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CHEMICAL ECOLOGY OF THE SETTLEMENT OF BENTHIC MARINE INVERTEBRATES*

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ABSTRACT Most benthic marine invertebrates produce planktonic larvae that must locate a suitable substratum on which to settle. This review considers evidence for chemical cues that promote or deter the settlement of marine invertebrates, with a particular focus on the isolation and identification of naturally occurring inducers of settlement. Chemoreception by marine invertebrate larvae is discussed, with a review of information on the larval sensory organs involved in the perception of chemical cues and with comparisons of chemoreception by marine and terrestrial invertebrates.

While there is considerable evidence for the existence of site-specific chemical cues that promote larval settlement, naturally occurring inductive compounds have been isolated and identified in only a few instances, and it is unclear whether any of these induce settlement under natural conditions. Conversely, a wealth of natural products have been characterised from extracts of unfouled sessile marine invertebrates to which an antifouling role has been ascribed, yet there is little evidence that these putative fouling inhibitors are released at concentrations that would influence settling larvae. The acknowledged importance of settlement and recruitment in structuring benthic communities warrants further interdisciplinary research on the identification, production, and perception of chemical signals in the marine environment.

INTRODUCTION

Unlike their terrestrial counterparts, benthic marine communities are dominated by a diverse invertebrate fauna representing most of the major animal phyla. A mystifying aspect of the life cycles of most of these invertebrates is that they include a planktonic larval phase that may last for minutes to months, during which time the larvae may drift from their place of origin for distances of metres to hundreds of kilometres. In most cases, the morphology of the larval form is totally unlike that of the adult, and if the larva feeds, it may have a vastly different diet. The disadvantages of pelagic dispersal are great: larvae face high levels of mortality due to predation and advection away from suitable adult habitats (Thorson, 1966;

*Review of literature completed 1 August 1991. This review is dedicated to the memory of Christopher Gardner Reed.

Day & McEdward, 1984; Young & Chia, 1987). Before the benthic phase of their lives can begin, these tiny larvae must somehow contact an acceptable substratum on which to attach themselves. Then, in a radical transformation, the larval organs are lost and the adult morphology is elaborated.

The extraordinary life histories of invertebrates with pelagic larvae have intrigued zoologists for decades. Research on the subject has produced an abundant literature (e.g., see the Proceedings of the Invertebrate Larval Biology Workshop, *Bulletin of Marine Science*, Volume 39(2), 1986). In this review, I shall focus attention on chemical cues in the marine environment that influence invertebrate larval behaviour at the time of settlement. In particular, I shall discuss evidence for inducers and inhibitors of settlement and for the larval chemosensory organs employed in their detection. This is not meant to be an exhaustive review of evidence for the existence of chemical cues that mediate settlement, anecdotal reports of which permeate the literature, but instead will concentrate on research that has resulted in the isolation and characterisation of an inducer or inhibitor. The reader may notice a bias in this review towards citations dealing with sessile, hard-bottom-dwelling invertebrates. This partiality reflects the preponderance of research in the field as much as it does the author's greater familiarity with that body of literature. In addition, because hard substrata are much less extensive, and far more patchily distributed, than sedimentary deposits in marine environments, selective pressures for a high degree of site-specific settlement among hard-bottom invertebrates may be more intense.

TERMINOLOGY

Planktonic (pelagic) larvae are classified into two groups depending on their source of nutrition (Thorson, 1950): 'planktotrophic' larvae feed while in the plankton and generally require long periods of time for development; 'lecithotrophic' larvae do not feed (but see Kempf & Hadfield, 1985; Jaeckle & Manahan, 1989), and generally stay in the plankton for much shorter periods (Fig 1). Non-pelagic development also occurs in benthic marine invertebrates and includes brooding of young by the adults, demersal and benthic development, and viviparity (see various definitions in Mileikovsky, 1971, 1974; Chia, 1974; Day & McEdward, 1984; Grahame & Branch, 1985; Turner, Pechenik & Calloway, 1986; Hadfield & Miller, 1987). Pelagic forms are, however, more common than non-pelagic; Thorson (1964) estimated that 80% of marine invertebrates, or about 90 000 species, produce larvae that develop in the plankton. Of these, the vast majority are planktotrophic.

It is unclear why long-term planktotrophic development predominates. Enhanced dispersal is most commonly cited as the primary advantage of a long-term pelagic life history stage (Crisp, 1974; Day & McEdward, 1984). Some brooding species have, however, wider distributions than closely related species with pelagic larvae (Johannesson, 1988). Dispersal by short-term lecithotrophic larvae should be sufficient to promote genetic exchange throughout the population of a given species. Indeed, variations in the life histories of marine invertebrates have attracted considerable recent research interest (Palmer & Strathmann, 1981; Todd & Doyle, 1981; Grahame & Branch, 1985; Hines, 1986; Strathmann, 1986; Scheltema, 1989; Levin & Huggett, 1990; Miller & Hadfield, 1990; Todd, 1991).

Planktonic larvae are generally not able to metamorphose until they mature sufficiently or become 'competent'. The attainment of competence may occur within minutes to days (most lecithotrophic larvae) or may require weeks to months (most planktotrophic larvae). Having attained competence, many pelagic larvae delay metamorphosis for variable periods of time, presumably until they encounter a suitable substratum (Thorson, 1950; Scheltema, 1961; Bayne, 1969; Strathmann, 1978; but see Fenaux & Pedrotti, 1988). Planktotrophic species may remain competent for extended periods (Hadfield, 1978b; Kempf, 1981; Pechenik, Scheltema & Eyster, 1984; Pechenik, 1986, 1987), which may vary considerably, depending primarily on nutritional limitations (Scheltema, 1986).

'Settlement' and 'metamorphosis' are variously defined, seemingly dependent on the organism or habitat most familiar to a given author. The result is confusing, particularly with regard to the former term. Scheltema (1974) defined settlement as a behavioural response resulting in the termination of a pelagic existence and assumption of a sedentary life; metamorphosis was defined as a morphogenetic term, referring to the morphological and physiological changes involved in the transition to benthic adulthood. Burke (1983a) restricted the definition of settlement to a reversible form of substratum-exploratory behaviour. He included the phenomena involved with permanent attachment to the substratum (e.g., extrusion of adhesive structures or cements) as part of metamorphosis. Crisp (1984) added complexity to the issue by subdividing settlement (*sensu* Burke, 1983a) into several behavioural components (attachment, exploration, inspection, settlement and orientation) and separately defining 'fixation' as the irreversible act of attachment preceding metamorphosis. Further confusing matters are reports of juvenile benthic invertebrates in the water column, having metamorphosed before reaching the benthos (Scheltema, 1974; Butman, 1987; Fenaux & Pedrotti, 1988). By the preceding definitions, these juveniles would not have undergone settlement at all.

Despite the foregoing definitions, settlement has more generally been taken to mean the overall transition from planktonic larva to benthic juvenile (Strathmann & Branscomb, 1979; Grosberg, 1981; Keough & Downes, 1982; Connell, 1985; Hadfield, 1986). In common usage, settlement does not solely refer to reversible contact with the benthos, but also to subsequent metamorphosis (e.g. 'gregarious settlement', 'settlement patterns', 'settlement sites', 'settlement cues'). In keeping with this usage, and for the purposes of this review, 'settlement' will be used as a general term that refers to the entire transition from planktonic larva to benthic juvenile. The definition of 'metamorphosis' (which includes fixation) is left unchanged from Burke (1983a), but is considered part of the process of settlement. Therefore, reversible contact with the substratum, exploratory behaviour, orientation, and metamorphosis are all part of the process of settlement (Fig 1). Having settled, a juvenile invertebrate is said to have undergone 'recruitment' to the substratum when its presence is recorded by an ecologist (Keough & Downes, 1982).

This review deals with environmental chemical cues that influence the induction of larval settlement; in particular, substratum exploration and the onset of metamorphosis. These cues may be present in the water column, but are more commonly associated with the substratum (Fig 1). Little is

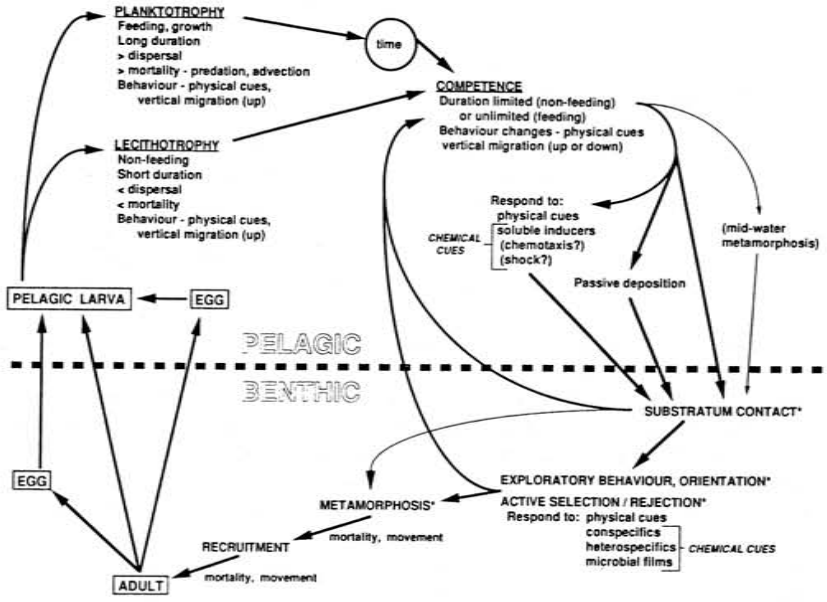


Fig 1.—Diagram of the generalised life histories of marine invertebrates with a pelagic larval phase. Components marked with an asterisk (*) are part of the overall process of settlement. Definitions of terms are in the text (page 274).

known about the endogenous chemical signals (hormones) that presumably orchestrate the complex metamorphic processes of many marine invertebrates (Chia & Rice, 1978; Burke, 1983a; Schwoerer-Böhning, Kroiher & Müller, 1990; see p. 307).

IMPORTANCE OF RECRUITMENT IN MARINE ECOLOGY

The processes that lead to the colonisation of substrata by larval invertebrates are among the most important in determining the ecology of marine communities. For rocky intertidal habitats, ecologists have focused on interactions of adult organisms with one another and with their environment, particularly the roles of competition, predation and disturbance (Dayton, 1971; Menge, 1976). Only recently has the significance of settlement and recruitment been recognised by some ecologists (Connell, 1985; Gaines & Roughgarden, 1985; Sutherland, 1990; Menge, 1991), although it has been acknowledged for decades by others (Thorson, 1950, 1966; Meadows & Campbell, 1972a; Scheltema, 1974; Lewis, 1976; Kendall, Bowman, Williamson & Lewis, 1982; Crisp, 1984).

Variability in the spatial and temporal patterns of larval recruitment may be attributed to a multitude of factors that are brought into play before, after, or coincident with settlement. Pre-settlement factors include the reproductive behaviour of adults (Barry, 1989), the availability of competent

larvae (Bousfield, 1955; Jackson, 1986; Olson & Olson, 1989; Farrell, Bracher & Roughgarden, 1991), and larval distribution in the water column (Grosberg, 1982; Shanks, 1983; Mathivat-Lallier & Cazaux, 1990). After settlement, juveniles may be subject to differential mortality or migration that will consequently alter their adult distribution (Cameron & Schroeter, 1980; Keough & Downes, 1982; Yund, Cunningham & Buss, 1987; Mullineaux, 1988; McCann & Levin, 1989; Osman, Whitlatch & Zajac, 1989). But differential larval settlement appears to be a major factor influencing recruitment, particularly on hard substrata (Strathmann, Branscomb & Vedder, 1981; Keough, 1983; Watanabe, 1984; Grosberg & Quinn, 1986; Bushek, 1988; Raimondi, 1988a; 1990; 1991; Young & Gotelli, 1988; Stoner, 1990), and chemical signals have been shown to influence settlement in the field (Strathmann & Branscomb, 1979; Chabot & Bourget, 1988; Le Tourneux & Bourget, 1988; Raimondi, 1988b).

PHYSICAL COMPARED WITH BIOLOGICAL AND CHEMICAL CUES

Invertebrate larvae are exposed to a multiplicity of environmental factors during their lives in the plankton and at the time of settlement and undoubtedly respond to a number of stimuli in the course of substratum selection. Physical factors such as light, gravity, hydrostatic pressure, temperature and salinity influence the behaviour of many species (Thorson, 1964; Crisp, 1974, 1984; Ryland, 1974; Sulkin, 1984; Young & Chia, 1987; Boudreau, Bourget & Simard, 1990; Kaye & Reiswig, 1991). Orientation and movement in response to light and gravity, in particular, are believed to affect the vertical distribution of larvae in the water column, and this may have a direct influence on settlement patterns (Grosberg, 1982; Sulkin, 1984).

Physical properties associated with the substratum may also be important. Settlement preferences have been demonstrated for variations in the contour, texture and thermal capacity of substrata (Ryland, 1974; Wethey, 1986; Raimondi, 1988a; 1990; Walters & Wethey, 1991), grain size of sediments (Gray, 1974), sediment cover (Hodgson, 1990), and water flow next to the substratum (Ryland, 1977; Crisp, 1984; Wethey, Luckenbach & Kelly, 1988). For most species, however, the importance of physical aspects of the substratum appear to be secondary to biological and chemical characteristics (e.g., Mihm, Banta & Loeb, 1981; LeTourneux & Bourget, 1988).

There may be a hierarchy of cues by which larvae select a generally favourable habitat and then a specific site for settlement (Meadows & Campbell, 1972a). A hypothetical sequence of larval behaviours has been illustrated by Crisp (1984) for a barnacle cyprid: at the time of settlement, the larva responds sequentially to light, current, presence of conspecifics, surface contour, surface hardness, and proximity of conspecifics. If a physical or biological condition is unacceptable to the larva, it returns to the previous position in the sequence and continues its exploratory behaviour. Planula larvae of the hydroid *Clava squamata* are photopositive and swim upward, but when they contact the brown alga *Ascophyllum nodosum*, their response to light reverses, causing them to settle on the shaded, interior stipes of the alga (Williams, 1965). Evidence for a hierarchy of chemical signals has been found for larvae of the nudibranch *Onchidoris bilamellata*, a predator of

barnacles (Chia & Koss, 1988). Sea water conditioned by the presence of adult barnacles induces competent larvae to cease swimming and begin exploratory behaviour. Larvae do not metamorphose, however, until they contact adult barnacles. In this case, independent chemical cues are thought to govern the onset of exploratory behaviour and the induction of metamorphosis.

RANDOM DEPOSITION, PASSIVE DEPOSITION, AND ACTIVE SUBSTRATUM SELECTION

Until well into this century, the prevailing view was that the site of deposition of competent invertebrate larvae was entirely a matter of chance; hence, settlement occurred at random (e.g., Colman, 1933). It was commonly assumed that larvae metamorphosed in the water column and then sank to the bottom with little or no ability to delay settlement or alter their distribution (Petersen, 1913; Yonge, 1937). With increasing frequency, however, studies of invertebrate larvae began to demonstrate selectivity at the time of settlement (Nelson, 1924; Visscher, 1928; Wilson, 1932, 1937) and delay of settlement in the absence of suitable substrata (Cole & Knight-Jones, 1939; Thorson, 1950; Wilson, 1952; Scheltema, 1961).

By the 1970s, descriptions of specific responses of settling larvae to particulars of the physical and biological environment were so pervasive in the literature that active substratum selection was advanced as the dominant factor determining the local distribution of marine invertebrates (Meadows & Compbell, 1972a,b). This was, however, probably an overstatement. Experimental evidence for active habitat selection was limited to laboratory assays of larvae in still water; little or no attempt was made to assess substratum selection under hydrodynamic conditions that might be expected in nature (Butman, 1987). Furthermore, objections were raised that, in addition to larval behaviour, habitat availability, ecological opportunity and passive transport might be important (DeWolf, 1973; Moore, 1975). Several recent studies suggest that passive transport and deposition strongly influence recruitment for some species (Eckman, 1983; Hannan, 1984; Banse, 1986; Wethey, 1986; Keen, 1987; Wethey *et al.*, 1988; Sammarco & Andrews, 1989; Webb, 1989; Black & Moran, 1991), but active substratum selection under realistic flow conditions has clearly been demonstrated for others (Butman, Grassle & Webb, 1988; Pawlik, Butman & Starczak, 1991).

Butman (1987) comprehensively reviewed evidence for active substratum selection versus passive deposition in determining patterns of invertebrate abundance in soft substratum environments. The passive deposition hypothesis proposes that larvae settle as passively sinking particles under the influence of local hydrodynamical conditions (Hannan, 1984). In contrast to random deposition, passive deposition takes into consideration the differential transport of particles in flowing water. Butman (1987) pointed out that although the evidence for active substratum selection is abundant, the importance of passive deposition of larvae has yet to be adequately addressed. She suggested that both passive deposition and active substratum selection may operate, but on different scales: larvae passively accumulate and are deposited under the influence of hydrodynamical processes operating at large spatial scales (tens of metres to tens of kilometres), while active substratum selection occurs only at much smaller scales (centimetres to metres).

On balance, the relative importance of passive and active processes in determining settlement patterns is likely to vary as much as the organisms settling and the habitats they occupy. Behavioural responses can affect the vertical distribution of larvae in the water column, and this in turn can influence their horizontal transport (Shanks, 1983; 1986; Chia, Buckland-Nicks & Young, 1984; Young & Chia, 1987; Bhaud & Cazaux, 1990). Active substratum selection has been amply demonstrated in the laboratory (see below) and in the field (Strathmann & Branscomb, 1979; Watanabe, 1984; Woodin, 1985; Bushek, 1988; Chabot & Bourget, 1988; Le Tourneux & Bourget, 1988; Raimondi, 1988a,b; 1990), and recently has been demonstrated in flumes under conditions designed to separate the effects of passive deposition from active choice (Butman *et al.*, 1988; Pawlik *et al.*, 1991). As Thorson (1950) explained, observations of larval behaviour "...seem further to show that the ability of postponing metamorphosis and actively seeking a substratum is widely distributed among marine larval invertebrates. In a water area with a bottom current of only half a knot the larvae forced towards the bottom by their photo-negativity and testing the substratum at intervals may be carried over a distance of 24 km in 24 h, i.e., 170 km per week, and their chance of finding a suitable substratum for settling and metamorphosis seems to be great". Although active substratum selection has figured prominently in past models of invertebrate larval settlement (Doyle, 1975), it is surprising that more recent models of recruitment have disregarded its importance (Roughgarden, Iwasa & Baxter, 1985; Roughgarden, Gaines & Possingham, 1988; Possingham & Roughgarden, 1990).

SPECIFICITY OF SETTLEMENT

Reports of active substratum selection by settling invertebrates abound in the literature. In almost all instances, the substratum is biogenic and the cues mediating specificity or enhancement of settlement are believed to be chemical in nature. References to studies of settlement preferences can be found in several volumes and reviews (Thorson, 1957, 1966; Gray, 1974; Meadows & Campbell, 1972a; Crisp, 1974, 1984; Giese, Pearse & Pearse, 1974–1987; Ryland, 1974; Scheltema, 1974; Chia & Rice, 1978; Burke, 1983a, 1986; Hadfield, 1986; Woodin, 1986; Hadfield & Miller, 1987; Butman, 1987; Chia, 1989; Svane & Young, 1989, Pawlik & Hadfield, 1990). The primary purpose of the present review is to discuss research that has advanced beyond the implication of a settlement cue to the full or partial characterisation of a chemical inducer. To begin, however, a brief description will be given of the categories of substratum-specific settlement exhibited by marine invertebrates.

GREGARIOUS SETTLEMENT

The formation of monospecific colonies and aggregations is very common among marine invertebrates. Colonies comprised 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 other 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 (Knight-Jones, 1953; Crisp, 1979; Chabot & Bourget, 1988; Hoffman, 1989; Raimondi, 1991), bivalves (Bayne, 1969; Eyster & Pechenik, 1987; McGrath, King & Gosling, 1988), and polychaetes (Knight-Jones, 1951; Wilson, 1968, 1970, 1974; Eckelbarger, 1978; Scheltema, Williams, Shaw & Loudon, 1981; Pawlik, 1986, 1988a,b). Gregarious settlement has been reported in at least 35 invertebrate species representing eight phyla; in 18 of these reports there was evidence of a chemical inducer of settlement (Burke, 1986).

The advantages of gregariousness are many (Crisp, 1979; Pawlik & Faulkner, 1988). Larvae that settle on or near adult conspecifics have chosen a habitat that is more likely to support postlarval growth than if they had settled indiscriminately (Jensen, 1989). Juveniles may derive additional benefits from adult conspecifics; for example, juvenile sand dollars that recruit to beds of adult sand dollars encounter less predation from tanaid crustaceans, which are displaced by the sediment-reworking activities of the adults (Highsmith, 1982). Adult invertebrates derive reproductive benefits from aggregation. Proximity increases fertilisation success for both internally fertilising and freely spawning species (Crisp, 1979; Pennington, 1985; but see Denny & Shibata, 1989); for the latter this is particularly true if spawning is synchronised (Thorson, 1950). Moreover, individuals in aggregations may live longer than if they had settled alone (Wilson, 1974) and thus benefit from greater fecundity over the course of a longer adult life span.

Patterns of gregarious recruitment are not always the result of larval settlement in response to conspecific adults. Several studies have demonstrated that some larvae preferentially settle near, or are attracted to, the presence of other larvae or recently settled juveniles (Cole & Knight-Jones, 1949; Van Duyl, Bak & Sybesma, 1981; Keough, 1984; Wethey, 1984; Grosberg & Quinn, 1986; Marsden, 1991). Restricted dispersal of larvae that spend a very short time in the plankton may promote a clumped distribution (Keough, 1989). Epibiotic invertebrates may become aggregated as a result of larval settlement preferences for living substrata (see p. 282). Aggregations may also arise as a result of the passive deposition and settlement of larvae on areas of the substratum that experience lower shear stress and have a thicker surface boundary layer (Keen, 1987; Havenhand & Svane, 1991). Hui & Moyse (1987) have proposed that the rejection of unsuitable substrata, rather than preferential settlement near adults, results in gregarious settlement. There has even been a suggestion that larvae may settle in response to cues emanating from predators of adult conspecifics if these cues provide a reliable indicator of a suitable habitat (Raimondi, 1988b); aggregation would similarly result.

Most species that form non-clonal aggregations do settle to various degrees in the absence of conspecifics. A certain level of non-gregarious settlement

is necessary for the colonisation of cleared substrata and the founding of new aggregations. Generally, enhanced settlement in the presence of conspecifics is enough to produce colonies, although some species may be more particular in their requirements than others (Pawlik, 1988b).

Gregarious settlement is not without cost. Larvae or juveniles may be eaten, absorbed or removed by conspecifics (e.g., Rinkevich & Weissman, 1987). Aggregated adults must compete for food, which may decrease individual fitness (Crisp, 1979). Some larvae that settle gregariously may space themselves far enough from conspecifics so as to minimise intraspecific competition (Hui & Moyse, 1987). This 'territoriality' of settling larvae has been ascribed to chemical cues (Knight-Jones & Moyse, 1961) and behavioural responses (Crisp, 1984). There are clear trade-offs between advantages and disadvantages, but the prevalence of gregariousness in hard-substratum marine communities suggests that the benefits outweigh the costs.

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 organisms.

Non-parasitic associations

Non-parasitic 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 specialised to an extreme in their substratum requirements (reviewed in Lewis, 1978). Hermaphrodite cyprid larvae of *Conopea galeatus* settle on the axial skeleton of specific gorgonians and cannot survive without access to this substratum (Gomez, 1973); this species also produces specialised male cyprids that settle solely on the external shell plates of the hermaphrodite adult barnacles, where they metamorphose into tiny complemental males. Other barnacles are host-specific for species of sponges (Van Syoc, 1988) and hard corals (Moyse, 1969). Phoretic barnacles include those that settle on whales and other marine mammals, turtles, and sea snakes (Crisp, 1974; Zann, 1980). Many of these are found on only one or a few species of vertebrate host, suggesting settlement cues may be involved (Lewis, 1978).

The planula larvae of cnidarians show a surprising degree of substratum selectivity, even though they may appear to be among the least sophisticated of larval forms. Anemone-like zoanthids that colonise the surfaces of sponges are highly specific in their choice of a host; their distribution is believed to result from larval recognition of host sponges (Crocker & Reiswig, 1981). Donaldson (1974) described the settlement of *Proboscidactyla flavicirrata*, a hydroid found solely on the tube rims of sabellid polychaetes. Nematocysts borne by the planulae of this species were specifically stimulated to discharge on contact with the feeding appendages or body surface of sabellids, resulting in larval attachment to the worm. Subsequently, the nematocysts became desensitised to the worm surface and would discharge only on contact with the worm tube, thereby effecting the transfer of planulae to the tube.

Epiphytic associations, whether transitory or permanent, are common among several species of marine invertebrates that have planktonic larvae. Encrusting red algae promote the settlement of various species of corals (e.g., Sebens, 1983; Morse, Hooker, Morse & Jensen, 1988), gastropods (Morse *et al.*, 1980c), polychaetes (Gee, 1965), and echinoderms (Barker, 1977; Rowley, 1989; Pearce & Scheibling, 1990b), while some bivalves prefer filamentous red algae (Eyster & Pechenik, 1987). Brown algae are the preferred substrata of hydroids, spirorbid polychaetes and bryozoans (Nishihira, 1965; Ryland, 1974; Scheltema, 1974; Hurlbut, 1991). Preferences for host algae may be genetically determined within a species. MacKay & Doyle (1978) performed laboratory settlement experiments with larvae of the polychaete *Spirorbis borealis*, which settle on brown algae of the genera *Fucus* or *Ascophyllum*. Larvae from a tidepool population preferred *Ascophyllum*, those from an embayment preferred *Fucus*, and those from transitional habitats had intermediate preferences. The differences in settlement were attributed to genetic variability of the localised populations. Besides brown algae of the genera *Fucus*, *Ascophyllum* and *Laminaria* (Wisely, 1960; Stebbing, 1972), various species of spirorbids settle specifically on red algae of the genera *Corallina* or *Lithothamnion*, sea grasses of the genera *Posidonia*, *Thalassia* and *Zostera*, or on the shells of crustaceans (Crisp, 1974; Dirnberger, 1990).

Parasitic associations

Most invertebrate phyla include parasitic groups; some are made up entirely of parasites (Pearse *et al.*, 1987). 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 parasitise (Hadfield, 1976). An unusual feeding habit is exhibited by *Cancellaria cooperi*, a parasitic snail normally found buried in sand with only the tips of its tentacles exposed (O'Sullivan, McConnaughey & Huber, 1987). On detecting the scent of the Pacific electric ray *Torpedo californica*, this snail crawls out of the sand, locates the ray, and inserts its proboscis into the mouth, gill slits or anus of the fish. The proboscis makes small wounds, from which blood and body fluids are sucked and ingested. The snails lay spatulate egg capsules, from which planktotrophic larvae hatch (Pawlik, O'Sullivan & Harasewych, 1988); it is probable that the presence of *T. californica* stimulates settlement of this species.

Among the crustaceans are several parasitic groups with pelagic larval stages, including isopods, copepods and cirripedes. The isopod *Hemioniscus balani*, a parasite of the acorn barnacle *Chthamalus dalli*, has a pelagic larval stage. A male larva of the parasite locates and mates with an adult female inside a barnacle, then moves to an unparasitised host barnacle and changes into a female. Blower & Roughgarden (1989) found a high proportion of solitary male parasites that had not yet changed sex in barnacles clustered next to a barnacle containing a female. They suggested that male larvae may be attracted to adult female parasites by a pheromone. Larvae of another isopod, *Probopyrus pandalicola*, swim from their intermediate, planktonic copepod host to their definitive, epibenthic host, the shrimp *Palaemonetes pugio*. Anderson & Dale (1989) conducted Y-tube choice experiments that demonstrated that isopod larvae swim upstream in water conditioned by shrimp, suggesting that these larvae may use chemoreception to locate their hosts from a distance.

Perhaps the most specialised of parasitic crustaceans are the rhizocephalan barnacles, which primarily parasitise other crustaceans (Høeg & Lützen, 1985). Female rhizocephalans form dendritic processes in the bodies of their hosts; when mature, they produce a reproductive sac external to the host from which larvae are released. Cyprid larvae may be male or female: the female larva must locate a suitable host to infect, usually a specific crustacean species; 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 an encounter between a female cyprid and its host, or even less likely, a male cyprid and a virgin female's reproductive sac, the involvement of chemical cues seems a necessity. In addition, the cyprid larvae of some rhizocephalans lack thoracic appendages and cannot swim (Pawlik, 1987), making the discovery of a virgin adult female by a male larva even less likely.

Herbivorous and predatory associations

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 the 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 & Ghiselin, 1983; Hadfield & Miller, 1987). The developmental mode and timing of settlement of some nudibranchs may result from their requirements for specific prey species that are seasonally abundant (Todd & Doyle, 1981; Todd, 1991). Some chitons and gastropod molluscs settle specifically on encrusting red algae and feed on the crusts after metamorphosis (Barnes & Gonor, 1973; Morse & Morse, 1984a; Shepherd & Turner, 1985).

Recent laboratory work has demonstrated, however, that specific dietary needs of adult invertebrates do not ensure settlement of their larvae near

food sources. Hubbard (1988) studied the larval development of the Hawaiian dorid nudibranch *Hypselodoris infucata*, which preys only on the sponge *Dysidea* sp. Surprisingly, competent larvae of the nudibranch settled in response to several species of sponges, including *Dysidea* sp, and in response to a film of microorganisms. In a similar vein, Pawlik (1989) found that larvae of the sea here *Aplysia californica* settled on a variety of macroalgae, even though juvenile and adult sea hares specifically consume red algae of the genus *Laurencia*. Newly metamorphosed juveniles of *Aplysia californica* ate the red algae *Laurencia pacifica* and *Plocamium cartilagineum*, but they would not eat any of the other algae on which they had settled and usually left them and crawled around the assay dish. Pawlik suggested that larvae of *Aplysia californica* may decrease their post-competent pelagic lifespan by settling relatively non-specifically and then locating the proper adult food after metamorphosis. This strategy may be an option for other invertebrates with mobile juveniles, but probably not for species with juveniles that are fixed to the substratum.

SETTLEMENT ON MICROBIAL FILMS

The presence of a surface film of microorganisms has long been recognised as a prerequisite for the settlement of many fouling invertebrates (ZoBell & Allen, 1935; Scheltema, 1974; but see Crisp, 1984). The microbial flora of sediments also stimulates settlement of soft-bottom species (see review in Gray, 1974). For example, larvae of the fiddler crab *Uca pugilator* develop much faster.and metamorphose sooner, when reared over sediment from the adult habitat than when reared in clean containers (Christy, 1989). Clean surfaces exposed to sea water 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 & Kirchman, 1984). Although microorganisms promote the settlement of many species, including hydroids (Müller, 1973; Freeman & Ridgway, 1987), polychaetes (Wilson, 1955; Knight-Jones, 1951; Gray, 1966; Kirchman, Graham, Reish & Mitchell, 1982a), bivalves (Cole & Knight-Jones, 1949; Weiner, Segall & Colwell, 1985), gastropods (Scheltema, 1961), bryozoans (Mihm, Banta & Loeb, 1981; Brancato & Woollacott, 1982), barnacles (Le Tourneux & Bourget, 1988) and echinoderms (Cameron & Hinegardner, 1974; Chen & Run, 1989; Johnson, Sutton, Olson & Giddins, 1991), microbial films inhibit the settlement of others (Ryland, 1974; Maki, Rittschof, Costlow & Mitchell, 1988; Maki *et al.*, 1989, 1990).

Microbial films may affect patterns of larval settlement by virtue of the altered wettability they confer on a hard substratum. Wettability describes the tendency of a substratum to induce the spreading of a liquid (in this case, sea water) on its surface. Brewer (1984) noted that planulae of the scyphozoan *Cyanea* sp preferentially settled on aged mollusc shells rather than on freshly vacated shells and attributed this preference to the decreased wettability of filmed surfaces. Mihm, Banta & Loeb (1981) found, however, that enhanced settlement of the bryozoan *Bugula neritina* on a film of microorganisms could not be attributed solely to its surface wettability; i.e., larvae were also responding to the biological or chemical nature of the microbial film.

THE CHEMICAL NATURE OF SETTLEMENT INDUCERS

Considering the many examples in which marine invertebrate larval settlement has been inferred or demonstrated to be substratum-specific, it is surprising that naturally occurring inducers of settlement have been isolated and identified for only a few species. This lack of knowledge stems largely from the difficulties associated with obtaining competent larvae. Only rarely can they be harvested directly from the plankton (e.g., Rice, 1986); generally, the identities of field-caught larvae are unknown 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 have narrow reproductive seasons (Strathmann, 1987). Should sufficient numbers of newly hatched larvae be 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 larvae, but most pelagic larvae are planktotrophic and require feeding for several weeks before competence is attained. Larval culture is fraught with pitfalls, from the quality of the sea water used, to the method of culture agitation, to the choice of dietary phytoplankton (Strathmann, 1987). Nevertheless, experiments have been performed on the larval responses of several species to chemical cues that have been purified and characterised to various degrees.

ISOLATED AND IDENTIFIED INDUCERS

To date, 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*. Information regarding compounds that affect the first three species is taken primarily from the natural products chemistry literature; biological evidence to support their putative function is somewhat equivocal.

Settlement of Coryne uchidai

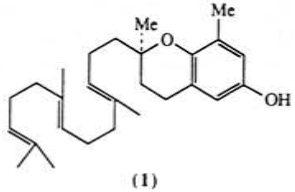
Nishihira (1968) studied the settlement specificity of the hydroid *Coryne uchidai* on brown algae of the family Sargassaceae. In assay dishes containing 20, 1-mm^2 pieces of *Sargassum thunbergii*, *S. confusum* or *S. tortile*, larvae of *Coryne uchidai* would stop swimming immediately and begin crawling. In contrast, in dishes wihout 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 2–3 days in dishes containing *Sargassum confusum* or *S. tortile*, within 3–4 days in dishes containing *S. thunbergii* and *Ulva pertusa*, and within 3–6 days in control dishes (no algae).

Boiled aqueous extracts of *Sargassum tortile* similarly caused larvae to cease swimming immediately, with metamorphosis occurring within 2 days.

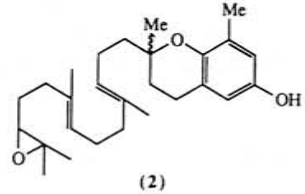
Extracts of *Ulva pertusa* had no effect on larvae beyond the gradual settlement observed in control dishes. Extracts of two other algae, *Dictyopteris divaricata* and *Symphyocladia latiuscula* (neither in the Sargassaceae), caused immediate cessation of larval swimming, but little or no metamorphosis. The extract of the latter alga killed larvae within 1 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 sea water 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**). Only limited settlement assay results were provided. Compounds were dissolved in a drop of ethanol and added to 20 ml of sea water containing 10 larvae. After 72 h, δ-tocotrienol at 37.5 μg/ml of sea water induced three larvae to metamorphose, but the remaining seven died after settlement. The epoxide induced all 10 larvae to metamorphose within 72 h at both 18.8 and 75 μg/ml of sea water. None of the larvae in control dishes (ethanol alone) completed metamorphosis within 72 h.

Unfortunately, no further information is available on the settlement responses of *Coryne uchidai* to algal metabolites. It is unclear whether chromanols are the only inductive compounds present in *Sargassum tortile*, and whether species of *Sargassum* produce these compounds to the exclusion of non-preferred 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.



(1)



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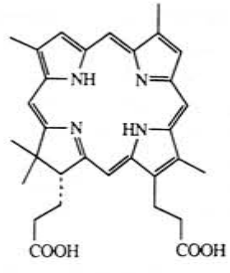

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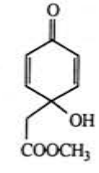


(4)

Settlement of Bonellia viridis

During the early part of this century, Baltzer (reviewed in Pilger, 1978; Jaccarini, Agius, Schembri & Rizzo, 1983) discovered that sexually undifferentiated larvae of *Bonellia viridis* were stimulated to settle and metamorphose into non-feeding dwarf males on 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 sea water. Herbst (in Pilger, 1978; Jaccarini *et al.*, 1983) found that similar effects could be triggered by altering the ionic composition or pH of the sea water to which larvae were exposed. Baltzer proposed that the masculinising 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 bonellin was described as an uncomplexed, alkylated chlorin (**3**) (Pelter *et al.*, 1978). 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, De Nicola Giudici, Zanetti & Prota, 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 effect larval settlement. However, Agius (1979) found the masculinising factor in aqueous extracts of proboscides and body tissues, and potent activity in the pigmented body secretion. Agius *et al.* (1979) reported that larvae were attracted to the proboscides of female worms and absorbed the green pigment from the proboscis at the site of their attachment. Larval assays performed with purified bonellin produced 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 sea water. Strangely, 0.5 and 0.2 ppm bonellin induced 35.8 and 14.4% masculinisation, respectively, but 0.01 ppm bonellin induced 44.5% of the larvae to turn into males.

Results of a more rigorous study were presented by Jaccarini *et al.* (1983). They concluded that the effects of bonellin on sex determination were inconsistent. Significantly higher levels of masculinisation were induced in larvae exposed to 10^{-6} M bonellin, but while purified bonellin induced 28% of the larvae to turn into males, the female body secretion triggered 96% masculinisation. Moreover, in three of five experiments with purified bonellin, there was no enhanced masculinisation over controls. There had been some suggestion that bonellin induced masculinisation 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; DeNicola Giudici, 1984). However, comparative larval assays of purified bonellin in light and darkness resulted in no significant effects over controls (Jaccarini *et al.*, 1983). Therefore, there is no unequivocal evidence linking bonellin to the masculinising 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.

Settlement of Pecten maximus

Yvin, Chevolot, Chevolot-Magueur & Cochard (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**), a compound previously isolated from *Jacaranda caucana*, a terrestrial vascular plant. Jacaranone stimulated maximum settlement of *Pecten maximus* at 0.5 mg/l ($\sim 3 \times 10^{-6}$ M), with increasing levels of larval mortality at higher concentrations (Cochard, Chevolot, Yvin & Chevolot-Maguer, 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 *Delesseria sanguinea*; its recruitment patterns are relatively indiscriminate (Cochard *et al.*, 1989).

Settlement of 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 & Faulkner, 1988). Wilson (1968, 1970, 1974) studied the larval settlement behaviour 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 behaviour. 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 p. 293).

Larvae of *Phragmatopoma californica*, a gregarious sabellariid from the coast of California, also settled on the sand tubes of adult conspecifics over other substrata (Jensen & 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). 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 nine FFAs that contributed 3% or more to the active

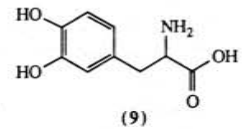
fraction, only palmitoleic, linoleic (18:2), arachidonic (20:4) and eicosapentaenoic acids (**5–8**, respectively) induced larval settlement.

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



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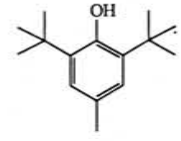

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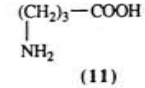


(11)

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 & 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 was determined both by the number of carbon atoms and the number of *cis* double bonds in the acyl chain. For example, although palmitoleic (16:1) was a potent inducer of larval settlement, oleic acid (18:1) was not, due to 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 & 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 stereochemical specificity was likened to that described in studies of chemoreception by terrestrial insects (Pawlik & Faulkner, 1986, 1988; see p. 307).

Larval settlement responses of *P. lapidosa*, a gregarious sabellariid from the tropical western Atlantic, were very similar to those of *P. californica* (Pawlik, 1988b). Inductive capacity of the tube sand was lost on extraction with organic solvents 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 fertilisation experiments. The hybrid larvae of both crosses developed and metamorphosed normally, prompting the synonymisation of the two species: *P. 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 chemical signals that caused settlement of *Phragmatopoma lapidosa 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 *Sabellaria alveolata* with organic solvents diminished its capacity to trigger settlement of conspecific larvae, but activity was not transferred to the extracts, and an inducer was not isolated or identified. Furthermore, the FFAs that elicited settlement of *Phragmatopoma lapidosa californica* and *P.l. lapidosa* were either not effective at inducing settlement of *Sabellaria alveolata* or actually inhibited settlement. Larvae of non-gregarious species from the Caribbean, *S. floridensis*, and from the eastern Pacific, *S. cementarium*, similarly did not respond to FFAs (Pawlik, 1988b; Pawlik & 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 *Phragmatopoma lapidosa 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 gregarious sabellariids of different genera is under the control of different chemical signals. Interspecific differences in larval responses of 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 have concurrently studied *P. lapidosa californica*, and have arrived at different conclusions regarding the induction of settlement of this species (Jensen & Morse, 1984; 1990; Yool *et al.*, 1986; Jensen, Morse, Petty & Hooker, 1990). Building on the hypothesis of 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 & Morse, 1984; Pawlik, 1990), but settlement occurred readily in response to a cresol-derived, lipophilic compound 2,6-di-tert-butyl-methylphenol, also known as butylated hydroxytoluene (BHT, **10**) (Jensen & Morse, 1990). BHT effected settlement of *P.l. californica* when adsorbed to surfaces in both laboratory and field experiments. Jensen & Morse (1990) proposed that BHT mimics the activity of the unknown, naturally occurring, inductive L-DOPA residue from tube cement (but see Pawlik, 1990). In addition, the authors have questioned whether FFAs function as a natural cue, as proposed by Pawlik (1986; 1988b), suggesting instead that FFAs induce settlement in a non-specific manner, possibly operating on the larval nervous system or parallel to the natural inducer (Jensen & 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 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 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 will be required to answer this query. Replication of experiments detailed in Jensen *et al.* (1990) have failed to confirm that freeze-drying or stirring decrease the inductive activity of natural inducer as compared with substrata coated with FFAs, or that induction by FFAs is temperature dependent (points 2 and 3 above; Pawlik, unpublished data). Moreover, the contention that larval response to FFAs is non-specific (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). Yet, 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 & 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, Grassle & Webb, 1988). *P. lapidosa californica* has proved to be a very useful subject in experiments with flumes, because (1) 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, Butman & Starczak (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 5×5, 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, behaviour may be important in the settlement process at two levels of *P.l. californica*: larvae respond first to flow conditions and then, as they sample the substratum, to chemical cues.

PARTIALLY PURIFIED INDUCERS

The studies described below have proceeded toward characterising the chemical induction of settlement but have not yet identified the stimulatory compounds. After field observations and laboratory assays have indicated

preferential settlement of larvae onto a specific substratum, research generally has 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 could be 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 lyophilised aqueous extracts of whole oysters or material from aqueous extracts of whole oysters that had been partitioned into diethyl ether (Keck, Maurer, Kauer & Sheppard, 1971). Hidu (1969) found 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 & 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 *O. 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 pp. 297 and 301).

Laboratory and field experiments have demonstrated than the sessile gastropod molluscs *Crepidula fornicata* and *C. plana* preferentially settle near adult congeners (McGee & 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 sea water conditioned by adult *C. plana* passed through both 10 and 15 kilodalton membrane filters and was retained on a reverse-phase chromatography column (McGee & 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 *Urechis caupo* settled rapidly in response to sediments from adult burrows or sediments that had been exposed to the epidermis of an adult worm (Suer & Phillips, 1983). The worm-derived factor triggered settlement only when adsorbed onto sediment. It was soluble in sea water and passed through dialysis membrane (3.5–14 kilodaltons), and it was heat-labile (>80 °C) but stable at ambient sea-water temperatures for several days.

Larvae of *Golfingia misakiana* settled in response to a low molecular mass (< 500 daltons), heat-labile factor present in sea water conditioned by the presence of adult worms (Rice, 1986). 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, microbially filmed sediment 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 a small peptide (< 10 kilodaltons). 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 & Scheibling (1990a) 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 and colleagues (Svane, Havenhand & Jørgensen, 1987; Havenhand & 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. Recruitment of *Ascidia mentula* was aggregated in the field. Larvae of *A. mentula* added to the middle of a seawater filled tube sealed at one end with the tunic of a living conspecific adult were preferentially distributed near the adult ascidian after 10 min. 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 *A. 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; the topic has been thoroughly reviewed elsewhere (Crisp, 1984; Gabbott & Larman, 1987). Most barnacle species liberate feeding nauplius larvae that moult through successive stages. With the last larval moult, each nauplius transforms into a non-feeding cyprid larva whose sole function is to find a suitable site for settlement. Knight-Jones first described gregarious settlement by *Elminius modestus*, *Semibalanus balanoides* (as *Balanus balanoides*) and *Balanus crenatus* (Knight-Jones &

Stevenson, 1950; Knight-Jones, 1953), although subsequent work focused primarily on *Semibalanus balanoides* (Knight-Jones & Crisp, 1953; Crisp & Meadows, 1963; Larman, Gabbott & East, 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 & Meadows, 1963; Larman & Gabbott, 1975). The factor was identified as "arthropodin", a proteinaceous component of arthropod cuticles (Crisp & Meadows, 1963).

The settlement-inducing substance was further purified and characterised by Gabbott & Larman (1971, 1987), Larman & Gabbott (1975), Larman *et al.* (1982) and Larman (1984). Protein precipitates of boiled extracts of adult *Semibalanus balanoides* were separated by electrophoresis to yield two fractions containing both 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 having amino acid compositions similar to that of actin. Proteins of this class are sticky; in particular, they adhere well to other proteins. Reversibly attached cyprid larvae (as opposed to those that have begun metamorphosis and cemented themselves for permanent attachment) required greater force to be removed from extract-treated surfaces than from untreated surfaces or surfaces treated with other proteins (Yule & Crisp, 1983; Yule & Walker, 1984). Moreover, reversibly attached cyprids left behind proteinaceous 'foot-prints' of their own making, which then might stimulate other cyprids to settle (Yule & Walker, 1987). Crisp & Meadows (1963) proposed a mechanism by which cyprid larvae detect the settlement factor that relied solely on the stickiness of the inductive proteins (Crisp, 1984; Gabbott & Larman, 1987). In this instance, settlement was theorised to result from a physical property of the chemical cue (adhesion), rather than receptor-mediated larval perception, an idea supported by the observed settlement of barnacles on slicks of oil and organometallic compounds (see pp. 301 and 304). 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 sort of result one would expect if the effects of arthropodins are purely physical. Bourget and colleagues studied the settlement of *Semibalanus balanoides* on the Atlantic coast of Canada and concluded that, in addition to physical cues, larvae respond to conspecifics (Chabot & Bourget, 1988) and to films of microalgae (Le Tourneux & Bourget, 1988), depending on the spatial scale examined. Mucus has also been observed to effect barnacle settlement (Johnson & Strathmann, 1989). Depending on its source, however, 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 & Williams, 1960). Extracts of two other fucoids, *F. vesiculosus* and *Ascophyllum nodosum*, also stimulated settlement. Similar responses were observed for larvae of another bryozoan, *Flustrellidra hispida* (Crisp & 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 (1965) 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.

Larvae of the wood-boring shipworm (bivalve mollusc) *Teredo norvegica* aggregated around the dried residue of alcohol or ether extracts of wood or around the opening of a capillary tube containing sea water saturated with these extracts or an aqueous extact of sawdust (Harington, 1921). Aqueous extracts of wood in the form of bog water (dissolved humic substances, or "Gelbstoff") also induced crawling behaviour in larvae of the shipworms *T. navalis* and *Bankia gouldi* (Culliney, 1972). *Lithophaga lessepsiana*, another boring bivalve, is found only in the scleractinian coral *Stylophora pistillata* (Mokady, Bonar, Arazi & Loya, 1991). Larvae of *Lithophaga lessipsiana* settled preferentially on *Stylophora pistillata* in choice experiments, and were induced to settle in response to tissue extracts of this coral species (Mokady *et al.*, 1991)

Larvae of the red abalone *Haliotis rufescens* preferentially settle on crustose red algae of the genera *Lithothamnion*, *Lithophyllum* and *Hildenbrandia* (Morse *et al.*, 1980c), although gregarious settlement onto the mucus of adult conspecifics has also been reported for this species (Slattery, 1987), and abalone raised in hatcheries are settled on plates filmed with benthic microalgae and bacteria (Hahn, 1989). The settlement of *Haliotis rufescens* was first attributed to the presence of γ-aminobutyric acid (GABA, **11**) molecules 'covalently linked' to proteins, and to phycoerythrobilin in the tissues of the algae (Morse, Hooker, Duncan & Jensen, 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 (Morse & Morse, 1984a; b). 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 (Morse & Morse, 1984a; Morse, Froyd & Morse, 1984). The responses of larvae to neuroactive compounds such as GABA are further discussed below (p. 298) and reviewed in 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 sea water or in natural sea water during the winter months in Woods Hole, Massachusetts. Larvae developed normally when raised in natural sea water during the summer at Woods Hole or during the winter at Hopkins Marine Station, California. They suggested that an exogenous factor, absent during the winter in natural sea water 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 were 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 sea water. They proposed that the source of the factors that induce both competence and metamorphosis was red macroalgae, and that the same compound controlled both processes. *A. californica* will metamorphose, however, on a variety of red, green and brown intertidal macroalgae (Pawlik, 1989), so it seems unlikely that the putative factor(s) are restricted to red macroalgae.

For over two decades, Hadfield and co-workers have studied the larval settlement of the nudibranch mollusc *Phestilla sibogae*, an obligate predator of hard corals of the genus *Porites* (Hadfield & Karlson, 1969; Hadfield, 1977, 1978a, 1984; Hadfield & Scheuer, 1985; Hadfield & Pennington, 1990). Larvae of the nudibranch settled in response to a water-borne inducer released from *P. compressa* or *P. lobata*, or in response to sea water containing an aqueous coral extract. The inducer was partially purified and characterised 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 sea water before re-exposure to the inducer (Hadfield & Scheuer, 1985). Despite intensive efforts, the inducer has not yet been identified (Hadfield & Pennington, 1990).

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

Preliminary data have been gathered on the chemical stimulation of settlement of the barnacle *Membranobalanus orcutti*, an obligate sponge commensal (Pawlik, unpubl. data). The barnacle settles on, and grows into, the surface of only two sponges in southern California; only one of these, *Spheciospongia confederata*, is abundant in shallow waters (Jones, 1978). Cyprid larvae of *Membranobalanus orcutti* settled readily on living sponge surface tissue or on surface tissue that had been freeze-dried and rehydrated. Removal of lipid-soluble constituents from the sponge surface tissue by extraction in organic solvents did not alter larval response. Settlement was greatly reduced, however, when freeze-dried surface tissue was boiled for 30 min, immersed in formaldehyde, or treated with a non-specific protease (followed by a 24 h sea-water rinse in all cases). 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 characterised. Müller (1973) described the settlement of the planula larva 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 non-dialysable. Metamorphosis of *H. echinata* was also induced by a heat-labile factor (≥ 8 kilodaltons) isolated from medium conditioned by metamorphosing larvae or recently metamorphosed polyps (Leitz & Lange, 1991), but the authors did not consider it likely that the factor functioned as a natural settlement cue.

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 in response to various peptides, large proteins, glycoproteins and cholera toxin, but the relationship of these compounds to the bacterially produced inducer is unknown (Fitt & Hofmann, 1985; Fitt, Hofmann, Wolk & Rahat, 1987; see p. 299).

Larvae of the spirorbid polychaete *Janua brasiliensis* settled preferentially on microbial films cultured from the surfaces 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 & Mitchell, 1985).

Bonar, Coon, Fitt, Weiner and colleagues have produced a recent body of work on the induction of settlement of oyster larvae (*Crassostrea*) by bacterial products and ammonia. Weiner, Segall & Colwell (1985) isolated a gram-negative, pigment-forming bacterium, designated LST, from oysters and oyster-holding tanks that enhanced the settlement of *C. virginica*. It was hypothesised that films of LST produced L-dihydroxyphenylalanine (L-DOPA), melanin precursors, and melanin itself, which stimulated larval settlement (Bonar, Coon, Weiner & Colwell, 1985). Coon, Bonar & Weiner (1985) had discovered that L-DOPA induced settlement behaviour of *C. gigas*, 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 behaviour under natural conditions (Coon & Bonar, 1987). A distinction was made between 'settlement behaviour' (larval foot extension beyond the shell margin) and 'metamorphosis' (loss of velum, growth of shell and gill) of *C. gigas*, with separate cues hypothesised for the onset of each (Bonar *et al.*, 1990; Coon, Fitt & Bonar, 1990); L-DOPA, for example, induced settlement behaviour, but not

metamorphosis (but see Bonar *et al.*, 1990, Table 2). Most recently, the induction of settlement behaviour 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 weight $\leqslant 300$ daltons. Low levels of activity were also detected in the control media 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 behaviour (Coon *et al.*, 1990; see p. 301). Metamorphosis of oyster larvae (as opposed to 'settlement behaviour') is thought to be induced by unknown, substratum-associated cues of bacterial orgin (Fitt *et al.*, 1990).

Extending the work of Scheltema (1961), Levantine & 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 & Hinegardner (1974) determined that competent larvae of the sea urchins *Lytechinus pictus* and *Arbacia punctulata* settled in response to a bacterial film or to sea water that had been incubated with particulate material from aquarium filters or sediment from the bottom of sea-water storage barrels. The sea-water-borne factor was non-volatile, 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 have varying effects on mature larvae, ranging from normal settlement and metamorphosis to abnormal metamorphosis and death (see review and Table 3 in Pawlik, 1990). Some of the earliest research employing marine invertebrate larvae concerned the induction of abnormal metamorphosis of tunicate tadpoles by compounds such as thyroxine (Bradway, 1936; Bell, 1955; Lynch, 1961).

Neurotransmitters and derivatives thereof that affect larval responses include choline and succinylcholine chloride (gastropods: Hadfield, 1978a; Harrigan & Alkon, 1978; Bahamondes-Rojas & Tardy, 1988; Todd, Bentley & Havenhand, 1991; polychaetes: Pawlik, 1990), DOPA and catecholamines (bivalves: Cooper, 1982; Coon *et al.*, 1985; gastropods; Pires & Hadfield, 1991; polychaetes: Jensen & Morse, 1990; Pawlik, 1990), and GABA (gastropods: Morse *et al.*, 1979; echinoderms: Pearce & Scheibling, 1990b). It has been hypothesised that bound 'neurotransmitter-mimetics' are responsible for the induction of settlement and metamorphosis in a variety of invertebrate larvae (Morse, 1985), but criticisms of this theory have been advanced (Pawlik, 1990). In the cases in which naturally occurring settlement cues have been isolated (p. 285), the compounds were unrelated to neurotransmitters; e.g., 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 transport amino acids into their bodies has been clearly established (e.g., Jaeckle & 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 & Hadfield, 1986; Coon, Fitt & Bonar, 1990).

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 (gastropod: Morse, Hooker & Duncan, 1980b; barnacle: Rittschof, Maki, Mitchell & Costlow, 1986), and those that affect the intracellular concentrations of cyclic AMP, such as cholera toxin (scyphozoan: Fitt *et al.*, 1987), dicapryloylglycerol (ascidian: Berking & Herrmann, 1990), and isobutylmethylxanthine (gastropod: Baxter & Morse, 1987). In some cases, the responses of larvae to these drugs have been used to formulate complex intracellular signal transduction mechanisms controlling metamorphic activation (Baxter & Morse, 1987). However, behavioural assays of whole larvae are not specific, neither in the application of the drug, nor in the assessment of the response, and the validity of models of the molecular pathways controlling settlement and metamorphosis have been called into question (Pawlik, 1990; but see Morse, 1990).

INORGANIC COMPOUNDS AS INDUCERS

In one of the earliest studies of larval behaviour, oyster settlement was attributed to the presence of copper salts in sea water. Prytherch (1931, 1934) observed that settlement of *Ostrea virginica* in Milford Harbor, Connecticut, peaked just after low tide, concurrent with lowest salinity resulting from an influx of fresh water from the Indian River. His analyses of the freshwater input revealed high concentrations of several heavy metals. Among them, copper was the only one that triggered oyster settlement, and it did so in metallic form and as various common copper salts. Prytherch measured the highest levels of dissolved copper at low tide (0.05 to 0.6 mg/l) and at these concentrations a colloidal precipitate of the oxychloride salt of copper was formed; he postulated that ingestion of these salt particles by larvae was both a requirement and a stimulus for settlement.

Prytherch's hypothesis was short-lived. According to Korringa (1940), Prytherch had over-estimated the concentration of copper in sea water by at least an order of magnitude. Treatment of settlement substrata with copper salts or metallic copper did not enhance oyster settlement. Particulate copper salts were rejected by oyster larvae as pseudofaeces rather than ingested. Most importantly, the peak in oyster settlement observed by Prytherch also corresponded with a peak in larval abundance in the harbour, a much more likely reason for increased settlement than decreased salinity or increased copper concentrations. It seems likely that the settlement observed by Prytherch was a sub-lethal toxic response of oyster larvae to high copper concentrations. Copper, iron and zinc salts have also been used to accelerate ascidian and bryozoan settlement (see review in Lynch, 1961); their toxicity was recognised in these studies.

Elevated concentrations of monovalent cations in sea water induce settlement of many invertebrate species, most probably by affecting the electrical potential across larval cell membranes (Pawlik, 1990; see p. 299). Müller and coworkers found that pulsed exposure of larvae of the hydrozoan *Hydractinia echinata* to sea water containing excess Cs^+, Rb^+, Li^+ or K^+ induced metamorphosis in a dose-dependent fashion (Spindler & Müller, 1972; Müller & Buchal, 1973; for a review of 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 been subsequently found to induce metamorphosis of the molluscs *Haliotis rufescens, Phestilla sibogae, Astrea undosa, Crepidula fornicata* and *Adalaria proxima* (Baloun & Morse, 1984; Yool *et al.*, 1986; Pechenik & Heyman, 1987; Todd, Bentley & Havenhand, 1991), and the polychaete *Phragmatopoma lapidosa californica* (Yool *et al.*, 1986). Larvae of the tunicate *Ciona intestinalis* metamorphosed in response to excess NH_4^+, Cs^+ and Li^+ (Berking & Herrmann, 1990). It seems unlikely, however, that invertebrate larvae would encounter significantly elevated concentrations of monovalent cations under natural conditions.

Two inorganic gases dissolved in sea water have recently been reported to stimulate settlement of invertebrate larvae: hydrogen sulphide (H_2S) and ammonia (NH_3). Cuomo (1985) demonstrated enhanced levels of settlement of larvae of a sediment-dwelling polychaete *Capitella* sp I in the presence of sulphide, with optimal settlement occurring in the 1.0–0.1 mM range. Larvae settled in response to sulphide whether sediment was present or not. Cuomo (1985) suggested that this specific response to sulphide would explain the recruitment of these worms to organically rich sediments. Dubilier (1988) further investigated the settlement of *Capitella* sp I and concluded that the apparent enhancement of settlement in the presence of sulphide was a toxic effect (larvae cease swimming and lay on the bottom in an apparently anaesthetised state), not the response of larvae to a specific settlement cue. She determined that recently hatched larvae of *Capitella* sp I settled and metamorphosed within minutes in response to organic-rich sediments in the absence of sulphide, whereas addition of sulphide resulted in delayed settlement. Sulphide in the absence of sediment enhanced settlement, but the response required 12–24 h and resulted in abnormal settlement behaviour. 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, Grassle & Webb, 1988; Grassle & Butman, 1989); sulphide levels were likely negligible under these experimental conditions.

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

Ammonia gas (NH_3) dissolved in sea water causes larvae of the oyster *Crassostrea gigas* to begin substratum exploration ('settlement behaviour' *sensu* Coon *et al.*, 1988; Bonar *et al.*, 1990; Coon *et al.*, 1990; Fitt *et al.*, 1990); an unknown, bacterial-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; the response was believed to be the result of increased intracellular pH, rather than a specific response to ammonia (Coon *et al.*, 1988, 1990). Weak bases, such as methylamine and trimethylamine, also induced similar behaviour. 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; see p. 298). 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.* (1990) suggest that it may play a rôle in oyster settlement.

Hydrogen peroxide (H_2O_2) at 10^{-4} M in sea water causes the loss of the velum (swimming organ) in larvae of the nudibranch mollusc *Phestilla sibogae* (Pires & 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 oxidised solutions of L-DOPA and catecholamines are often very different from those to freshly prepared, unoxidised solutions (e.g., Pawlik, 1990), an effect that may be attributable to the production of H_2O_2 as these compounds oxidise (Pires & Hadfield, 1991).

INDUCTION BY PETROLEUM PRODUCTS AND ORGANIC SOLVENTS

Holland and co-workers (Holland, Crisp, Huxley & Sisson, 1984) discovered that oil extracted from Blackstone oil shale contained a factor that enhanced 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 mobilisation of lipophilic inducers from the kerogen matrix of the shale (Huxley, Holland, Crisp & Smith, 1984). Smith & Hackney (1989) also found that crude oil or mixture of gasoline and engine oil spread onto clam shells promoted the settlement of the barnacles *Balanus improvisus* and *B. eburneus*, but petroleum treatment inhibited settlement of the oyster *Crassostrea virginica*.

Hill & 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 as nickel- and vanadium-chelated porphyrins by ultraviolet spectrometry. 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/m^2, depending on the valence of the chelated metal ion. Metalloporphyrins were hypothesised to stimulate settlement in much the same way as arthropodin: the compounds are sticky and presumably bind the proteins associated with the cyprid attachment disk (Hill & Holland, 1985; see pp. 294 and 305).

Common organic solvents at high concentrations elicited settlement of the nudibranch *Phestilla sibogae* (Pennington & Hadfield, 1989). Five alcohols, including ethanol and methanol, ethanolamine, acetonitrile, acetone, dichloromethane and toluene were effective at inducing settlement, but ethylene glycol, dimethyl sulphoxide, benzene and hexane were not. A maximum of 65% settlement occurred in response to ethanol at 0.1 M 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, i.e., contact with the substratum is required for recognition of the cue. This has been demonstrated repeatedly and across phylogenetic lines, for cnidarians (Donaldson, 1974; Morse *et al.*, 1988), polychaetes (Wilson, 1948, 1968; Williams, 1964; Kirchman *et al.*, 1982a), molluscs (Bayne, 1969; Morse & Morse, 1984a), barnacles (Knight-Jones, 1953; Crisp & Meadows, 1962), bryozoans (Crisp & Williams, 1960) and echinoderms (Highsmith, 1982). Settlement can be stimulated by water-soluble neuroactive agents (Morse *et al.*, 1979; Pawlik, 1990) or soluble preparations of inductive substrata (Harington, 1921; Veitch & Hidu, 1971; Müller, 1973). Molluscan larvae have been stimulated to settle in enclosed volumes of sea water 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 & Shibata, 1989). In point of fact, the few naturally occurring settlement cues that have been isolated and identified are insoluble in sea water (Kato *et al.*, 1975; Yvin *et al.*, 1985; Pawlik, 1986).

Nevertheless, soluble compounds are thought to effect settlement in some species. Larvae of the mud snail *Ilyanassa obsoleta* (as *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 & Scheuer, 1985; although larvae may not respond until very near the substratum, see Hadfield & Miller, 1987). Larvae of another nudibranch *Onchidoris bilamellata* may begin substratum exploration after perceiving soluble cues associated with barnacle prey (Chia & Koss, 1988). Similarly, larvae of the oyster

Crassostrea gigas may respond first to soluble cues, which initiate substratum exploration, and then to substratum-bound cues, which initiate metamorphosis (Coon, Fitt & Bonar, 1990). Sand dollar larvae (*Dendraster, Echinarachnius*) settle in response to small molecules, produced by adults and transferred to adjacent sediments, that may be perceived in the water column (Highsmith, 1982; Burke, 1984; Pearce & Scheibling, 1990a).

Larvae of the cephalaspidean mollusc *Haminoea callidegenita* may be stimulated to metamorphose by a diffusible compound present in the jelly mass that surrounds the developing embryos (Gibson & Chia, 1989). Under normal circumstances, 30–50% of the hatchlings emerge from egg masses as veligers, with the remainder crawling away as juveniles. Embryos removed from egg masses but cultured in the presence of egg jelly exhibited a similar ratio, but 80% of the embryos cultured without egg jelly developed into veligers. Jelly also induced metamorphosis of veligers that had already hatched. Unlike the previous cases, the soluble cue thought to affect larvae of *H. callidegenita* did not diffuse freely in sea water, but probably remained concentrated in the egg mass jelly.

Marsden (1987) performed laboratory experiments with larvae of the tube worm *Spirobranchus giganteus*, an obligate associate of corals (Hunte, Conlin & Marsden, 1990). She noted that, in still water, precompetent larvae swam toward some coral species in preference to other species, coral rubble, or control sea water. The preferences of immature larvae for various coral species were assessed in the same manner (Marsden, Conlin & Hunte, 1990; Marsden & Meeuwig, 1990). It was suggested that larvae may respond to a chemical cue diffusing from the preferred coral species. 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 could 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 (see Butman, 1986), hence larval response to a diffusing cue would be little different than contact chemoreception. Secondly, larvae are of sufficiently small size as 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, e.g., 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 larvae subjected to flow characterised by low Reynolds numbers are more apt to travel along with a mass of water than through it (see Denny & Shibata, 1989). The sperm of algae (Maier & Müller, 1986) and some invertebrates (Miller &

King, 1983) are attracted to their eggs by chemotaxis, but the process occurs over a distance measured in micrometres and within the viscous boundary layer surrounding the egg. Larvae of coral fishes appear to respond to diffusible chemical cues emanating from adult conspecifics and heterospecifics (Sweatman, 1988), but fish larvae are both larger and better swimmers than invertebrate larvae. Juvenile benthic invertebrates apparently respond to soluble cues with directed movements (Rittschof, Williams, Brown & Carriker, 1983), and chemotaxis certainly occurs among adult marine invertebrates (Reeder & Ache, 1980; Atema, Fay, Popper & Tavolga, 1988), which may obtain directional information from temporal patterns of diffusing chemical signals released into turbulent water flow (Moore & Atema, 1988; the subject of chemical orientation is extensively reviewed in Bell & Tobin, 1982).

CHEMOSENSORY ORGANS

Sensory organs transduce environmental cues (light, gravity, mechanical or chemical stimuli) into signals within the organism (neutrotransmitters, hormones or electrical impulses). The sensory organs of invertebrate larvae are poorly known (Laverack, 1974; Chia & Rice, 1978; Lacalli, 1981, 1988; Burke, 1983a; Chia, 1989). Their perceptive functions are usually presumptive, inferred from observations of larval behaviour or based on histological and ultrastructural evidence. The small size and delicate nature of most larvae make them 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 should come as no surprise that no larval chemoreceptive organs that respond to identified chemical signals have been unambiguously characterised, although some recent research shows considerable promise toward this end (Chia & Koss, 1988; Arkett, Chia, Goldberg & Koss, 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 so as to trigger metamorphosis. This has been achieved by exposing larvae to sea water with an altered ionic composition (Baloun & Morse, 1984; Yool *et al.*, 1986; see p. 300), and to various neuroactive agents (see p. 298), and by direct electrical stimulation (Cameron & Hinegardner, 1974; Burke, 1983b; Satterlie & Cameron, 1985). Compounds that 'shock' larvae (e.g., H_2S) may cause settlement without the involvement of a specific chemoreceptor. There is greater 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 recognised to have a chemosensory role in selective settlement (Knight-Jones, 1953). Cyprid larvae use brush-like 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 & 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 brush-like 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 & Nott, 1971). Nott & Foster (1969) advanced a theory of the mechanism by which the attachment disks might be used to detect the arthropodin cue of conspecific adults: the disks expel proteases as they contact the substratum, resulting in the localised breakdown of arthropodin and release of characteristic amino acids that are then recognised by the sensory hairs. As discussed earlier (p. 294), an alternative view, that of the 'tactile chemical sense', was elaborated by Crisp & Meadows (1963) and Crisp (1974, 1984) who proposed an analogy to an antigen-antibody reaction whereby the attachment disk adheres to the substratum-bound inducer by non-covalent 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 & Crisp, 1983) and with the discovery of sticky proteins that are exuded by the attachment disk during reversible attachment (Walker & Yule, 1984; Yule & Walker, 1987). Yet, species-specific responses by cyprid larvae to arthropodin cues have been demonstrated (Crisp, 1990), implying that chemoreception does occur.

The presumptive chemosensory organs of molluscan larvae have been described for a few species. Bonar (1978) characterised 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 & Koss (1982) described the putative sensory organs of the larvae of *Rostanga pulchra*, a nudibranch that settles specifically on its sponge prey *Ophlitaspongia pennata* (Chia & Koss, 1978). Competent veligers of *Rostanga 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 & 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 hypothesised to detect the chemical factor produced by adult barnacles that stimulate cessation of swimming and onset of substratum exploration (Chia & Koss, 1988; Chia, 1989). Arkett *et al.* (1989) have successfully made preliminary intracellular recordings from cells in the sensory field of larvae of *O. bilamellata*. These cells respond to barnacle-conditioned sea water with a slow, small-amplitude depolarisation, but do not respond to control sea water. The depolarising cells were revealed by injection with lucifer yellow 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* (Morse, 1990; see p. 299). The receptors for both the natural inducer of settlement (derived from encrusting red algae) and for water-borne amino acids that regulate this induction are hypothetically located on epithelial chemosensory cilia. Morse *et al.* (1980a) described the secretion of glycopeptides from the cephalic sensory organ as larvae underwent "behavioural matamorphosis" in response to GABA, a neurotransmitter that is 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 & Morse (1986) determined that a radio-labelled inducer of settlement, baclofen (an analogue of GABA), became dissociated from metamorphosing larvae after 20 h 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 & Morse, 1991). It is not clear, however, whether the cilia used in these investigations 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 behaviour. Using intracellular recording techniques, she monitored electrical responses of velar cells to GABA and determined that the receptor for the compound was most likely not present on velar cells, although her results did not necessarily preclude their presence on velar cilia. Barlow (1990) 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 characterised for reef-building sabellariids of the genus *Phragmatopoma*. Eckelbarger (1978) described tufts of cilia scattered over the body of larvae of *P. lapidosa lapidosa* and suggested that these structures might have a role in substratum selection because they are concentrated on parts of the body used by the larvae when exploring the substratum. Amieva & Reed (1987) and Amieva, Reed & Pawlik (1987) used video microscopy to study the behaviour of *P.l. californica* at settlement and examined the ultrastructure of the larval tentacles of this subspecies in detail. They determined that the tufts of cilia on the tentacle surfaces were immotile and borne by cells in direct communication with the larval nervous system. The morphological evidence and observations of settlement behaviour 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, Ninos & Woollacott, 1988). The putative larval chemosensory organ consists of a long bundle of cilia called the vibratile plume, which project from the anterior midline of the larva (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 behaviour 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 & 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 & Cloney, 1988).

COMPARISONS WITH TERRESTRIAL INSECTS

The chemical ecology of terrestrial insects is much better understood than that of marine invertebrates. Not only have compounds responsible for various insect behaviours been isolated and identified, the chemosensory structures involved in signal perception have been well characterised through the use of electrophysiological techniques, and the neuroendocrine mechanisms controlling development have been intensively studied (Hansen, 1978; Vinnikov, 1982; Downer & Laufer, 1983; Bell & 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 diet 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 2). Gregariousness, with all its concomitant advantages, is common among insects, but is restricted in most orders 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. Examples include pierid butterflies that oviposit only on plants of the family Cruciferae that produce glucosinolates (Chew, 1977), sawflies that lay eggs only on willows that synthesise specific phenolic glycosides (Roininen & Tahvanainen, 1989) and some parasitic wasps that 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: Oehlschlager *et al.*, 1988; Birgersson, Schlyter, Bergström & Löfqvist, 1988).

Insect olfactory cues have received particular attention (Kramer, 1978; O'Connell, 1986). Volatile compounds are used as sex attractants, as

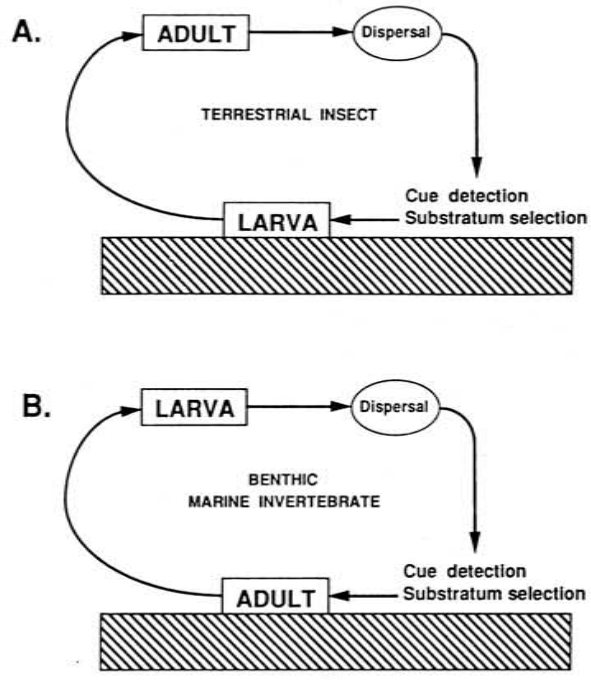


Fig 2.—Comparison of the generalised life histories of (A) a terrestrial insect and (B) a benthic marine invertebrate. Dispersal and substratum selection are undertaken by adult insects with sedentary larvae, while the opposite occurs among marine invertebrates.

trailmarkers, 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 characterised 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 & Foster, 1969; Gibson & Nott, 1971). Some authors have compared chemically-mediated substratum selection of invertebrate larvae to pheromonal communication by terrestrial insects (Burke, 1984, 1986; Pawlik & Faulkner, 1986, 1988), although insects can 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 & Faulkner, 1986; Pawlik, 1988b). Among insects, specific fatty acids stimulate electrophysiological responses in sensory receptors of *Necrophorus* 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 moults, pupation, and to adulthood (Downer & Laufer, 1983). In barnacles, synthetic analogues of insect juvenile hormones trigger metamorphosis without attachment (Gomez, Faulkner, Newman & Ireland, 1973; Freeman & Costlow, 1983); compounds similar to insect juvenile hormones have been identified in extracts of crustaceans (Laufer *et al.*, 1987). As in the case of some insects, fouling barnacles could potentially be controlled by disrupting their normal development through manipulation of the endocrine system (Fingerman, 1988).

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; Johnson, MacIntosh & Somerton, 1986). Isolation and identification of the compounds responsible for the localisation 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.

CHEMICAL INHIBITION OF SETTLEMENT

Competition for space among benthic marine organisms living on hard substrata is generally believed to be intense, and the production of allelopathic chemicals is a suggested mechanism by which slower-growing species persist (Jackson & Buss, 1975) or established organisms deter the settlement of colonising larvae (Goodbody, 1961). Marine organisms inhibit surface fouling through a variety of physical means: Cnidarians bear stinging nematocysts, echinoderms and bryozoans elaborate pinchers or movable spines, and crustaceans groom themselves and completely replace their external surfaces with each successive moult. Indeed, the periodic or continuous sloughing of a mucoid or epidermal coating is an attractive alternative pursued by various algae, sponges and cnidarians (Rublee, Lasker, Gottfried & Roman, 1980; Filion-Myklebust & Norton, 1981; Dyrynda, 1986; Barthel & Wolfrath, 1989; Wahl & Banaigs, 1991). Davis, Targett, McConnell & Young (1989) and Wahl (1989) have recently reviewed the literature on the establishment of fouling communities and the inhibition of settlement and overgrowth by marine algae and invertebrates. I shall restrict the scope of this review to what is known about the chemical inhibition of invertebrate larval settlement.

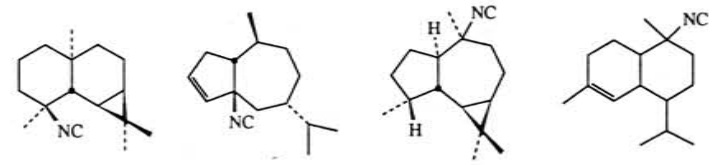
Invertebrate larvae may recognise established competitive species and forego settlement in their presence. In laboratory experiments, Young & Chia (1981) demonstrated a delay in the settlement of the bryozoan *Bugula pacifica* in response to sea water conditioned by the presence of the ascidian *Diplosoma macdonaldi* or an ethanol extract of the ascidian. Water conditioned by two other ascidians or a sponge had little or no effect on larval settlement. Field

experiments performed by Grosberg (1981) revealed that the larvae of nine invertebrate species (three polychaetes, two barnacles, four bryozoans) were sufficiently selective at the time of settlement to avoid glass plates bearing 15 colonies of the ascidian *Botryllus schlosseri*. Grosberg discounted an allelopathic response, however, because larvae of the nine selective species that did settle on the plates frequently did so immediately next to a colony of *B. schlosseri*. Larvae of another ascidian, *Podoclavella moluccensis*, were found to avoid settlement on two species of subtidal sponges, *Mycale* sp and *Crella incrustans*, when larvae were individually followed in the field (Davis, Butler & Van Altena, 1991). Johnson & Strathmann (1989) found that settlement of the barnacle *Balanus glandula* was diminished on panels that were treated with the mucus of the snail *Nucella lamellosa*, a predator of adult barnacles. As discussed previously (p. 280), competition for space may result in spacing-out or avoidance behaviour by settling barnacle larvae, but the stimuli involved are unclear (Hui & Moyse, 1987). Among soft-bottom invertebrates, there is evidence for avoidance of sediment associated with the adult polychaete *Abarenicola pacifica* by larvae of the polychaete *Pseudopolydora kempi*, ostensibly to prevent burial of juveniles of the latter species by the sediment reworking activities of the former (Woodin, 1985).

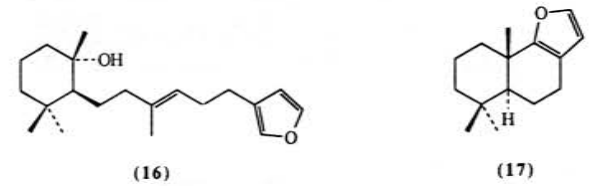
Well over 2000 natural products have been described from marine organisms (Faulkner, 1991, and earlier reviews by the same author cited therein). The biological importance of these compounds is the subject of considerable speculation. Marine algae and soft-bodied invertebrates have yielded a wealth of novel compounds. Because many species are conspicuously free of epibionts, an antifouling role has often been suggested for the unusual secondary metabolites isolated from them (Bakus, Targett & Schulte, 1986; Davis *et al.*, 1989). Unfortunately, only in a few instances has experimental evidence been provided to support these claims.

Sponges have yielded an abundance of novel compounds. They are also infrequently fouled. Thompson, Walker & Faulkner (1985) assayed 18 purified natural products from seven species of southern California sponges employing larvae of three invertebrate species: *Phidolophora pacifica* (bryozoan), *Salmacina tribranchiata* (polychaete) and *Haliotis rufescens* (gastropod). A natural mixture of isonitriles **(12–15)** from *Axinella* sp was active against all three species at 10 μg/ml. Two compounds from *Dysidea amblia*, ambliol-A **(16)** and pallescensin-A **(17)**, at the same concentration inhibited settlement of *Salmacina tribranchiata* and *Haliotis rufescens*, but not *Phidolophora pacifica*. Larval responses to the other compounds were variable. One of the sponge species, *Aplysina fistularis*, was further studied to determine whether its natural products, the dibromotyrosine-derived metabolites aerothionin **(18)** and homoaerothionin **(19)**, were elaborated on or near the surface of the sponge where settling larvae might be exposed to them (Thompson, 1985; Walker, Thompson & Faulkner, 1985). Sea water conditioned by *A. fistularis* caused inhibition of metamorphosis or death of larvae of *Haliotis rufescens*, but had no effect on *Phidolophora pacifica* or *Salmacina tribranchiata*.

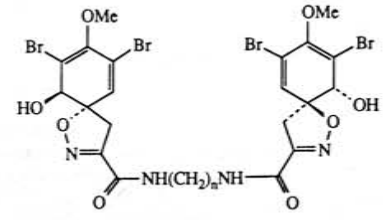
Bingham & Young (1991) tested for the release of allelopathic chemicals by sponges in the field. Three sponge species were chosen at each of three study sites (one in Belize, two in Florida). Living sponges were positioned next to ceramic recruitment tiles, with synthetic sponges similarly positioned as controls. Surprisingly, only one recruiting species at one site (an unidentified



(12) **(13)** **(14)** **(15)**



(16) **(17)**



(18) n = 4

(19) n = 5

sponge) had significantly lower recruitment next to living sponge. Five species exhibited enhanced recruitment next to a sponge, however, suggesting that sponge exudates may promote the settlement of some species.

Organic solvent extracts of several sponges have been demonstrated to deter invertebrate larval settlement. Ethyl acetate extracts of *Lissodendoryx isodictyalis* dissolved in sea water inhibited settlement of the barnacle *Balanus amphitrite* in laboratory assays, as did several fractions purified from the extracts (Sears, Gerhart & Rittschof, 1990). Two sponges, *Mycale* sp and *Crella incrustans* were tested for their ability to inhibit settlement of the compound ascidian *Podoclavella moluccensis* (Davis *et al.*, 1991). Individual tadpole larvae were offered the choice of an area soaked in sponge extract or an equal area soaked in solvent alone (control). In all but one case, larvae settled preferentially on the control area, a result which supported the authors' view that sponge natural products deterred larval settlement. It is unclear, however, whether a paper surface coated with an organic extract accurately approximates the sponge surface, where organic compounds are ostensibly bound in cellular inclusions. Impregnating paper with lipophilic compounds may alter its surface wettability; larvae may respond to the different surface properties, rather than the metabolites *per se* (see Brewer, 1984; Mihm, Banta & Loeb, 1981). The fact that the primary metabolite cholesterol inhibited settlement of *P. moluccensis* (Davis *et al.*, 1991), supports this possibility.

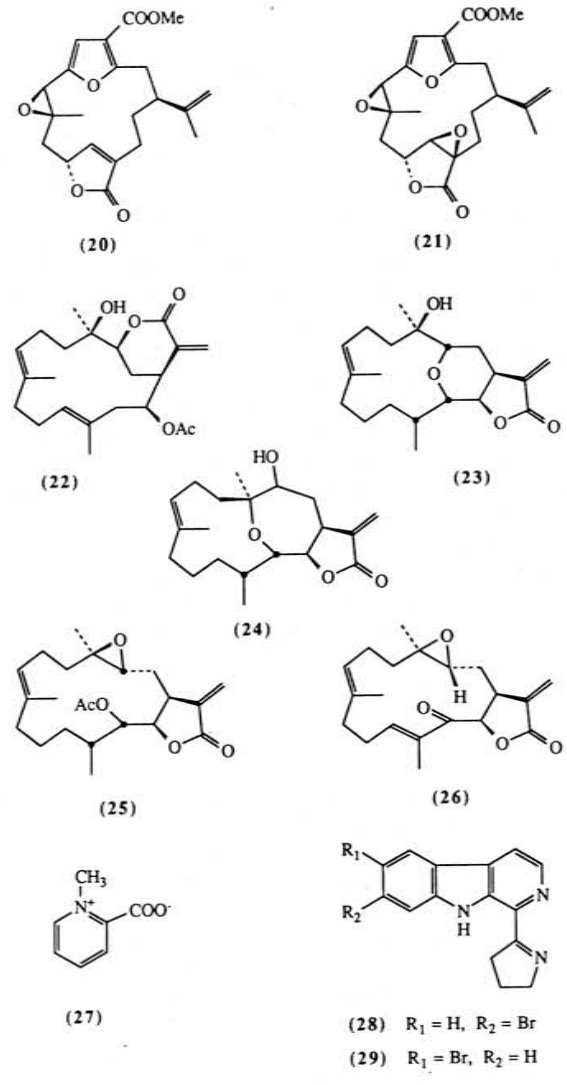
Excised tissues of sponges, bryozoans, ascidians and a soft coral were assayed for their effects on the larvae of two bryozoan species (*Bugula flabellata*

and *B. turbinata*) in small volumes of sea water (Dyrynda, 1985). The presence of pieces of most species was moderately to acutely toxic to larvae of *B. turbinata*, but had no effect on *B. flabellata*. Of course, larvae are probably not exposed to high concentrations of substances leaking from the damaged tissues of adult benthic invertebrates under natural circumstances.

The natural products of two octocorals, the gorgonian *Leptogorgia virgulata* and the pennatulacean *Renilla reniformis*, have been studied for their antifouling properties. Standing, Hooper & Costlow (1984) isolated both inducers and inhibitors of settlement of the barnacle *Balanus amphitrite* in homogenates of soft tissues, dialysates of the homogenates, and sea water conditioned by whole animals. Inhibitors were low molecular mass compounds (< 20 kilodaltons), while inducers were larger molecules (> 20 kilodaltons) that adsorbed to surfaces. The inducers were thought to effect barnacle settlement in much the same way as sticky proteins adsorbed to surfaces (see pp. 294 and 305). These studies were expanded upon by Rittschof and colleagues (Rittschof, Hooper, Branscomb & Costlow, 1985; Rittschof, Hooper & Costlow, 1986, 1988; Gerhart, Rittschof & Mayo, 1988). The barnacle settlement inhibitors of the two octocorals had different chromatographic properties, but both inhibited settlement once adsorbed onto polystyrene surfaces. The inhibitors of barnacle settlement were ineffective against larvae of the bryozoan *Bugula neritina*. A different fraction inhibited bryozoan settlement, but it had no effect on barnacle larvae. The surface-bound inhibitors were not otherwise toxic to larvae. Two of the antifouling agents from *Leptogorgia virgulata* were identified as diterpenoid hydrocarbons, pukalide **(20)** and epoxypukalide **(21)**, both previously described from the octocoral *Sinularia* sp. A third, unidentified compound inhibited settlement because it caused cyprids to become stuck to the walls of assay vials. There is no evidence that any of the compounds or fractions isolated from these octocorals influence invertebrate larvae under natural conditions.

Very few other cnidarians have been studied for the inhibitory effects of their secondary metabolites on settling larvae. Cembranolides from some Caribbean gorgonians were assayed for toxic effects (particularly loss of ciliary activity) on larvae of the tropical Pacific nudibranch *Phestilla sibogae*, a specific predator of hard corals (Hadfield & Ciereszko, 1978). All five compounds, crassin acetate **(22)**, eunicin **(23)**, jeunicin **(24)**, eupalmerin acetate **(25)** and peunicin **(26)** killed larvae within 24 h at concentrations of 1, 5 or 10 ppm. Most of the compounds stopped larval ciliary movements within an hour. Homarine (N-methyl picolinic acid, **27**), isolated from cnidarian tissue homogenates, inhibited metamorphosis of planulae of the hydroid *Hydractinia echinata* (Berking, 1986), although interest in this effect concerned the compound's action as an endogenous morphogen rather than its antifouling property.

For ascidians, surface acidity and high concentrations of vanadium were thought to inhibit the settlement of epibionts (Stoecker, 1978). However, several heavily fouled ascidians have acidic tests (Davis & Wright, 1989), and high vanadium concentrations in their tissues (Stoecker, 1980; Davis *et al.*, 1989). Davis & Wright (1989) noted that colonies of the highly acidic *Eudistoma capsulatum* were fouled by epifaunal invertebrates, while a non-acidic congener *E. olivaceum*, was free of epibionts. Ethyl acetate extracts of *E. olivaceum* inhibited settlement of the bryozoan *Bugula neritina*, an



effect attributed to the presence of eudistomins in the extracts. Assays were conducted in which plastic squares were coated with fractions from extracts of *Eudistoma olivaceum* (Davis & Wright, 1990); the possibility of confounding effects of organic films on larval settlement have already been discussed (see p. 311). Two toxic and one non-toxic inhibitors of settlement were investigated; the toxic compounds were identified as eudistomins G and H (**28** and **29**, respectively). The identity of the non-toxic inhibitor was not determined. Again, there is no evidence that these compounds are elaborated on the surface of the organism at sufficient concentrations to deter larval settlement.

CONCLUSIONS AND FUTURE DIRECTIONS

There is considerable evidence that chemical stimuli induce the settlement of marine invertebrate larvae in nature. The importance of settlement cues appears to vary with the species; some may be relatively non-specific, but the highly localised distributions of many adult invertebrates can ultimately be traced to patterns established at the time of larval settlement. Chemical signals are likely to be important for species that form aggregations, those associated with heterospecific organisms (various symbioses and predators settling on or near prey), and those that settle preferentially on a surface film of microorganisms. Settlement preferences have been characterised for species representing each of these groups, and in some cases the chemicals providing the stimuli have been partially purified, but natural compounds that induce settlement have been isolated and identified in only a few instances, and it remains to be demonstrated that any of these truly function as inducers in nature. Putative chemosensory organs have been described from larvae of several phyla, but their functions have not been unequivocally established.

Clearly, this subject area is ripe for further research. Virtually nothing is known about the perception of chemical stimuli by larvae of parasitic and mutualistic invertebrates, even though their responses are likely to be extremely specific. As greater use is made of modern natural products and biochemical techniques to isolate and identify chemical signals, patterns in the structural classes of compounds that induce settlement may become evident. The relative solubility of these compounds in sea water will be of particular interest. Among the unanswered questions are: Do larvae perceive soluble compounds, in addition to substratum-associated cues, under natural conditions? Are soluble inducers detected with chemosensory organs, or do the compounds 'shock' larvae, causing them to fall out of the water column? Does chemotaxis occur? If so, how are concentration gradients detected by miniscule larvae under natural conditions of water flow?

On the subject of water flow, it has become evident that hydrodynamical processes must also be considered when addressing settlement phenomena. Experiments performed in still sea water on laboratory benches do not accurately reflect the environmental conditions faced by most larvae. Greater effort should be devoted to testing stimulatory substrata or compounds under more realistic flow regimes, i.e., in flumes or in the field, perhaps with a concommitant effort toward tracking larval movements (see Levin, 1990).

More data are needed on the chemosensory organs and receptors of invertebrate larvae. In this regard, studies of marine invertebrates may follow the path of research on terrestrial insects. Once the chemical signals have been identified, characterisation of the chemosensory cells and receptors can proceed by employing electrophysiological and biochemical techniques.

If studies of the chemical induction of settlement are in their infancy, research on the inhibition of marine invertebrate settlement by naturally occurring chemical cues has yet to leave the delivery room. While it is relatively easy to demonstrate that a purified natural product has a toxic effect on competent larvae, it is not so easy to show that the compound is externally elaborated by the source organism in such a way that larvae are deterred from settling on or near the source. There is no shortage of marine natural products to which an antifouling role has been tentatively assigned. Further advancement on this topic awaits (1) evidence of the release of compounds into the water or onto the surface of their source organisms, and (2) demonstration of their role as settlement inhibitors against a natural population of competent larvae at natural concentrations and under realistic conditions of water flow.

Over thirty years ago, Lynch (1961) wrote a review of the effects of various physical and chemical factors on the settlement and metamorphosis of invertebrate larvae. The final passage from that review will close this one as well: "It is evident that there is need for new viewpoints, for more observations and, perhaps, for team-work between various disciplines not only of biology but of physics and chemistry as well before there will be a clearly acceptable hypothesis of metamorphosis. Only the beginnings have been made in this interesting field."

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