MARINE BIODETERIORATION

Advanced Techniques Applicable to the Indian Ocean

Editors

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39. The Gregarious Settlement of Sabellariid Polychaetes: New Perspectives on Chemical Cues

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Polychaete worms of the family Sabellariidae have planktonic larvae that in some species settle gregariously to form colonies of amassed sand tubes. Evidence for site-specific larval settlement and metamorphosis in the family is reviewed, with particular emphasis on the recent isolation of naturally occurring, lipophilic inducers of larval settlement of *Phragmatopoma californica*. The amenability of larval sabellariids as experimental organisms and the diversity of larval responses within the family make them particularly well suited to address the complex set of factors governing invertebrate larval settlement and the development of marine fouling communities.

INTRODUCTION

The vast majority of benthic marine invertebrates that constitute fouling communities release planktonic larvae that are transported some distance through the water column prior to their assumption of sessile adulthood. Site selection by these larvae is no longer regarded as stochastic, as manifested by the large body of accumulated work on the physical and biological properties of potential substrates that influence larval response (recent reviews by Chia and Rice 1978, Burke 1983, Crisp 1984). Interest in the biological conditions influencing settlement has concentrated on larval preferences for: (1) substrates bearing an organic-microbial film (e.g., cnidarians: Brewer 1984; polychaetes: Wilson 1955; echinoderms: Cameron and Hinegardner 1974); (2) host plants or animals (e.g., cnidarians: Nishihira 1968; polychaetes: Potswald 1978; gastropods: Hadfield 1976; Morse et al. 1979; bryozoans: Ryland 1974); and (3) sites on or near adult conspecifics (e.g., cnidarians: Williams 1976; echiuroids: Suer and Phillips 1983; bivalves: Bayne 1969; crustaceans: Crisp 1979; echinoderms: Highsmith 1982). Many of these studies attributed the initiation of settlement and metamorphosis to an interaction between the larvae and the surface chemistry of the chosen substrate.

Chemical cues of larval settlement have been of particular interest,

perhaps because an understanding of the chemical basis for settlement in fouling organisms might result in some degree of control over the processes involved. The important successes of earlier work on the initiation of barnacle cyprid settlement by proteinaceous extracts of adults (Knight-Jones 1953, Crisp and Meadows 1962) and on the induction of gastropod metamorphosis by vertebrate neurotransmitters (Morse et al. 1979) seem to have biased the search for natural inducers of larval settlement and metamorphosis in other fouling species. Subsequent research focused on hydrophilic biomolecules as chemical inducers: proteins for barnacle cyprid larvae (Larman 1984), proteins, amino acids, choline derivatives, and related compounds for molluscs (Veitch and Hidu 1971, Morse et al. 1984, Hadfield 1984), and sugar moieties for spirorbid polychaetes (Kirchman et al. 1982).

In contrast, there have been some accounts of induction of larval settlement and metamorphosis by lipophilic (i.e., lipid soluble) substances (e.g., oysters: Keck et al. 1971). Nishihira and coworkers (Kato et al. 1975) found that a hexane soluble fraction of *Sargassum tortile*, one of the preferred algal substrates of the hydroid *Coryne uchidai*, contained delta-tocotrienol and its epoxide, both of which proved to be active at inducing larval settlement. There is, in fact, growing evidence that the natural chemical cues to site-specific settlement and metamorphosis of larval invertebrates may be as diverse as the organisms involved. This paper affords an opportunity to discuss recent evidence for lipophilic cues to larval settlement and metamorphosis in the polychaete family Sabellariidae and the considerable advantages of these worms as experimental organisms in investigating the complex factors that lead to the formation of marine fouling communities.

THE SABELLARIIDAE

The family Sabellariidae is a relatively small, morphologically distinct group of polychaetes that build tubes out of a combination of available sediment and a worm-derived cement secretion (Hartman 1944, Vovelle 1965). The worm body plan is modified for a tube-dwelling existence, with a coalescence and modification of the most anterior setae to form an operculum that seals the tube when the animal withdraws (Dales 1952).

Fossilized structures attributable to sabellariids have been found in strata dating to the lower Cambrian (Kirtley 1974). There are at least six extant genera encompassing more than 50 species, of which approximately two-thirds build solitary tubes, usually on shells and stones, at intertidal to abyssal depths worldwide (Hartman 1944, Achari 1972). About 20 species, predominantly of the genera *Phragmatopoma*, *Sabellaria* and including the monospecific genus *Gunnerea*, construct small to

extensive reefs of aggregated tubes in the low intertidal to subtidal of temperate and subtropical coasts in many parts of the world (figure 1, references cited in Achari 1972, Kirtley 1974).

Prerequisites for reef formation include a hard substrate for initial larval settlement, adequate water motion to provide a continuous source of dietary plankton, and sufficient suspended sediment to allow for tube construction at a rate exceeding that of overgrowth by competitive fouling organisms. Worm reef morphology varies considerably, apparently depending on the hydrodynamic conditions of the locality. Intertidal patch reefs of *Phragmatopoma californica* and *P. lapidosa* along the open coasts of southern California and southeastern Florida, respectively, are densely packed with adult worms so that the surface of these reefs resembles that of a honeycomb. The large, subtidal reefs of *P. lapidosa* along the eastern coast of Martinique, however, are much less crowded, the worms aligning their tubes in meandering rows so as to form loosely packed mounds resembling large heads of brain coral. Tube reefs may reach hundreds of meters in width and stretch over tens to hundreds of kilometers of coastline (Dollfus 1960, Kirtley and Tanner 1968). They have been implicated in shipwrecks, in the stabilization of beach sand (Kirtley 1967), in dominating the community structure of intertidal habitats (Taylor and Littler 1982), and in fostering communities of invertebrates and fish within and around their confines (Gruet 1971, Gore et al. 1978).

Reproduction in the Sabellariidae is strictly sexual, with the dioecious worms spawning their gametes directly into the water column. Therefore, reef formation is entirely dependent on the recruitment of feeding larvae, which may spend from several weeks to months in the plankton (Wilson 1968a). Curtis (1978) reviewed the literature concerning the occurrence of sabellariid larvae in the plankton from which broadly defined breeding seasons were extrapolated. The larvae of many species were found in the plankton throughout much of the year. Spawning may also be induced by colony damage, as evidenced by anomalously high recruitment rates following intense storms (Barry 1985).

Both the advantages and disadvantages of gregarious settlement were reviewed by Crisp (1979). Among reef-forming sabellariids, the close proximity of adults would allow for synchronization of spawning, particularly if a water-borne pheromone were involved. The proximity of freely-spawning invertebrates also strongly influences the percentage of successfully fertilized gametes (Pennington 1985), hence, a gregarious lifestyle would tend to minimize the risks of excessive gamete dilution upon synchronous spawning. Additionally, members of large aggregations are more likely to survive physical disturbances and competitive interactions with other fouling organisms and, consequently, gain a longer adult
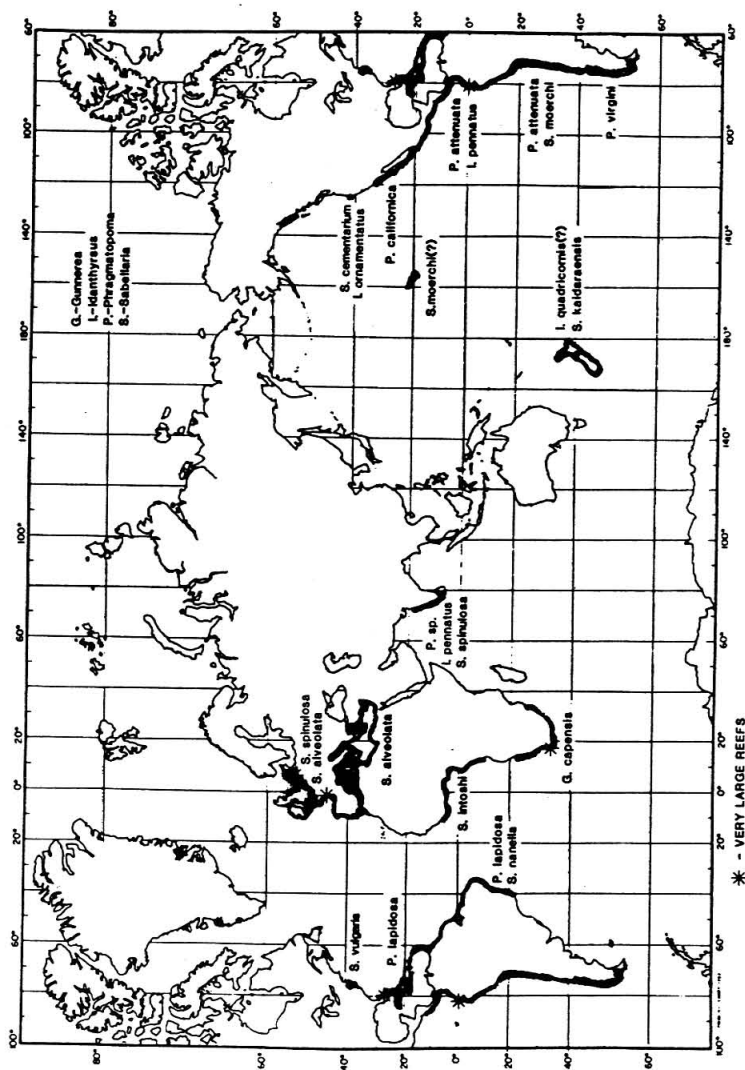
Figure 1. Distribution of reef-forming polychaetes of the family Sabellariidae.

life-span resulting in increased overall fecundity. In point of fact, Wilson's (1974) recurrent surveys of Britain's Cornwall coast have indicated that members of colonies of *Sabellaria alveolata* had survived for more than 10 years!

Eckelbarger (1978) has reviewed sabellariid larval development, settlement, and metamorphosis in considerable detail, with emphasis on larval morphology and ultrastructure. To provide the proper perspective, earlier work and more recent findings on substrate selection in the Sabellariidae will be summarized here.

Douglas P. Wilson (1929; 1968a, b; 1970a, b; 1974; 1977) devoted much of his career to exhaustive studies of larval development, settlement, and metamorphosis of the sabellariids from British waters. In one of the earliest experimental demonstrations of substrate specificity in marine invertebrate larvae, he discovered that larvae of the reef-building species *S. alveolata* were stimulated to settle upon larval contact with adult tubes, tube remnants or the mucoid tubes of juvenile worms. Factors such as surface contour and roughness, sediment type, water motion, and the presence of surface microorganisms had only a minor influence on larval behavior. The metamorphosis-inducing capacity of the tubes did not dissolve in water and was unaffected by drying, but was destroyed upon treatment with cold concentrated acid. Wilson concluded that a chemical cue in the tube cement induced larval response in a fashion similar to that proposed by Knight-Jones (1953) involving the settlement of barnacle larvae on contact with quinone-tanned, cuticular proteins of adult barnacles. Larvae of a sympatric species, *Sabellaria spinulosa*, which forms reefs in the North Sea, behaved in a similar manner, and were additionally found to metamorphose preferentially on the tubes of their own species over those of *S. alveolata*. Surprisingly, the converse was not necessarily true. Whereas larvae of *S. alveolata* preferred the natural tubes of their own species, they contrarily preferred tubes that had been built by adult *S. spinulosa* out of shore sand in laboratory aquaria over tubes that had been similarly constructed by adults of their own species, a result that Wilson could not explain.

Eckelbarger (1978) observed that the larvae of the four species of North American sabellariids that he studied (*Sabellaria vulgaris, S. floridensis, Phragmatopoma californica,* and *P. lapidosa*) would settle in the presence of tube sand from any of the other species, although preferences were not assessed experimentally.

Jensen and Morse (1984) extended Wilson's findings of the contact-dependent, chemical nature of sabellariid larval settlement to include *P. californica,* a reef-building species from the coast of central and southern California. They demonstrated that larval contact with the anterior portions of adult tubes initiated settlement and metamorphosis, while the

presence of various sympatric algae and invertebrates, sandstone, and the posterior portions of adult tubes resulted in little larval response. Tubes that had been boiled in water had lost their inductive capacity. They similarly discussed the likelihood that the chemical cues to larval settlement were quinone-tanned proteins, precursors or enzymes involved in their synthesis.

Less is known about the larval responses among nongregarious sabellariids. The larvae of *Lygdamis muratus*, a solitary, subtidal species, show no settlement preference for adult sand tubes, although they are capable of differentiating between sediments, preferring nonsterile sands containing pebbles and mud (Wilson 1977). Eckelbarger (1977) noted that more than half of the larvae of the nongregarious *S. floridensis* he had cultured had metamorphosed normally in the complete absence of tube-building materials. In a small-scale experiment, Smith and Chia (1985) found that the larvae of the mostly nongregarious *Sabellaria cementarium* required sediment to initiate settlement, but showed no apparent preference for beach sand over sand from the tubes of adults of its own species or from the tubes of *P. lapidosa* or *Idanthyrsus ornamentatus*.

ISOLATION OF NATURALLY OCCURRING LIPOPHILIC INDUCERS OF LARVAL SETTLEMENT AND METAMORPHOSIS OF *PHRAGMATOPOMA CALIFORNICA*

We are currently employing a bioassay-directed, natural products isolation procedure in a search for chemical cues to larval settlement in several southern Californian site-specific marine intertebrates. One species, which was particularly easy to culture and assay for metamorphosis, was the reef-building sabellariid *P. californica* (Pawlik 1986). Sequential extraction of the tube sand of *P. californica* in a series of organic solvents diminished its capacity to induce larval settlement and metamorphosis: assays of unextracted tube sand, extracted tube sand, and clean control sand resulted in a mean of 72%, 13%, and 2% metamorphosis, respectively. The inductive activity was retained in organic extracts of natural tube sand and was restricted to a single peak isolated by high-performance liquid chromatography. This active fraction consisted of a mixture of free fatty acids (FFAs), which was shown by gas chromatography-mass spectrometry of the corresponding methyl esters to be dominated by eicosapentaenoic (20:5), palmitic (16:0), and palmitoleic (16:1) acids. Of the nine FFAs that contributed 3% or more to the active fraction, only palmitoleic (16:1), linoleic (18:2), arachidonic (20:4), and eicosapentaenoic (20:5) acids induced larval metamorphosis, while the others were ineffective. Active FFAs were extracted from tube sand at concentrations within the level of a significant larval response, although these concentrations

were thought to be an inordinately low estimate of the actual FFA concentration naturally available to competent larvae on the surface of adult tubes.

In further assays of an additional 28 FFAs of variable acyl chain length and unsaturation (Pawlik and Faulkner 1986), it was discovered that larval response was highly stereospecific, with metamorphosis peaking in response to palmitoleic (16:1), linolenic (18:3), eicosapentaenoic (20:5), and docosahexaenoic (22:6) acids. Palmitelaidic acid, the *trans* isomer of the highly active palmitoleic acid (16:1), was ineffective at inducing larval metamorphosis. Inductive activity was strongly 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 acid (16:1) was a potent inducer of larval metamorphosis, 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 16:1.

The induction of larval metamorphosis by FFAs was also found to be dependent on the presence of the free carboxyl group (Pawlik and Faulkner 1986). Modification of the carboxyl terminus of the molecule by esterification or reduction resulted in the loss of inductive activity.

There are a number of advantages to free fatty acids as cues to larval settlement and metamorphosis in the marine environment: (1) Fatty acids are rare in the nonesterified, free carboxyl form (Wood 1974), thus, the presence of high concentrations of FFAs would provide a highly site-specific chemical signal. (2) FFAs are relatively water insoluble; they would remain adsorbed on the substratum and not diffuse into the surrounding water column. Crisp and Meadows (1962), in their studies of the gregarious settlement of barnacle cyprid larvae, suggested that the larvae of marine invertebrates may be incapable of perceiving chemical signals at a distance, although some exceptions may exist (Crisp 1984). Sabellariid settlement, like that of cyprids, is dependent upon larval contact with the substratum. The proteinaceous cement produced by the adult worms may additionally act to enhance the binding of FFAs to the sand grains in a fashion similar to that seen by Hoering and Abelson (1965). This may explain our inability to suppress fully the inductive capacity of tube sand by sequential organic extraction alone. (3) FFAs are relatively stable and would persist over a sufficient length of time to be of use as a surface-bound chemical signal. The loss of inductive capacity as tubes age (Jensen and Morse 1984) may reflect the eventual degradation of FFAs by oxidation and microbial attack. (4) FFAs would be simple to produce from a metabolic standpoint. The enzymatic machinery for lipolytic cleavage of esterified fatty acids could readily be co-opted from a digestive function to

the production of a chemical signal. The similarities in the composition of the free fatty acids derived from tube sand and the esterified fatty acid composition of marine phytoplankton are striking (cf. Volkman et al. 1980), and inducer production may represent the direct cleavage of dietary fatty acids by the adult worms, with FFAs produced and incorporated into the tubes as they are built.

Members of the Sabellariidae are exceptionally homogeneous in terms of morphology and life history patterns, and free fatty acids may be responsible for gregarious settlement in other species as well. We have recently determined that FFAs are also responsible for the induction of larval settlement and metamorphosis in the western Atlantic species *P. lapidosa*. Wilson's (1968b) descriptions of treatments influencing the inductive capacity of the tubes of *S. alveolata* (water insolubility and stability to drying, but not to acids) are also consistent with the chemical nature of FFAs.

THE APPLICABILITY OF SABELLARIIDS FOR CONTINUED RESEARCH OF LARVAL SETTLEMENT AND METAMORPHOSIS

Sabellariid polychaetes provide a highly tractable experimental organism for the study of larval invertebrate settlement and metamorphosis. Based on experience with the four species used to date in our laboratory, gravid adults can be obtained throughout the year, assuring a continuous supply of larvae. Larval culture is simple compared to other planktotrophic larval invertebrates and, under controlled conditions, development is uniform and synchronous (Pawlik 1986). Both larvae and adults can be successfully shipped by airmail, larvae in oxygenated, 1 μ-filtered seawater; small adult colonies are best sent with just enough seawater in the bottom of the shipping container to wet the top of the colony by capillary action. Fully gravid adult colonies can be kept in laboratory aquaria flushed with flowing seawater for six months or more on a diet of cultivated phytoplankton.

Sabellariids display a full range of settlement strategies that represent a microcosm of the span of larval behaviors found among marine fouling organisms. The larvae of reef-forming species such as *P. californica* and *P. lapidosa* will delay metamorphosis indefinitely until inductive tube sand is encountered. On the other end of the spectrum, larvae of solitary species such as *S. floridensis* metamorphose in the absence of sediment altogether, as though on a set developmental schedule (Eckelbarger 1977). Intermediate between these two strategies are species that form aggregations in some localities but are solitary over much of their geographic ranges. *S. vulgaris* is nongregarious over much of its range (eastern coast of North America), yet forms patch reefs in Delaware Bay (Curtis 1978).

The same is true for *S. cementarium*. Found throughout the North Pacific, this species builds reefs only near Coos Bay, Oregon (Posey et al. 1984). The reasons for this "facultative gregariousness" are still not clear (see Curtis 1978 for possible explanations), however, some tradeoff between the delay of larval metamorphosis and substrate specificity appears likely. The retention or concentration of larvae under the hydrodynamic conditions offered by bays and estuaries may shift the balance towards gregarious settlement. Although the substrate requirements of the larvae of *S. cementarium* have been investigated to some extent (Smith and Chia 1985), the importance of chemical cues to larval settlement of these facultative reef formers is unknown.

Many species of sabellariids live sympatrically and some appear to settle gregariously in a species-specific fashion (see earlier discussion of *S. alveolata* and *S. spinulosa*). *P. lapidosa* and *Sabellaria bella* form species-specific aggregates along the southern coast of Brazil (Nonato and Pérès 1961). *Sabellaria fucicola* from the coast of western Africa settles gregariously onto algae (Day 1967). Investigation into the potential differences in the chemical cues of larval settlement for these species may prove particularly rewarding.

Sabellariid larvae are well suited for studies of the receptor mediation of larval response. Eckelbarger (1978) described presumptive chemoreceptors from *P. lapidosa* larvae. Sensory structures are concentrated on the larval tentacles, which play an important role in substrate selection. The stereochemical specificity and concentration dependence of the response of *P. californica* larvae to FFAs (Pawlik 1986, Pawlik and Faulkner 1986) are suggestive of the type of receptor phenomenon common to studies of insect chemoreception (Hansen 1978). In particular, stereospecific responses to short-chain FFAs have been described in research on some beetles and flies. Analogous to a situation in which the antennae of an insect detect volatile pheromones, larval sabellariids may factually detect adsorbed lipophilic inducers (also pheromones) with their larval tentacles. These tentacles are within the range of effective microcannulation for neurophysiological study, hence, the sophisticated techniques of electrophysiologists may be applicable to studies of sabellariid chemoreception as well. Similarly, advanced techniques used in the study of pharmacologic and sensory receptors may prove useful in further elucidating sabellariid larval response at a molecular and ultrastructural level.

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