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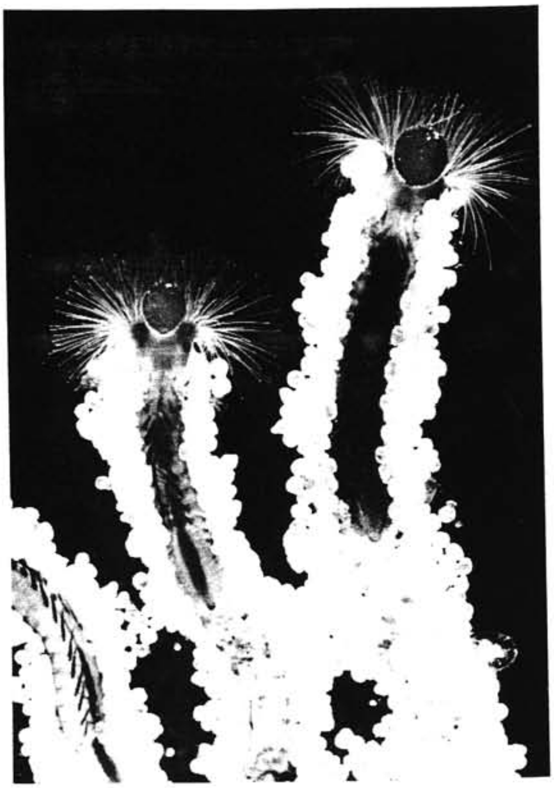
Tubeworms

Marine worms of the polychaete family Sabellariidae live in tubes constructed of cemented grains of sand. Some species are gregarious and form reefs of



Adult sabellariid worms (*Phragmatopoma californica*) in their sand tubes, built on a pane of glass, which allows them to be viewed in cross section. The black structure near the tentacles of each worm is an operculum; it blocks the tube opening when the worm retracts. The inside diameter of the tube is approximately 0.2 in. (5 mm).

amassed sand tubes. The planktonic larvae of these species recognize specific chemical cues in the sand tubes of adult worms that induce the larvae to settle and metamorphose. For one species, the chemical signals controlling larval settlement have been isolated and identified as a mixture of free fatty acids. Larval response is highly specific and dependent on the length, shape, and functionality of the free fatty acid molecule. These molecules are thought to be perceived by ciliated chemoreceptor cells that dot the surface of the larval tentacles.

Reefs. Many marine invertebrates construct tubes to protect their soft bodies. These tubes can be formed of calcium carbonate (vermetid snails, serpulid worms) or a mucopolysaccharide matrix (cerianthid anemones, sabellid and chaetopterid worms). Sabellariid worms form tubes (see **illus**.) by catching grains of suspended sand and shell fragments with their feeding tentacles and cementing them together with a proteinaceous glue produced by glands near their mouths. Unlike most other tube-dwelling invertebrates, sabellariid polychaetes form large mounds and reefs of aggregated sand tubes.

Fossilized structures attributable to sabellariids have been found in strata dating to the Lower Cambrian. Most of the extant species build solitary tubes in deep water, but approximately 20 species, predominantly of the genera *Phragmatopoma*, *Sabellaria*, and *Gunnerea*, construct small to extensive reefs of sand tubes in the low intertidal and subtidal of temperate and tropical coasts in many parts of the world. 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 tube construction at a rate exceeding that of overgrowth by other fouling organisms.

Tube reefs may reach hundreds of meters (1 m = 3.3 ft) in width and stretch over tens to hundreds of kilometers (1 km = 0.6 mi) of coastline. Particularly large reefs are found off the eastern coast of Florida and in Mont Saint-Michel Bay in northern France; the former have been blamed for at least one shipwreck. Sabellariid reefs stabilize sandy beaches and can be important in preventing coastal erosion. In addition, the reefs provide substrate and shelter for complex communities of invertebrates and play an important role as "nursery grounds" for juvenile fishes.

Reef formation by larvae. Unlike colonies of reef-forming corals, which grow primarily by asexual division of preexisting polyps, colonies of sabellariid worms are entirely dependent on the recruitment of planktonic larvae for reef maintenance and growth. Adult worms have separate sexes and spawn their gametes directly into the water column. The resulting larvae may spend several weeks to months drifting in the plankton and feeding on phytoplankton prior to settlement and metamorphosis. To deter predation during their long planktonic phase, sabellariid larvae bear characteristic bundles of barbed setae, which they erect around themselves when disturbed. After several weeks, the larvae develop a pair of anterior tentacles which they use to explore potential substrates prior to settlement. Gregarious species settle and metamorphose in response to contact with the tube sand of adult worms.

The advantages of gregarious settlement are many: the proximity of adults allows for synchronization of spawning and greatly increases the percentage of successfully fertilized gametes. Moreover, members of large aggregations are more likely to survive physical disturbances and competitive interactions with other fouling organisms, thereby gaining a longer adult life-span and greater fecundity. Some individual worms in sabellariid colonies from the coast of Britain have survived for more than 10 years.

Role of chemical cues. During the 1960s and 1970s, in studies of a reef-building sabellariid from European waters, *Sabellaria alveolata*, it was discovered that settlement was stimulated 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. It was concluded that a chemical cue in the tube cement induced larval settlement and metamorphosis.

Larvae of *Phragmatopoma californica*, a gregarious sabellariid from the coast of California, were similarly found to settle on the sand tubes of adult conspecifics over other substrates. Sequential extraction of the tube sand of *P. californica* in a series of organic solvents diminished its capacity to induce larval settlement and metamorphosis. The inductive activity was retained in the organic extracts of natural tube sand. An active fraction was isolated from the extracts by high-performance liquid chromatography, and it was found to consist of a mixture of free fatty acids.

Fatty acids in their esterified form occur as important components of cell membranes and other lipids in all living cells. Fatty acids possessing a free carboxyl group, however, are quite rare in nature. Yet, extracts of worm-free tube sand from reefs formed by *P. californica* contained concentrations of free fatty acids sufficient to induce larval settlement.

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

In further assays of an additional 28 free fatty acids of variable carbon-chain length and unsaturation, it was discovered that larval response was highly stereospecific, with metamorphosis peaking in response to palmitoleic, linolenic (18:3), eicosapentaenoic, and docosahexaenoic (22:6) acids. Palmitelaidic acid, the trans isomer of the highly active palmitoleic acid, 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 by the number of cis double bonds in the acyl chain. For example, although palmitoleic acid was a potent inducer of larval metamorphosis, oleic acid (18:1) was not, owing to its greater molecular length. Linoleic and linolenic acids 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 metamorphosis by free fatty acids was also found to be dependent on the presence of the free carboxyl group. Modification of the carboxyl terminus of the molecule by esterification or reduction resulted in the loss of inductive activity. In summary, larval response was found to be dependent on the presence of at least one cis double bond in the molecule, conservation of overall molecular shape with increasing acyl chain length by addition of cis double bonds, and the presence of a free carboxyl group.

Similarities to insect chemoreception. The stereochemical specificity and concentration dependence of the larval response of *P. californica* to free fatty acids are suggestive of the type of receptor phenomenon common to insect chemoreception. Stereospecific responses to short-chain free fatty acids have been described for the chemoreceptive organs of some beetles and flies. Analogous to a situation in which the antennae of an insect detect volatile pheromones, larval sabellariids may tactually detect adsorbed lipophilic inducers (also pheromones) with their larval tentacles. Detailed studies of the ultrastructure of the larval tentacles of *P. californica* have revealed the presence of putative ciliated chemosensory cells that synapse directly with the larval nervous system. 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.

Different species, different cues. *Sabellaria alveolata*, a reef-building sabellariid from European waters, did not respond to the same chemical signals as *P. californica*. In reciprocal assays, settlement of both species occurred to a greater extent on conspecific tube sand than on heterospecific tube sand. Extraction of the tube sand of *S. alveolata* diminished its capacity to induce metamorphosis of conspecific larvae, but the capacity was not transferred to the organic extracts, and a lipophilic inducer was not isolated or identified for this species. Furthermore, the free fatty acids that induced metamorphosis of *P. californica* either were ineffective at inducing settlement of *S. alveolata* or inhibited the response. Free fatty acids were present in the natural tube sand of *S. alveolata* at less than one-tenth the concentration found in natural tube sand of *P. californica*. Therefore, the larval settlement of gregarious sabellariids appears to be under the control of different types of chemical signals for two species in different genera. Whether differences exist between species within a given genus is the subject of current research.

For background information *SEE* CHEMORECEPTION; PHEROMONES; POLYCHAETA in the McGraw-Hill Encyclopedia of Science & Technology.

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Turbine propulsion

System studies performed in response to concerns about the fuel consumption of transport aircraft show that advanced turboprops could have propulsive efficiencies about 1.3 times as high as those of