Fouling Organisms of the Indian Ocean

R. Nagabhushanam

ROUTLEDGE

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Biology and Control Technology

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Preface

While this book focusses on the fouling organisms of the Indian Ocean, the destructive potential of biofoulers can be found in all marine environments. The Indian Ocean was selected because of the vast numbers and species of fouling organisms found there and because of the research done on them in recent years through funding from the U.S. Office of Naval Research, Oceanic Biology Program as well as from the Government of India.

The biofouling effects on man-made structures in marine waters have had increasingly greater economic impacts as oceans are used more and as antifouling prevention and protection costs increase. All types of surfaces can be fouled—boats, ship moorings, offshore platforms, aquaculture nets, onshore power stations—literally, any object in the water. Materials are degraded, become rigid or brittle or plugged, or are made less buoyant due to the weight of the fouling communities. Moving parts of vessels are affected as are their operating speeds and fuel consumptions. Fouling-related costs are huge, for example, the U.S. oil industry spends 16–18 billion dollars per year, the Tasmanian-Atlantic salmon industry $ 800,000 per year, and the U.S. Navy 75–100 million dollars per year (see page 46, this volume). It is obvious why antifouling prevention and protection are of deep interest to various industries and navies, and to scientists and engineers.

Over the years there has been much research directed on this problem. In some areas there is a wealth of information but in many others, very little. Numerous books and scientific articles are now in the literature, but the problem is still unsolved. It is hoped that the material in this volume will help augment what is already known as well as provide new information. Specifically, (1) to provide basic knowledge on the diverse structural and physiological adaptations of fouling organisms that have successfully invaded submerged structures in the Indian Ocean, and (2) to highlight strategies for fouling control.

The book has 16 chapters. The first presents an overview of research efforts on the fouling organisms of the Indian Ocean. It also includes a summary of research on marine wood borers as India has made considerable advances in the last three decades in this area. The next five chapters are written by international experts on recent advances involving the biological and technical aspects of marine aufwachs, chemical cues in larval settlement, succession of fouling communities, and natural antifouling compounds. This is followed by a chapter on control methods. The remainder, and largest part of the book, covers the basic biology and distribution of fouling organisms normally recorded in Indian waters and their control (wood borers are excluded as they would require a book of their own). Depending upon the interests of the contributors as well as the extent of research done, some of the topics are dealt with in greater detail while others are primarily descriptions of the basic biology of the fouling communities.

Although this book is intended for use by scientists engaged in research on marine fouling organisms of the Indian Ocean, it is anticipated that it will have a wider, less ephemeral appeal. Anyone engaged in any manner with the use of underwater marine structures should find much to interest them, while undergraduate and graduate students in Indian universities will discover many principles presented in a form that should help them in their understanding of biology. Indian readers will also find relevant information concerning marine animals familiar to them. We hope that this book, in particular, will stimulate interest in further research on the biology and control of fouling organisms.

It is with pleasure and gratitude that we express our sincere appreciation to all those who contributed. We appreciate their hard work, dedication, and willingness to share their expertise. Special acknowledgement must go to Dr. Bernard J. Zahuranec, U.S. Office of Naval Research, who has been instrumental in reactivating biofouling research in India as well as seeing it through by generous funding for research and, through the American Institute of Biological Sciences, for international meetings, proceedings, and consultant travel.

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An Overview of Indian Research Efforts on Marine Wood-boring and Fouling Organisms

R. Nagabhushanam and R. Sarojini

Introduction

The problem of controlling biofouling and marine-borer infestation is extremely complex not only because of the multitude of organisms and processes involved but also because of the many chemical and physical environmental conditions. Even the materials used in tests and the infested structures are often variable (Turner 1988). Marine biodeterioration today affects the entire economic balance of the Indian fishing industry, which depends upon the efficient service of its fishing fleet. In addition to a large investment for improvement of the industry, a vast sum is spent yearly on the maintenance of ships in the fleet. The losses due to biodeterioration of materials are enormous. While there are no accurate assessments, rough estimates can be made. For example, in 1988 losses due to wood-boring organisms cost the fishing industry $7.4 million. Removal of biofouling organisms from an offshore platform amounted to $4 million as cleaning operations required 20 days at $20,000 per day for underwater operations. Today, India has about 30 offshore platforms for oil and gas and the Oil and Natural Gas Commission is planning to add many more every year. The cost of biofouling removal will be staggering (Qasim 1988). The only figures available are 18 years old. The cost of cleaning Indian merchant naval ships was estimated to be $28.6 million. This was based on data from Lloyd's registery of shipping, which does not include naval vessels or barges used for inland transport (Qasim 1988). Obviously, this is much higher today.

The warm tropical waters of India provide excellent support for the development, growth, and survival of its varied marine life. The organisms responsible for biological deterioration are not only numerous but also diverse.

Although the historical background of marine fouling dates back to the 18th century to the days of Sir Humphry Davy (1824) in India, the foundation for studies on biodeterioration was laid by Erlanson in 1936, when a detailed survey of boring organisms in the harbor of Cochin was made. Systematic and detailed investigations on the biology, physiology, and ecology of borers and foulers were initiated in 1952.

Knowing that a thorough study on every aspect of biodeterioration is essential before further progress on its prevention can be made, a committee was constituted at the Forest Research Institute (FRI), Dehradun. The "Marine Organism's Scheme" was initiated and great strides were made in obtaining knowledge in every area of biofouling, from systematics and physiology to development of antifouling paints. At the same time, realizing the magnitude of fouling in Indian waters, the Crafts Material Section of the Central Institute of Fisheries Technology (CIFT) at Cochin conducted detailed studies on several aspects of marine fouling towards the development and use of effective measures to control the fouling of the rapidly expanding fishing fleet.

Research and active interest in biodeterioration were also generated in other institutions such as the Zoological Survey of India in Calcutta, the National Institute of Oceanography (NIO) and its regional research centers along the western coast of India, the Forest Research Laboratory in Bangalore, the Naval Chemical and Metallurgical Laboratory in Bombay, and the universities of Visakhapatnam, Madras, Trivandrum, Cochin, and Bombay. These institutions took up the task of combating biofouling.

Much of this work has been published in various research journals in India and abroad over the last four decades. The first comprehensive report by the FRI Dehradun Wood Preservation Branch, covering a span of 17 years from 1953 to 1970, was compiled by Purushotham and Rao (1971), and was followed by subsequent reports by the same authors (Tiwari et al. 1984). A book, *Marine Borers, An Annotated Bibliography,* prepared by Clapp and Kenk in 1963 is used as a guideline by those studying fouling and biodeterioration. However, it only covers the literature published through 1954. *Marine Wood Borers of India—An Annotated Bibliography* compiled by Santhakumaran (1985) is the major reference in the field in India. It amasses all the work done on every aspect of the borer problem. The report prepared by Becker (1958) for the Indian Government on the protection of fishing craft against borer attack also offers useful suggestions and guidelines.

Marine Wood Borers and Wood Foulers

Crustaceans and Molluscs

For a better understanding of protective measures against foulers and borers, knowledge of their ecology, distribution, seasonal variation, physiology, and systematics is necessary. From the eastern coast of India, reports on the incidence, distribution, and ecology of wood-boring organisms from the Sunderbans were compiled by Roonwal (1966) and from Visakhapatnam harbor by Ganapati and Nagabhushanam (1955). Three species of isopod wood borers, *Sphaeroma terebrans, S. vastator,* and *Metaponorthus pruinosus* were recorded from the wooden jetties and piles in Visakhapatnam harbor. From the port of Madras, Daniel (1958a, b) provided details on the distribution, ecology, and systematics of two classes of wood-boring molluscs and crustaceans. Nair and Dharmraj (1980) studied the incidence and activity of eleven species of shipworms and two of piddocks along the coast of Mannar and Palk Bay. Palekar and Bal (1955) described the wood-boring organisms in Bombay waters.

From the western coast of India, Nair (1965b, 1966) extensively studied the seasonal settlement and vertical distribution of the wood borers of Cochin harbor. *Teredo furcifera* and *Nausitoria hedleyi* were examined in detail in relation to their settlement during different seasons. He found that *T. furcifera* settles less primarily during the premonsoon period (February to June) and *N. hedleyi* confines its settlement to the low saline periods of the monsoon and postmonsoon (August to February). The occurrence and distribution of borers from Mangalore to Kandla were surveyed by Santhakumaran (1982). In addition, he (1983a) studied the wood borers of the Goa coast as did Karande at Bombay harbor (1968a). Santhakumaran's survey reports three species of *Teredo,* one of *Lyrodus,* and two of *Bankia* among the teredinids; one species each of *Martesia* and *Pholas* from the pholads; and *Sphaeroma* (pill bugs) species as the chief wood borers.

The most detailed landmark publication on wood borers is that of Nair (1984). The entire coast of India was studied by him with respect to their distribution and their variations in relation to hydrographical conditions. He reported that the borers of India belong mainly to the Mollusca and Crustacea. The molluscs are represented by 5 genera of pholads, namely, *Pholas, Martesia, Xylophaga, Barnea,* and *Lignopholas,* and by 12 genera of shipworms of the family Teredinidae. The crustacean wood borers are mainly confined to the order Isopoda and are represented by two well known genera, *Sphaeroma* and *Limnoria* (gribbles). Thirty-four species of shipworms, seven of piddocks, five species and one variety of pill bugs, and no less than nine species of gribbles have been reported from Indian waters, in addition to bacteria and fungi. Thus, according to Nair, attacks on timber are a joint effort by at least 55 species of crustaceans and molluscs.

The wood-boring molluscs of the Andaman and Nicobar Islands were studied by Das and Dev Roy (1980, 1981). From Lakshadweep Island 19 species of bivalves, 16 belonging to the family Teredinidae and 3 to Pholadidae, were reported by Nair and Dharmraj (1983). Biofouling associated fauna of shipworms, crustacean wood borers, and various other aspects of biodeterioration were also discussed by them. The most dominant and highly destructive species were *Teredo fulleri, T. clappi,* and *Lyrodus massa.* Species such as *Teredora palanensis, Teredo aegypas,* and *T. somersi* were recorded for the first time from the Arabian Sea territorial waters of India.

Biology

The biology of individual organisms forming the entire heterogenous assemblage of wood borers was also investigated by various biologists. The general anatomy, biology, distribution, and ecology of *Martesia* have largely been the efforts of Srinivasan (1959, 1960, 1962 a,b; 1963 a,b; 1965; 1966). The biology and anatomy of *Martesia striata* from Visakhapatnam harbor were extensively studied by Nagabhushanam in a series of papers (1955; 1956a,b; 1961d).

Much work on the distribution and various aspects of the life cycle, physiology, and biology of *Bankia indica* from the Madras harbor was done by Nair. He studied the occurrence and described a new species of *Neobankia bipinnata* (1955a), the digestive enzymes of *Bankia* (1955b), the nature and properties of crystalline-style enzymes (1955c), sex changes (1956b), and the developmental biology of *Bankia* from fertilization to metamorphosis into the adult form (1956c). The wood-boring pelecypod *Teredo* was also investigated in some detail. A preliminary study of its sex changes (Ganapati and Nagabhushanam 1954) and its biology (Ganapati and Nagabhushanam 1955) were examined.

Among the crustaceans, the isopods, *Limnoria* and *Sphaeroma,* belong to the wood-boring community. Innumerable protective measures and remedies have failed to achieve complete control over these pests. Systematic and distribution studies on *Limnoria* in India were pioneered by Ganapati, Pillai, Santhakumaran, and Srinivasan. Five species of *Limnoria* from the Andamans were described by Ganapati and Rao (1960). The role of *Limnoria* in the destruction of submerged timber was studied by Pillai (1965), and the differential responses of this organism to chemically treated timbers to assess timber resistance were investigated by Srinivasan and Leela Vallabhan (1984). *Sphaeroma* was examined in great detail by a number of others workers. Its biology, ecology, and physiology were assessed by John (1968, 1971). In a survey of isopods from Bombay, Joshi (1957) described three new species. Physiological studies related to osmotic behavior and the effect of exposure duration to air were done by George (1965, 1967). Molting and associated changes in calcium content of the cuticle of some *Sphaeroma* species and the structural and chemical pecularities of the cuticle were worked on by Leela Vallabhan (1979, 1981, 1982).

Marine Fungi

Gupta and Ravindran (1988) described the fungi from fishing craft in Cochin waters. The traditional craft that land 60 to 70% of the marine fishes in India undergo rapid biodeterioration, which results in a serious economic problem. Fungal decay is, by far, the most important cause of deterioration of these boats, which are built exclusively from a variety of timber. An examination of wood samples of mango (*Mangifera indica*) and aini (*Artocarpus hirsuta*) from aged fishing craft still in operation showed the presence of some cellulolytic and lignicolous fungal species: *Botryodiptodia theobromae* Pat., *Fusarium equiseti* (Corda) Sacc, *Aspergillus niger* Van Tiegham, *Trichoderma koningii* Oudem, *Curvularia lunata* Wakker, *Penicillium citrinum* Thom., and *Pestatoliopsis mangiferae* (Henn) Steyart. A study was conducted to assess quantitatively the effectiveness of different oil-based wood preservatives, traditionally applied on craft, by determining the ultimate compressive stress of preservative-treated wood samples exposed to fungal attack. The results showed that traditional preservatives afforded only marginal protection to the boats. The occurrence of fungi in timbers treated with various preservatives was reported by Raghukumar et al. (1988).

Seven wood species (13 samples)—untreated and treated with preservatives (copper-chrome-arsenate, copper-chrome-borate, creosote fuel oil)—were examined for fungal colonization following submergence in the Mandovi estuary for periods up to 36 months. All samples except one had fungi. *Periconia prolifica* was the most common, while *Halosphaeria quadricornuta* was generally observed on untreated panels. Preliminary experiments with the fungi *Cirrenalia* sp., *Clavariopsis bulbosa*, and *Arthrobotrys* sp., on their tolerances to copper-chrome-arsenate indicated that these species could best tolerate the preservative at 20 ppt salinity, which is also the optimum salinity for their growth. Growth was observed up to 0.50% copper-chrome arsenate concentration in these fungi.

Control of Borers

Wooden structures have been known to last for 20 centuries in Indian waters. How this was accomplished in ancient times is unknown. A survey of indigenous methods of preservation revealed that fish oil, crude oil, cashew-nut oil, cashew-nut shell oil, coconut oil, and calophylum oil have been in use along with some "special compositions." However, the nature and proportions of the special preparations were never disclosed (John and Cheriyan 1964).

Indigenous resins obtained from *Canarium stricium, C. euphylum, Veterina indica, Hopea odorata,* and *Shorea robusta* were found to be not only effective but also economical in the prevention of borer attack. Sand, cement, bitumen, black tar, coconut-fiber coir rope, coir mat, copper-chromate-arsenate, creosote, and fuel oil are some of the substances applied on timbers for protection. The fishermen of Bengal have an unusual protective measure: they suspend a boat infested by shipworms across two poles and light a fire beneath it to destroy the worms. Dessication is fatal to the soft parts of the organisms and charring of the boat offers protection from borers for some time. This practice has been accepted for centuries.

The use of treated wood, steel, fiberglass, ferrocement, and aluminum in the construction of modern fishing boats is now gaining considerable importance. Wood needs careful seasoning and preservation, and no indigenous protective measures have been effective in providing marine wooden structures complete freedom from borers. A number of alternative and more modern preventive measures have evolved in the course of recent years. The efficiency of a number of treated timbers and the duration for which they are effective in the control of borers have been studied periodically. Creosote and fuel-oil treated timbers from 15 species showed good resistance to borers for 8 years in the Cochin harbor (Cherian and Cherian 1980).

In a study conducted by Ganapati and Nagabhushanam (1964) over a period of 10 to 12 months, 12 chemicals were tested for timber treatment in the Visakhapatnam harbor. It was found that ASCU, creosote, creosote-coal-tar, and copper abietate impart the most immunity. A pure creosote application inhibited the population intensity and burrowing activity of *Sphaeroma.* Creosote was also found to resist the settling of *Sphaeroma,* but once settled, the preservative had little effect on its metabolic activities according to a report by John (1965).

Investigations conducted by the wood preservation branches of FRI at Dehradun, Visakhapatnam, Madras, Cochin, and Bombay revealed that chemically treated timbers have at least three times the life of untreated ones. Copper-chromate-arsenate creosant, and creosote-coal-tar mixtures were reported as highly effective borer controllers. With the help of wood preservatives, easily available nondurable timbers after adequate processing can be substituted for the more expensive ones. Krishnan et al. (1983) found that timber with very poor natural durability when treated with copper-chromate-arsenate and creosote had twice the life span as untreated timber. Copper-chromate-arsenate treated timbers were very effective against *Martesia* while creosoted panels were better against *Teredo. Limnoria* attacked only panels treated with low concentrations of copper-chromate-arsenate.

Ravindran and his colleagues have been continuously engaged in developing antiborer measures. In their relentless efforts they reported two very effective wood preservatives, copper creosote and Creoscor, which are produced by fortifying copper with creosote. Their use on fishing craft results in a saving of 70% compared to traditional treatment according to a report by the CIFT-Cochin (Ravindran et al. 1984). Coatings based on melamine-treated cashew-nut oil, polymerized rubber with carbon additives, and polyster gel coatings were also developed for this purpose. In addition to tributyltin-oxide, silicon carbide in a finely divided state was introduced into a matrix to create a condition hostile to marine borers. The affinity of certain components in creosote for inorganic salts has also been explored in an effort to find biologically active stable compounds that could check the settlement of marine organisms.

For hundreds of years, attempts have been made to invent methods for preventing wood from marine-borer attack. It was found that some woods are more resistant than others. The degree of resistance varies with different localities, probably due to different species of borers, quality of timber, and the physical conditions of the environment. Timbers of tropical regions have greater durability in seawater, probably due to the presence of various natural substances such as oils, resins, gums, tannins, and alkaloids, which may serve as deterring agents to the settlement of foulers.

Natural Resistance and Durability of Indian Timbers

A systematic survey of the natural durability of various species of wood in India was conducted by Troup as early as 1909. He found that among Indian woods, *Fragrea fragrans* and *Acacia catechu* were absolutely free from borer attack. Pearson and Brown (1932) listed some commercial timbers of India suitable for harbor work. Among them are *Artocarpus gomeziana, Lagerstroemia flos-reginae, Melanorrhaea usitata, Shorea robusta, Tectona grandis,* and *Terminalia tomentosa.*

A detailed study of the durability of various wood species in Visakhapatnam waters was done by Nagabhushanam (1960). Eighty species belonging to 33 families were tested for resistance to borer attack. Of these, none was immune. However, *Terminalia paniculata* was barely attacked by shipworms even though it was infested with *Martesia.* The timber *Dysoxylum binectiferum* (Family Meliaceae) was resistant to *Martesia* but was moderately attacked by teridenids.

In 1956, Nair studied the natural resistance to borers offered by 16 species of indigenous timbers in Madras and Kayamkulam waters. Only light attacks were noticed on *Cocas nucifera* and *Borassus* sp. in their green state during a 12-month period, whereas all other species suffered heavy damage in their dry state (Nair 1956a).

Among the characteristics essential in a timber for the manufacture of fishing craft, lightness and resistance to decay and foulers are of prime importance. *Tectona grandis* (teak), *Artocarpus hirsutus,* and *Lagerstroemia microcarpa* were recommended. Balan (1980), in discussing the service life of *kattumaran* logs recommended *Melia dubia* and *Albizia molluscana,* two log species from Sri Lanka and Kerala forests, as preferable for *kattumaran* building.

A study of the natural resistance of 85 timber species exposed for 9 months in different test sites in Bombay waters showed that none of the species escaped borer attack. Twenty suffered average destruction, below 25%; 12 between 26 and 50%; and the remaining 53 species over 50% destruction (Santhakumaran and Alikunhi 1983).

The built-in canoes of the Kerala coast called *thanguvallam* are made of light-weight timber. A recent estimate notes nearly 106,000 of these indigenous craft are in use. They have to be repaired or replaced every two to seven years due to borer destruction. These canoes contribute nearly 62% of the fish landings and are of considerable economic importance. Fungus infection has been recognized as the fundamental cause of their biodeterioration, next to weathering. Indigenous methods, such as the application of cashew-nut oil and natural resins, have proved inadequate protection. In 1936, Erlanson suggested the possibility of protecting marine timber by dry docking sea vessels every two to three months and scrubbing them with a "poisonous wash" concocted of copper sulfate, mercuric chloride, hot brine, and eye solutions. But even Erlanson noted the ineffectiveness of these methods and recommended the use of sheathing wooden structures with copper or concrete.

Biofouling Organisms

Marine biofouling, as with marine boring, is of great economic importance to all maritime nations. Settlement of marine fouling organisms is common on all structures exposed to seawater made of wood, steel, aluminum, fiberglass reinforced plastic (FRP or GRP), and even ferrocement. As a result of fouling organism accumulation on hulls constantly exposed to seawater, problems of frictional resistance, loss of speed, and increased fuel consumption arise. Loss of efficiency of underwater propellers and frequent malfunctioning of underwater electronic installations may also occur. Fishing vessels have to be dry-docked periodically, an added economic loss, in addition to the destruction of the surfaces of the vessels.

Fouling is a biological process aided by various hydrographical and geographical factors. The marine fouling complex along the 5,000 km Indian coastline appears to be a typical representation of tropical fauna and flora.

The microscopic fouling forms found in Indian waters are bacteria, diatoms, fungi, protozoans, and rotifers. The macroscopic are sponges, coelenterates, flatworms, bryozoans, tube worms, amphipods, barnacles, and molluscs, in addition to some planarians, nemertines, polychaetes, isopods, decapods, gastropods, and pisces. Barnacles, tube worms, bryozoans, and mussels are by far the most important in regards to surface coverage, volume, and weight.

The first publication giving some information on organisms that foul hulls of boats in Indian waters was that of Erlanson (1936). Subsequently, several workers collected data on this aspect from the important commercial harbors of India.

The establishment of a fouling community can be divided into different phases. Initially, a primary film develops comprised of bacteria, fungal spores, diatoms, and colloidal organic matter. In the second phase, there is the establishment of macrofoulers, which in Indian waters usually consist of hydroids, barnacles, tubicolous polychaetes, bryozoans, mussels, oysters, and compound ascidians. As a submerged substratum ages, the fouling complex passes from the establishment to the extinction of different communities, whose compositions are influenced by the abundance of local species and physicochemical conditions of the environment. Studies carried out at different important commercial harbors in India have revealed that only a few groups remain in the fouling community for a long period. Various species of barnacles are the most important members. Documented evidence from test panels maintained at various levels supports this.

Ganapati et al. (1958) provided a detailed account of the distribution and growth rates of the fouling community at Visakhapatnam harbor, on the eastern coast of India. They reported species of *Nitzchia*, *Pleurosigma*, and *Rhizosolania* among the diatoms, the colonial ciliate *Zoothamnium* in large numbers, sporadic folliculinids among protozoa, and unidentified encrusting sponges from porifera. The colonial hydroid *Laomedia bistriata* and serpulids were dominant foulers and a host of other hydroids were representatives from the class Coelenterata. Six species of serpulid worms with their calcareous tubes formed a substantial part of material scraped from the bottoms of boats and buoys. *Nereis glandulata*, *Lycastis indica*, and *Morphysa sanguinea* were the polychaetes collected from mud and organic detritus from jetties and test panels.

Among the crustaceans, barnacles constituted the most important fouling group. Four species were reported throughout the year. Amphipods and isopods were also found. Only three species of bryozoans were observed from the jetty piles and test panels: the common encrusting forms of *Membranipora* sp., *Bowerbankia caudata*, and *Bowerbankia* sp. These organisms were present sporadically, probably because they are short lived. Molluscs were represented by lamellibranchs and gastropods. Simple and compound tunicates also formed part of the fouling complex. The occurrence of scyphistoma larvae was studied by Ganapati and Rao (1958).

The importance of entoprocts as fouling organisms in Visakhapatnam harbor was discussed by Rao et al. (1988). During the course of an investigation on marine biofouling at the harbor, it was noticed that entoprocts were an important component, especially in the early stages of development of test-block communities. As many as five species belonging to the families Pedicellinidae and Urnatellidae—*Pedicellina cernua* (Pallas), *Barentsia gracilis* (M.Sars), *B. discreta* (Busk), *B. ramosa* (Robertson), *Loxosomatoides laevis* Annandale—were found. Of these, *B. ramosa* is a new record for the Indian Ocean region and *B. gracilis* is reported for the first time from Indian waters. *Pedicellina cernua* is a new record for the Bay of Bengal. All these species are new locality records for Visakhapatnam. Brief descriptions of the species encountered using modern terminology, measurement of taxonomically important meristic characters, and notes on their distribution were provided and thre species illustrated. Data on seasonal occurrence, abundance, and growth rates for important species were given and their role in fouling discussed (Rao et al. (1988). The study indicates that these organisms are probably more common in fouling communities than was generally thought in the past—a view that is increasingly gaining support in recent years.

Rao and Balaji (1994a) described the succession of fouling communities at Visakhapatnam over a two-year period. The study was conducted at two stations, Station I and Station II, having widely differing ecological conditions. While rapid colonization was a feature common to both stations, there were differences in the emergence of dominant species and sequence of events of community development. In the polluted waters of Station I, the introduced bivalve *Mytilopsis sallei* gained virtual monopoly within 30 days, almost eliminating all other species. Dominance was shared by different species—spirorbids, bryozoans, barnacles, sponges, oysters—at different stages in the relatively cleaner waters of Station II. Factors involved in community development such as new recruits, biological interactions, and physical disturbances, were considered. Because the dominance gained by some species in a community does not appear to involve an orderly or directional process that is predictable or involves modifications of the physical environment, it is argued that they should best be regarded as "multiple stable points" rather than "climax communities." This appears to be applicable in many Indian, subtropical, and other tropical harbors (Rao and Balaji 1994a).

Results of fouling investigations conducted for the first time at the fast developing intermediate port of Kakinada in the Godavari estuary, Andhra Pradesh during 1983-1984 were presented by Rao and Balaji (1988). The fouling species collected from different structures and craft were identified and listed. Several of the species were reported for the first time from the area and some are new records for the Bay of Bengal. The main species were the serpulid *Mercierella enigmatica*; the barnacle, *Balanus amphitrite*; and the bryozoans, *Electra bengalensis*, *Membranipora amoyensis*, *Alderina arabiansis*, and *Victorella pavida*. Panel tests (timber and glass; short and long term) were conducted at two selected stations (Station I: Kakinada canal, port area; Station II: new fishing harbor) with widely differing hydrographic conditions. The data obtained for one year were presented. Variations in the nature and composition of the fouling communities were found between the two stations. Station I supported a low number of highly tolerant (estuarine) species, whereas a high number of species and a more complex community structure were found at the more stable Station II. Data on seasonal settling patterns, fouling biomass fluctuations, and growth rates of important species were given and relevant comparisons made with other Indian harbors.

Another survey on fouling from the eastern coast of India comes from the port of Madras by Daniel (1954). Tube-dwelling amphipods, *Stenothoe gallinsis*, *Elasmopub pectinicrus*, and *Corophium madrasensis* and the caprellial *Protogeton* were abundant. The polyzoan, *Brisia* sp., and the ascidian, *Diandrocarpa brackenheilmi*, formed the fouling complex. The biology of fouling at the Gulf of Manner and Palk Bay was studied by Kurian (1953).

Antony Raja (1959) dealt with the distribution and succession of sedentary organisms of Madras harbor with a discussion on the influence of environmental factors. Subsequently, he (1963) described in detail the rate of growth, sexual maturity and breeding of four sedentary organisms — *Modiolus striatulus, Bowerbankia* sp., *Cynthia* sp., and *Dasychone cingulata* — from the harbor. All the forms studied attained their maximum size within six months. While *M. striatulus, Bowerbankia* sp., and *D. cingulata* breed throughout the year with peak period(s) of intensity during specific time(s) of the year, *Cynthia* sp. breeding does not last the whole year.

Nair (1976) described the settlement and growth of major fouling organisms in the Cochin harbor. Those recorded were hydroids, the tube worm *Hydroides norvegica, Balanus amphitrite, Ostrea* sp., *Modiolus* sp., and encrusting bryozoans. Data analyses of test panels showed that the settlement and growth of the various fouling groups are very reduced during the monsoon (June to September), when salinity drops considerably. Salinity plays a decisive role in the breeding and subsequent settlement of the larvae of marine foulers at Cochin.

Balasubramanyam et al. (1973) reported that tropical marine fauna and flora are unique in many respects, in particular, their heavy and dense growth of protective shells. They also noted that although fishing trawlers in India maintain an average speed of 7 to 11 knots, they tend to get heavily fouled while in port. The intensity of fouling is confined to selected zones on the hull below the water line, such as at the turn of the bilge, below the keel, rudder surfaces, and the water-line belt. Bronze propellers and copper-metallic surfaces are also heavily fouled under their galvanic inactivation.

Menon et al. (1977) made a comprehensive study of the fouling organisms encountered at the port of Mangalore. Barnacles, oysters, bryozoans, polychaetes, and hydroids were the dominant groups of foulers there. Barnacles were, by far, the most important. Distinct seasonal abundance in settlement was noticed in the different groups. Major settlements of the barnacles occurred in November and December, and polychaetes in April and December. The pattern of oyster settlement indicated that the spat of *Crassostrea madrasensis and C. cucullata* settled during January, March, May, and October in this region. The differences in the quality and quantity of the fouling communities were controlled by their breeding periodicity, seasonal hydrographic fluctuations, and species composition of the sedentary community of the region. Nageshwar Rao et al. (1982) described the foulers of Karwar coast.

Anil and Wagh (1988) reported the results of biofouling on aluminum panels placed at different depths in the Marmagoa harbor from February 1983 to May 1984. Panels were exposed for different durations to determine the effects of various exposure periods on biofouling during different seasons: premonsoon (February–May), monsoon (June-September), and postmonsoon (October-January). Environmental data (salinity, dissolved oxygen, pH, water temperature, particulate organic carbon, total suspended matter, chlorophyll *a*, phaeopigments, nitrates, nitrites, phosphates) were collected at fortnightly intervals. Biomass variations on aluminum panels and their correlation with the environmental parameters were discussed. During the period of observation, the presence of the scleractinian coral *Astrangia cavatus* was recorded on the panels.

Marine biofouling at the Ratnagiri coast was reported for the first time by Alam et al. (1988). A seasonal study of fouling organisms was conducted at three sampling stations. The fouling organisms found were diatoms, fungi, protozoans, coelenterates, polychaetes, some bryozoans, and cirripede species. The important molluscan fouling community were the bivalves. Heavy settlements of hydrozoans and barnacles were noted. Seasonal occurrence, growth, and settlement of all classes of the biofoulers were studied in relation to changes in the physicochemical environmental parameters.

Among the diverse assemblages of organisms that form the fouling complex in the marine environment of Bombay, barnacles constitute an important group. They commonly occur on the underwater structures of ships. Wagh and Bal (1969) described 11 species of intertidal barnacles and teridinid worms over a span of 4 years. The major fouling genera belong to the classes Hydrozoa, Cirripedia, Polychaeta, Bryozoa, and Tunicata. The barnacles were chiefly Indo-Pacific forms (Karande 1968a), some with wide distributions and abundances. Of the bryozoans, a large number of both erect and encrusting forms were reported. They also form a major fouling group of Bombay waters.

Marine fouling and its composition in the suboceanic islands of the Andamans were investigated by Karande (1978) as part of a biofouling sampling program of different sites at Port Blair. As a result of uniform hydrographic conditions, an atmosphere devoid of industrial effluents, and natural beds of sedentary organisms, fouling was found to be very heavy. The most common were polyzoans of the genus *Bugula*. Barnacle growth, though very rich, is subject to competition from other sedentary organisms such as bryozoans, hydroids, ascidians, and bivalves. Of the nine species of balanomorphs, *Balanus variegatus* and *B. amphitrite* were dominant and settled throughout the year. Both calcareous and mud-dwelling serpulids like *Hydroides norvegica*, *Spirorbis* sp., and *Pomatoceras* sp. were also encountered year round. *Hydroides* species were found to be highly tolerant to chlorine, which is used as a biocide. The presence of these organisms in abundance causes blockage of water-front installations. Several species of fast growing bivalves, sometimes outnumbering all other sedentary forms, cause severe infestation in underwater installations. *Pteria, Spondylus, Ostrea,* and *Mytilus edulis* are of concern in Port Blair waters. In addition to being surface foulers, they can also create choking problems.

Important contributions on the systematics of barnacles and new records of intertidal barnacles were made by Wagh and Bal (1969, 1974)

In summary, a total of 54 species of fouling organisms have been recorded from the Visakhapatnam harbor, 60 from Madras harbor, and 50 from the waters of Bombay.

Biology

Effective measures for the prevention of fouling can be put to use only after a thorough study of the different physiological aspects, complete life cycles, and larval development stages of these sedentary organisms.

The culturing and rearing of dimorphic larvae of the ascidian *Aplidium multiplicatum* were investigated by Karande (1981) to assess chemical antifoulants and for harbor pollution studies involving the monitoring of seawater quality. In order to rear *B. amphitrite communis* to obtain their cyprids for the screening of antifouling chemical compounds, a new technique was developed by Karande (1968b). Studies of the various stages of barnacle larval development of *Teraclitella karandei* reared in the laboratory were also conducted by him (1974).

Detailed investigations on barnacle respiratory metabolism related to body size, temperature, salinity, and other factors were conducted by Ganapati and Prasad Rao from Visakhapatnam (Ganapati and D.G.V.P. Rao 1960, 1962; Rao and Ganapati, 1972). Comparisons were made of the respiratory metabolism of three tropical barnacles—*Balanus amphitrite amphitrite, B. tintinnabulum tintinnabulum, Chthamalus witherisi*—in relation to temperature (Rao et al. 1988). In general, respiration and the rate of respiratory movements increased with increasing temperature up to a specific limit (30°C in *B. amphitrite amphitrite* and *B. tintinnabulum tintinnabulum* and 40°C in *C. withersi*), beyond which they declined. These differences in the three species in their critical thermal limits might by due to their different level shore habitats. Comparison of metabolism/habitat temperature curves of these tropical forms to those of Arctic and temperate ones showed a shift towards higher temperatures in the tropical forms.

Meenakumari and Nair (1988) reported the growth of the barnacle *B. amphitrite communis,* an important fouling organism in Cochin backwaters, based upon its incidence on short- and long-term panels immersed in Cochin waters. *Balanus amphitrite communis* exhibited fluctuating growth rates during various months. A maximum growth rate of 0.47 mm per day in rostro-carinal diamaeter was recorded in December followed by 0.45 mm per day in May; maximum growth of 22 mm in the rostro-carinal diameter was significantly linear, showing that the von Bertalanffy growth curve would be an appropriate fit for growth in barnacles. Growth predicted on the basis of the von Bertalanffy growth curve agreed with the observed growth in these studies.

The endocrinology of the Indian barnacle *B. amphitrite* was reported by Sarojini et al. (1988). Two types of neurosecretory cells were observed in the central nervous system: large and small. High concentrations of PAF-staining granules were found in the large neurosecretory cells in March and April. During these months the ovaries were quiescent and no breeding took place. However, in May, June, and July when breeding activity was at its peak, PAF-staining granules were at their lowest. Molting was observed for one year. The rate fell sharply in November-December and the animals underwent a period of anecdysis for six to eight weeks. They resumed molting at a lower rate, reaching a maximum in March-April. During this period the PAF-staining granules in the small neurosecretory cells were at their minimum.

An histological study of the ovary and testis of the goose barnacle *Lepas* sp., a marine hermaphroditic cirripede crustacean, was conducted by Machale et al. (1994 a). They also described endocrine control of oogenesis (1994b) and the neurosecretory cells (1994c).

The free-swimming larvae of marine organisms such as barnacles, tube worms, and bivalves become a fouling menace only when they settle and secrete a calcareous shell. The cement glands, histology, and histochemistry in *Balanus kondakovi* were studied in detail by Karande and Gaonkar (1977). Inhibition of calcium secretion in shell dwelling organisms can be effective in preventing their settlement and growth. Karande and Menon (1972) exposed pediveligers to graded concentrations of natural amd synthetic chemical compounds and studied the mechanism of shell formation and calcium cycling.

Wagh and Sawant (1982) observed biofouling on metallic surfaces around Goa waters. The effects of copper sulfate and mercuric chloride, illumination, and current velocity on the settlement of marine foulers and borers in the Madras harbor were observed by Daniel (1956, 1957, 1958a) and Antony Raja (1959, 1963).

Cadium effects on the tissues of the bivalve *Mytilopsis sallei* were described by Vinayakumari et al. (1994). They were exposed to lethal and sublethal concentrations for different periods of time for histological study. Changes in the histopathology of the gills, hepatopancreas, gonads, and kidneys were clearly seen. The behavior of seven representative marine organisms towards tributyltin oxide (TBTO) was studied under controlled laboratory conditions by Karande and Ganti (1994). Sensitivity varied from species to species. The highest tolerance was shown by the fouling species *M. sallei* (LC_{50}/28 days = 13.0 μg/TBTO) followed by Indian rock oyster *Saccostrea cucullata.* The most sensitive species seemed to be the green mussel *Perna viridis* (LC_{50}/28 days = 0.28 μg/1). The environment quality target for TBTO in India is proposed to be 0.03 μg/1 (an advisory recommendation). Rao and Balaji (1994b) reported the results of experiments conducted to study the toxicity of copper to *M. sallei* at Visakhapatnam. The LC_{50} values obtained indicated that the species is highly resistant to copper compared to several other bivalves. None of the antifouling paints or wood preservatives presently used in India offers adequate protection against this species. Chlorinated rubber-based paints containing TBTO fare relatively better. The adaptive strategies contributing to the success of *M. sallei* in Indian harbors were outlined in their report.

The biology of serpulid worms in relation to biofouling was discussed by Chandramohan and Aruna (1994). These worms form an important component of marine fouling substrata. The family Serpulidae is represented by 50 genera and 350 species. Eight species were recorded from fouling substrata found on buoys, harbor jetties, and hulls of ships and fishing trawlers in Visakhapatnam waters. Of these, *Hydroides elegans* and *Mercierella enigmatica* are known to have wide distributions and extreme limits of tolerance in varying salinities. These worms form characteristic communities with other organisms such as barnacles, bryozoans, ascidians, and isopods. Factors that determine their settlement rate, survival duration, and ecological distribution are of interest as are the predators, encrusting gelatinous material (e.g., filamentous algae and sponges), and sediment settlement that control their abundance. Studies pertaining to the introduction of many new species from different areas and the biogeographical distributions of many of the cosmopolitan species are also of great importance in relation to their role in association with other biofouling organisms. The chemical nature of substrata and the effects of other animal associations in regulating their settlement are studied to determine the necessary control measures that can be adopted to prevent their settlement.

Role of Microbial Film in Biofouling

When a surface is immersed in seawater, adhesion of many microorganisms is observed within a short time. This initial covering of the exposed surface is called the slime film, biofilm, or primary film. Once this attachment process is initiated, a succession of settling organisms is observed leading to the development of a microbial population. The predominant organisms are bacteria, algae, unicellular fungi, and protozoa in a matrix of detritus, which provides a continuous source of nourishment. At the Visakhapatnam harbor, Nagabhushanam (1959) studied the settling process of two borers, *Martesia striata* and *Teredo furcillatus*, and the role of primary film in their settlement and behavior. He concluded that some microorganisms (e.g., bacteria, fungi, algal spores) have to condition the wood by decomposing it superficially to "welcome" the fouling and boring organisms. The study also concluded that metamorphosis of *T. furcillatus* takes place on primary filmed surfaces.

At the Madras harbor, Daniel (1955) observed that the primary film was chiefly composed of diatoms and algal spores with a small proportion of bacteria. He also saw that fouling commenced after 48 hours, i.e., only after the surface film was formed. According to him, larvae of foulers avoided nonfilmed surfaces by behavioral and structural necessity, and perished rather than settle on these surfaces.

The composition of the primary film, the succession of its various constituents, and its probable role in the subsequent settlement of the fouling organisms in the Cochin harbor were studied by Nair and Pillai (1977). They found that bacteria were the first settlers, followed by diatoms after 18 hours. The slime-filmed surfaces, according to their studies, provided a favorable base for the settlement of barnacle cyprinids and *Bugula* larvae, although it was not essential for their attachment.

Karande (1968a) examined test panels from the Bombay harbor that showed only a few bacteria and cell detritus on them after the first 24 hours of settlement. The diatoms, which settled 48 hours later, were *Melosira, Navicula, Achananthes, Bascillaria, Amphora, Nitzchia, Surirella, Rhopalodia,* and *Mastogloia.* Among the protozoa, *Epostylis* and *Vorticella* were recorded. Some of the fungi isolated from submerged wood included *Plectomycetes, Aspergillus, Cladosporium,* and *Halosphaeria.* The soft-rot fungus *Halosphaeria quadricornuata* was present on the superficial layers of submerged wood. One common factor of the slime films was the presence of *Halosphaeria* on all test sites.

The effects of slime film on barnacle settlement were reported by Meenakumari and Nair (1994). They compared the ratio of settlement of cyprids to young barnacles on panels with slime films and panels that had been sterilized. Settlement was greater on the panels with slime. Settlement rate varied significantly during different months and different exposure periods. Similar patterns were found on the sterile as well as the panels with slime. Venugopalan et al. (1994) described the biological and biochemical aspects of biofilm development. Bacteria and diatoms constitute two major groups of microorganisms that colonize solid surfaces immersed in coastal waters. Their paper reports the results of studies characterizing the biofilm that develops in Kalpakkam coastal waters and elucidating the effects of bacterial films on the settlement of fouling diatoms. The physiochemical, microbiological, and biochemical characteristics of the films that developed on Perspex panels were studied in the initial 120 hours of immersion at 24-hour intervals. Bacterial strains isolated from the biofilms were used in a laboratory experiment to determine their effects on the settlement of three diatoms, *Nitzschia*, *Navicula*, and *Amphora*, on glass slides. One strain was capable of significantly promoting diatom settlement; the other two induced significant suppression of settlement in the initial 24 hours. The results indicate that bacteria, as pioneer colonizers on submerged surfaces, elicit variable responses from subsequent settlers such as diatoms (Venugopalan et al. 1994).

Biochemical analyses of microfouling material settled on aluminum and glass panels were carried out at two Goa stations: one at the Dona Paula jetty and the other at Marmagao harbor, located on either side of the mouth of the Zuari estuary. This study dealt with the composition of microfouling in terms of organic carbon, carbohydrates, proteins, bacterial counts, and chlorophyll *a* concentrations. The study was conducted to assess the effects of oil slicks on primary film build up (Tulaskar et al. 1994).

Bhosle et al. (1994) described the carbohydrate metabolism of a marine fouling diatom *Navicula* sp. It was cultured in the laboratory under a 12-hour light, 12-hour dark condition. Cells in suspension and attached to the flask walls were analyzed for chlorophyll *a*, cell organic carbon, total cell carbohydrate, and carbohydrate fractions. Maximum chlorophyll *a* concentrations were obtained on the fifth and eighth days of cultivation for suspended and attached cells, respectively. For both cell types, total carbohydrate production increased with the cultivation period. The total carbohydrate : cell carbon ratio also increased with cultivation, being marginally higher for the attached cells. During the initial four-hour dark cultivation period, the attached cells had more alkali-soluble carbohydrates. Following this period, the acid-soluble carbohydrate was the major component of the total carbohydrate of the attached cells. In general, more acid-soluble carbohydrate was observed for attached cells, whereas alkali-soluble and residual carbohydrates were more abundant in the suspended cells.

Nair and Ravindran (1994) studied the dynamics of bacterial colonization and barnacle settlement on surfaces treated with selected repellents and attractants such as amino acid, benzoic acid, tannic acid, copper-chrome-arsenic composition, straight and fortified creosotes, tributyltin oxide, and Teflon inert control surfaces. The chemicals were impregnated into porous ceramic plates and their performances under marine conditions evaluated to provide a mechanistic approach to fouling control technology. Bacteria and barnacles showed a distinct preference for rough surfaces over polished ones. The chemical preference was: benzoic acid > amino acid > copper-chrome-arsenic composition > tannic acid > creosote > copper creosote > formalin > tributyltin oxide.

Control of Biofouling Organisms

Paints

The problem of successfully combating the settlement of marine organisms is of considerable magnitude. Marine fouling is a common process occurring on all submerged surfaces in an unprotected state. Fishing vessels built of steel, wood, fiberglass, reinforced plastic, aluminum, and ferrocement are no exception to the settlement of foulers. One method to rid foulers is the periodic scraping of the submerged portions of trawlers and boats. But the disadvantage of this is an increase in frictional resistance of the boat and a consequent decrease in speed.

From the number of preventive measures adopted from time to time, a periodic coating of paint possessing antifouling properties seems to be the only accepted method. Antifouling paints are poisonous in nature and, on gradual dissolution in seawater, inhibit larval settlement and other marine organisms due to their toxicity. Such paints are only effective while a sufficient loading of 'poison' is present in them. In practice, many of the commercial antifouling paints manufactured in India provide useful service only for a period of four to five months, after which they become ineffective.

The rate of leaching is the guiding factor in determining paint efficiency. A cold plastic medium paint with 40 to 45% loading of cuprous oxide prevents fouling for eight to nine months. Compounds such as copper aceto-arsinate and organometallic compounds like tributyltin oxide give longer service.

Biological control

Another approach to the problem of fouling prevention is biological control. Introduction of predatory organisms that feed on larval forms can be successfully employed. But, this method also has its limitations.

Bioactive compounds

Recently, attempts have been made to identify bioactive compounds from marine organisms of the Indian Ocean that may prevent biofouling.

Vitalina Mary et al. (1991) discovered compounds from Indian Ocean octocorals that inhibit barnacle settlement. Methlene-chloride extracts from the gorgonian octocorals *Solenocaulon tortuosum, Suberogorgia suberosa, Echinogorgia complexa, Juncella juncea,* and the alcyonacean octocoral *Spongodes* sp. prevent larval settlement of *B. amphitrite.* Settlement is inhibited at levels ranging from several parts per million to as low as several parts per billion. Inhibitory substances are not toxic to cyprids. Inhibitors isolated from *J. juncea* are most potent.

Evelyn Mary et al. (1994a) also discovered bacteriostatic compounds from several marine animals of the Indian Ocean. Eighteen bacterial isolates from five genera, *Aeromonas, Alcaligens, Flavobacterium, Iseudomonas,* and *Vibrio,* were isolated from biofilm associated with *Perna* sp. These marine bacteria were tested for sensitivity to extracts from sponges, anemonie, and a polychaete worm. The sponges, *Spirastrella inconstans* and *Spongia officinalis,* were found to be bacteriostatic. In the future, natural products will be used as tools to study the interactions of bacteria and the settlement of barnacle larvae.

Sarma et al. (1991) studied the effect of the sponge metabolite, herbacin, on macrofouler settlement. They reported the results of exposure trials conducted with test compounds of *Mangifera indica* treated with herbacin, a recently described furanoses quiterpene isolated from the marine sponge *Dysidea herbacea* at Visakhapatnam. Seven species of fouling organisms common to the test site—the spiorbid, *Neodexiospira pseudocorrugata*; serpulids, *Hydroides norvegica* and *Serpula vermicularis*; bryozoans, *Hippoporina americana* and *Bowerbankia gracilis*; and the hydroid *Loomedia bistriata*—were selected to study their settling and growth responses to the compound. In addition, information on such aspects as fouling build up, general progression of the community, and growth of selected species was provided. The study suggests that the sponge metabolite appears to exert an inhibitory influence on some species *(L. bistriata, H. americana, H. norvegica, S. vermicularis)* while acting as an attractant to others (*B. gracilis, N. pseudocorrugata*). The barnacle *B. amphitrite* seems to be unaffected by the compound.

Mokashe et al. (1994) reported the antimicrobial properties of poriferan species belonging to class Demospongia, extracted with methanol. The methanol extracts were tested for antimicrobial activity against six fouling bacterial strains. Extracts from *Craniell* sp. at a concentration of 50 µg/disc (7 mm diameter) were positive against all strains, suggesting the use of these extracts for further antifouling studies.

The biological potency of methylene extracts of ascidians was investigated by Evelyn Mary et al. (1991). Extracts of *Styela pigmentata* and *Pyura pallida* were toxic to *Artemia salina* at 8 and 4 mg ml^{-1} wet weight of the animal upon 96 hours of exposure, affected the growth of the marine microalgae *Dunaliella tertiolecta* and *Isochrysis galbana* at 10 mg ml^{-1}, and showed a sharp inhibitory effect during the exponential growth period of *L. galbana* at 10 mg ml^{-1}.

Methanol extracts of the fruits of the terrestrial plants *Randia brandistii* and *Sapindus trifoliatus* were screened for their antifouling activities on the marine fouling diatoms *Navicula subiflata* and *N. crucicula* (Sawant and Wagh 1994). Both extracts inhibited the growth of these diatoms on glass surfaces. Lethal concentrations varied with the types of plants and diatoms used. The extracts were found to act both as a stimulant and as an inhibitor depending on their concentrations in the media. Data suggest the possible potential of these extracts as antifouling agents.

Broad spectrum natural products from soft corals were reported recently by Evelyn Mary et al. (1994b). Compounds from the soft coral *Euplexanora nuttingi* inhibited barnacle settlement in the laboratory. These compounds were tested against 18 bacteria from five genera — *Aeromonas, Alcaligens, Flavobacterium, Pseudomonas,* and *Vibrio* — found in the biofilm associated with the macrofouler *Perna* sp. All 18 bacterial isolates inhibited barnacle settlement in the laboratory, and two were bacteriostatic.

Anticorrosion measures

The protection of steel in seawater by paints as an anticorrosive measure has many problems, and innovative methods to solve them are needed. Without protective paints, underwater structures develop blisters, pits, perforations, and gradual thinning of hull plates. The primary method of protection for boat hulls is the use of paint coatings, which are very effective and economical, plus the use of supplementary cathodic protective measures, mostly at stern areas. Ravindran and his colleagues (1969) at CIFT developed an anticorrosive paint formulated with CNSL (cashew-nut shell liquid), a condensated product called SILIX. SILIX coatings on cathodically protected structures withstood alkalinity and did not show any blistering or softening. Pillai (1971) designated a single-pack wash primer for aluminum surfaces, primarily suitable for coating aluminum-magnesium alloy sheathing on the wooden hulls of fishing boats.

In addition to the application of protective anticorrosive paints, mechanized wooden boats are sheathed with copper or an aluminum magnesium alloy. This alloy (Indal MSTS), due to its high potential, occupies an important position in the galvanic series of metals and alloys in seawater. Cathodic protection has to be used to control the corrosion of metals and alloys. In India, investigations employing anodes have been conducted by De and his team (1980) on the cathodic protection of naval ships at the Naval Chemical and Metallurgical Laboratories in Bombay. Kelkar (1968) from the same laboratory, developed an anticorrosive paint based on metallic manganese pigment. Incorporation of manganese into zinc-rich paint showed remarkable improvement and corrosion resistance of paint films.

Since 1960, investigations and experiments conducted at the CIFT-Cochin have resulted in the finding that indigenous aluminum alloyed with magnesium and rolled in the form of sheets can be used to protect the wooden hulls of fishing boats at only one-fifth the cost of copper.

Anaerobic bacteria are probably the most studied organisms in biological corrosion investigations. Excessive corrosion of metal structures as well as unsatisfactory performance of anticorrosive cathodic protection in polluted waters were reported from the Bombay harbor by De et al. (1980). They attributed this to the growth of sulfate-reducing bacteria such as *Desulphovibrio desulphuricans* and *D. vulgaris.* An ecological survey was conducted by Srivastava and Karande (1984) to determine permissible concentrations of hydrogen sulfide as well as sulfate-reducing bacteria in seawater. They also elaborated on a method for estimating sulfate reducers.

De and his colleagues (1980) were pioneer workers in India who contributed to our knowledge of understanding the corrosion behavior of certain structural metals in the Bombay and Cochin harbors. Ravindran and Pillai (1984) are probably the first to have elaborated upon the interrelationship of marine corrosion and fouling in India from the Cochin harbor.

Summary

From this review it can be seen that marine biodeterioration has almost passed through the basic research stage in India. Considerable work has been done on the biology, ecology, and control of marine borers. Similarly, fouling communities from the various coasts of India have been identified and their seasonal occurrence, succession, and biology fully studied. However, there is insufficient information on the physiology, biochemistry, and the role of microbes on fouling and borer communities. Research on these are still in preliminary stages.

Future Direction and Needs

Looking to the future, attention must be focussed first on the importance of innovative basic research in all aspects of marine biodeterioration. Without question, more progress has been made in the last fifteen years than at any time in the history of marine biodeterioration research in India. This has been mainly due to the financial support provided to the Indian marine biologists by the American Institute of Biological Sciences and Office of Naval Research through United States PL-480 grants.

Probably less than ten percent of the boring and fouling organisms are known biologically and, of these, only a few have been studied in detail in all phases of their life history. The biological bases of normal functioning and behavior must be fully understood to interpret the effects of toxicants or to design new means of controlling these pests effectively.

Broadly, five areas of research, equally important for all wood-boring and fouling organisms, should be pursued:

- The first and most important area—initial events in the settlement of organisms, especially a better understanding of the principles of bioadhesion. Basic knowledge is needed on the microfouling process: elucidation of the biophysical properties of the spontaneously adsorbed conditioning film, and how they relate to the properties of the original substrata and to the subsequent attachment and distribution of bacteria and other cellular or particulate matter.
- Larval biology of fouling and boring organisms. Applications to fouling problems have naturally led to placing greater emphasis on larval settlement, behavior, and structure of pelagic phases; larval nutrition; factors controlling the length of pelagic life and the function of larval sense organs; and, especially, the means by which information on pressure and vibration is received. This type of research should continue.
- Biochemical clues that control larval settlement, attachment, and metamorphosis. The development of wood-boring and fouling organisms is regulated by a complex of biochemical factors that act by controlling the expression of genetically programmed behavioral and developmental processes intrinsic to these communities. The design of new effective countermeasures must be based upon strategies for the identification and interdiction of these essential, underlying biochemical mechanisms. An understanding of the basic biochemical requirements, signals, and mechanisms that underlie and control marine wood borers and foulers is thus required for the design of specific and effective inhibitors and countermeasures.
- Bioactive compounds. In the last two decades, a wide range of organotin copolymer toxicants was developed in the United States and Europe and quite recently by the Indian Naval Chemical Laboratory to control marine biodeterioration. With certain formulations, suppression of fouling was obtained for up to seven years; these coatings were used in ship trials (Alberte et al. 1992). However, these organotin compounds have brought about considerable environmental and health problems. Therefore, there is need to develop alternate technology by discovering nontoxic antifouling compounds from marine organisms that can be incorporated in the antifouling paints. India has a rich source of marine communities that can be profitably exploited for this purpose.
- Field trails. There is a need to test, in the field, the use of potentially biodegradable organic compounds and marine natural products as

possible antifoulants for inhibition of microbial, algal, and invertebrate components of the biofouling community. It is important to develop new antifouling coatings to deliver such inhibitors at sustained, constant rates to obtain a long coating life.

- To achieve these objectives, there is a need for much closer cooperation and improved understanding between marine biologists, chemists, engineers, and others involved with the practical problems of controlling biodeterioration in the oceans.

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Living Attached: Aufwuchs, Fouling, Epibiosis

Martin Wahl

Introduction

This synopsis presents an overview based on recently published work (mostly 1985 through 1994) on the biological and technical aspects of marine aufwuchs, e.g., life forms growing attached to solid/fluid interfaces (substrata) without depending trophically on their substrata. Aufwuchs encompasses the general phenomenon, while fouling and epibiosis refer to aufwuchs on nonliving and living substrata, respectively. The central theme will be the interaction between organisms and the substrata. For this reason, only sessile and hemisessile species are taken into account. Vagile organisms are not considered true aufwuchs organisms here because they have the potential for switching habitats and, therefore, are less definitively linked to the substrata. The substrata bearing aufwuchs may be extremely variable in size, consistency, chemistry, and longevity. They may be of geochemical, biological or man-made origin.

In the first section some reasons are given why attached life is a typically aquatic phenomenon and rarely encountered on land. The latter part of the section deals with the mechanisms of substratum colonization. The second section treats the subject of "fouling". This rather partial term designates the aufwuchs on nonliving substrata, which in the case of man-made, immersed structures often interferes with human interests. "Epibiosis" on the other hand (third section), describes the association of organisms growing attached to other living organisms. Here, the occurrence of epibiotic associations and epibiosis-caused biological and ecological effects are dealt with. The last section speculates about antifouling solutions as derived from epibiosis research.

Aufwuchs

Attached Life: A Typically Aquatic Phenomenon

With regard to the evolution of sessile life forms, air and water differ drastically in several relevant parameters. Viscosity is 55 times smaller in air (18.1×10^{-6} Pa*sec) than in water (1×10^{-3} Pa*sec). Density of air (1.2 kg*m^{-3}) is 833 times lower than that of water (1×10^{3} kg*m^{-3}). Both these parameters strongly (but differently) influence drag, lift, and acceleration force, the three main forces responsible for the displacement of organisms by winds or currents. In addition, density significantly lowers the relative weight of submerged organisms, increasing their floatability and decreasing gravity-induced friction between organism and substratum. The mathematics of these forces are not simple (for details see Vogal 1988, Denny 1988, and Gaylord et al. 1994). Yet, most of us have certainly experienced that while it is easier to float in water than in air, it is much more difficult to stay put in a moderate current than in a strong wind. Relative humidity and the risks of desiccation are obviously very different in the two media. The role of this parameter will be discussed later in this chapter. Finally, both density and chemistry of water (e.g., dipoles) make this medium a more universal solvent than air, especially for large molecules.

These physicochemical differences between water and air have multiple consequences for terrestrial and aquatic life. In contrast to air, water is rich in dissolved and particulate matter (floatability). Solute concentrations in air (perfumes, pheromones, etc.) are typically thin and the dissolved substances are of relatively small molecular size. "Air plankton" is restricted to very small particles like viruses, bacteria, and pollens. Representatives of the "air nekton" (insects, birds, bats) spend considerable energy staying aloft, and resting phases are inevitable. On the other hand, suspended life in water is incomparably richer in individuals and species, with representatives of almost any aquatic animal and plant phylum spending at least one developmental phase floating or swimming. Plankton density may reduce visibility to less than a meter.

In contrast to oceanic environments, terrestrial life is almost two-dimensional. This is illustrated by a strictly surface-bound primary production on land depending, in the great majority of cases, on nutrient uptake from the soil. In the sea, nutrients are distributed throughout the water column (and in the sediment), thus neutralizing trophic dependency of algae on soil and roots.

The abundance of dissolved and suspended matter makes the aquatic medium an ideal food vector. This opens the possibility for water-dwelling animals to live directly from the surrounding and continuously renewed "broth" by suspension feeding or uptake of dissolved nutrients. For this latter nutritional mode, the absence of evaporation underwater is of relevance. On land, at least those sessile organisms that may not escape the heat, have to fight desiccation by thick cuticles, waxes, and the like. These protections would severely impair the transcutaneous uptake of medium-dissolved nutrients. Underwater, the climate is generally more benign, and for isothermic, isosmotic animals, thin skins do not represent a major risk in this regard. The uptake of dissolved nutrients by marine animals is probably of greater and more general importance than suspected.

Thus, in the aquatic habitat, locomotion is not a prerequisite for feeding. Sessile life, under submerged conditions, is possible even for consumers. Because the suspension of particulate organic matter in air is so thin, suspended prey has either to be hunted for, involving locomotion (some birds, bats, frogs), or filtering devices have to be unproportionately large (e.g., sedentary, net-building spiders). Suspension-feeding, attached animals do not occur on land.

Low relative weight of submerged organisms, especially those without calcareous body parts, leads to reduced friction between benthic organisms and the substratum. In combination with high viscosity and high density of the medium, this raises the danger of dislodgement by currents or wave action. Staying put in a favorable habitat becomes a serious challenge in a submerged flow environment, unknown to all but the tiniest land animals. Only those terrestrial animals with high surface to body mass ratios and/or living in exposed habitats, like tree tops, may experience comparable dangers.

Aquatic shallow-water animals have developed a multitude of anchoring devices: hydrophobic surfaces, fibrils, habtic cilia or cirri, "roots", claws, glues, suction cups, and many more (e.g., Crisp 1972). The most secure and presumably least costly are cements that irreversibly fix an organism to the substratum. A prerequisite for the evolutionary success of this adaptation is the capacity of the settling life form (larva, spore, etc.) to select a favorable spot with regard to physical and biological parameters. The literature on settling cues and larval site selection is rich (e.g., Henschel and Cook 1990, Boudreau et al. 1990, Chevolot et al. 1991, Roberts et al. 1991, Morse 1992, Pawlik and Butman 1993, Kjelleberg and Holmstroem 1994). Strictly sessile species cannot switch habitats when ambient conditions change. Therefore, most attached forms in variable environments exhibit great flexibility in behavior, body form, growth regime, reproduction mode, physiology and/or genetics.

In conclusion, due to physical characteristics of water compared to air, a sessile mode of life is possible (food vector water) and favorable (risks of dislodgement) in the aquatic realm. It is not surprising, that many thousand species with representatives from most of the marine phyla have adopted this mode of life for at least one ontogenetic phase: many bacteria, many protozoa, many diatoms, most macroalgae, all sponges, most cnidarians, many molluscs (bivalves, gastropods), some rotifers, most bryozoans, most phoronids, many brachiopods, many tube-building polychaetes, some echinoderms, a few crustaceans (especially cirripedia), some hemichordates, all ascidians.

In many shallow, hard-bottom habitats, sessile life forms dominate the benthic community by number of individuals and species. The decoupling of feeding medium (water) and attachment medium (substratum) may make suitable settlement area a limiting factor in marine habitats. Colonization pressure is a function of locally and seasonally available colonizing species as well as physicochemical and nutritional properties of the water. While never nil, it may vary enormously seasonally and geographically: it may take months in the western Baltic winter for the first visible biofilm to show, while salmon cage netting has to be changed weekly because of heavy fouling in Tasmanian summer waters (Hodson and Burke 1994). Wahl and Lafargue (1990) introduced an index to evaluate the suitability (or rather unsuitability, defense) of a substratum for colonization.

$$\text{Antifouling Potential} = (1 - E/CP) \times A/(FP + A)$$

with E = number of aufwuchs species found on a substratum, CP = numbers of species of local colonizer pool, A = longevity of the substratum, FP = time between immersion and arrival of first metazoan larvae (as an arbitrary estimate colonizing intensity). The index may be used to evaluate the unsuitability of a substratum (e.g., efficiency of antifouling paint or biological defense), but is primarily thought to illustrate the parameters controlling colonization intensity. Thus, a long lived (high A) surface exposed to intense fouling pressure (short FP, high CP) but remaining scarcely fouled (small E), may be expected to be unsuitable for settlement or well protected against colonizers.

Colonization of an Immersed Substratum

Surface Properties

"On immersing a surface in sea water, a complex process of colonization is initiated" (Davis et al. 1989). This statement, or variations of it, can be found in the introductions of most publications treating the subject. It can be, and sometimes is, phrased more sharply: "*Any* hard substratum immersed *anywhere* in the ocean will *inevitably* become colonized—if it is not continuously disturbed or well defended." This is bad news (although not really new) for the antifouling industry (see section on fouling). The two restrictions "disturbance" and "defense" will be treated in the following sections. A closer look at the three main items of this generalization in reverse order, follows.

Inevitable Colonization: Regardless of place and substratum type, an aufwuchs community will establish. Yet, this process will vary in colonization speed, density, and species composition with latitude, depth, exposure time, season, colonizer pool, water chemistry, and substratum characteristics.

Anywhere: As suggested by the widespread occurrence of sessile species across prokaryote, animal, and plant kingdoms, it is not surprising that some potential colonizers can be found anyplace in the ocean: from the poles to the tropics, from the sea surface to hadal depths, from estuaries to offshore waters, from sewage outflows to low-nutrient gyres. Again, intensity of colonization will depend on such local parameters as temperature and nutrient availability, and species composition will be a subpopulation of the local colonizer pool.

Any Substratum: Maybe the most amazing observation of previous reports is, that any stable surface is subject to some kind of colonization. Substrata as diverse as glass, aluminum, steel, copper, titanium, sandstone, granite, slate, concrete, PVC, Teflon, Plexiglas, coral, algal surfaces, mollusc shells, crustacean carapaces, polychaete tubes, diatom valves, soft animal tissue, wood, and many more will develop aufwuchs communities—albeit often featuring only a small subpopulation of locally available colonizer species.

Usually, substratum types do not only differ by their chemical composition, but also one or more of other properties such as wettability, color, consistency, roughness, longevity, size, irradiation, inclination, orientation.

Wettability, a function of surface free energy, ranges from hydrophobic to hydrophilic. This surface property strongly influences the spreading and adhesion of the attachment glues or cements used by many settling colonizers.

The color (or grey shade) of the substratum is important for optically cueing larvae, but its importance will decrease with water depth.

The consistency of a substratum may range from steely hard to watery mucus (some algae, cnidaria) and from rigid to flexible, and should have implications especially for larger, shell secreting or rigid colonizers.

Surfaces may be anything from smooth (e.g., glass, many algae) to granular (e.g., sand stone, some carapaces), scaly (e.g., some bivalve shells), hairy (e.g., some algae and polychaetes), and so on. Microtopography of the surface may influence settlement by modulating small scale hydrodynamics or by reducing available flat area for attachment. Although promising, the role of surface roughness in colonization processes has not yet been investigated to any extent.

The significance of substratum longevity obviously depends on the life cycle of a given colonizer species. Successful settlement and reproduction on a surface can be achieved within weeks by bacteria, diatoms or protozoa, while higher animals or algae depend on surface stability over months or even years. Substratum longevity, meaning the persistence of conditions as they are at the onset of colonization, may be delimited by abiotic changes (emersion, drastic changes in salinity, oxygen concentration, pH, etc.), by mechanical alteration of the surface (overturning of sand grains or boulders, abrasion, erosion, ablation, sloughing, etc.) or by the life expectancy of a living substratum (leaf, carapace, integument, whole organism). A successful colonizer should be able to develop and reproduce before its substratum vanishes or surface conditions become intolerable.

Appropriate size is a prerequisite for colonization. Available, reasonably flat, surface area should exceed the dimensions of the settling form (cell, larvae, spore) and, better still, the attachment area of the adult. An oyster larva will not settle on a diatom, a diatom not on a bacterium.

The remaining three parameters — irradiation, inclination, orientation — affect the substratum's exposure to light, water movement, and siltation.

As mentioned before, all undefended surfaces will be subject to some sort of colonization. The development of an aufwuchs community may be slowed down on certain substrata, the aufwuchs may be less dense or less diverse. But no combination of the above properties makes a substratum wholly unsuitable for all potential settlers. There are two reasons, at least, for this phenomenon. First, among the multitude of locally available colonizer species, there will always be some (especially among the bacteria) that can cope with a given set of surface conditions. Second, the development of aufwuchs is a multistep, selforganizing process (see next section). Many of the surface properties will be altered, neutralized or masked by the first layer(s) of pioneer colonizers, and thus become less relevant to later settlers.

Colonizing Sequence

The physical, biochemical, and biological events leading to the establishment of an aufwuchs community have been thoroughly investigated. Details can be looked up in the more general references given in this section or the literature cited in these. In the following, the sequence of events most commonly observed is outlined very roughly. While most descriptions are based on the colonization on artificial substrata (metals, glass, polymers) immersed in the sea, similar processes have been observed in other media (freshwater, blood, saliva) and on different substrata (wood, stone, teeth, coral skeletons, living organisms). The model thus seems to be of some general value. Yet, in each particular set of conditions, variations can be expected with regard to speed of colonization, number of steps involved, species settling, etc.

The colonization of a substratum is generally viewed as a four-step process: biochemical conditioning of the surface, bacterial colonization, diatom and protozoan colonization, settlement of larvae and spores (figure 1). These steps usually set in sequentially, but the different subcommunities continue evolving throughout the life span of the substratum, interacting with each other.

Colonization pressure begins acting the instant of first contact between seawater and substratum: launching of a ship, hatching of a larvae, splitting of a boulder, appearance of new surface through sloughing of a cuticle or growth of a seagrass blade. For simplicity, this instant will be called "immersion".

Biochemical conditioning: Seawater does not only contain inorganic salts, but also a variety of organic compounds such as sugars, amino acids, proteins, lipids, a multitude of secondary metabolites, etc. Physical properties (surface free energy, polar and nonpolar components, wettability) of substratum and water are virtually never identical (Dexter 1976). The resulting thermodynamic forces across the solid/liquid interface are the motor of the adsorption of organic macromolecules (mostly glycoproteins, polysaccharides and proteoglucanes) onto the substratum. As this process (de-mixing) reduces the randomness of molecular distribution,

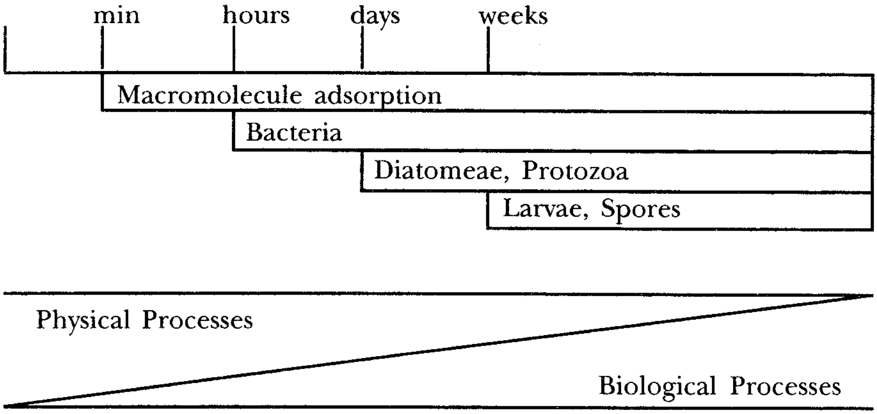

Figure 1. Schematic of colonization sequence figuring the four overlapping phases and the change of dominant forces from physical to biological (logarithmic time scale, modified after Wahl 1989).

the accompanying loss of entropy must be compensated by a diminution of the system's total free energy. This is apparently ensured by the replacement of the initially high-energy solid/liquid interface by a lower energy organic layer (Dexter 1978, Dexter and Lucas 1985). This adsorption is purely physical and spontaneous (Baier 1984). It begins within seconds to minutes after immersion. As most substrata, independently of their original surface properties adsorb similar, often amphoteric macromolecules, their surface free energy and associated wettability, usually converge toward a 30–50 mN/m range during this process (Baier 1981, Becker and Wahl 1991), with hydrophobic surfaces increasing and hydrophilic ones decreasing in wettability. Furthermore, conditioning films forming on different substrata exposed under the same conditions are similar (Little 1985). These are examples of how substratum properties may become masked during colonization (e.g., Schneider 1994). However, on substrata with initial wettability in the range 20–30 mN/m, binding strength and compactness of the conditioning film appear to be reduced (Baier 1981). A further aspect of this adsorption is that physical, chemical, and biochemical characteristics of this macromolecular film are quite different from those of the surrounding seawater. In particular, the concentration of macromolecular nutrients at the interface is thought to have an impact on subsequent colonization steps (e.g., Wardell et al. 1983).

Bacterial colonization: Beginning within hours after immersion, this phase is of mixed physical and biological nature (figure 2). While settlement of bacteria (small size, low Reynold's numbers) has been compared to that of colloid particles (e.g., Marshall 1972, Characklis 1981), bacterial behavior (motility, chemotaxis) undoubtedly contributes significantly to this process (Chet and Mitchell 1976, Mitchell and Kirchman 1984). The nature of forces involved in bacterial transport changes with distances (from the surface) considered: water currents (km, m, cm), cell motility, microturbulence, Brownian motion, gravity (mm, µm), electrostatic and Van der Waal interactions between cell and substratum, fibril contraction (µm, nm) (e.g., Characklis and Cooksey 1983). In this context it is important to realize that water layers near a surface behave physically differently from bulk water. Mostly due to friction, any surface bears an almost perfectly stationary water "skin", called the viscous layer (thickness 40–100 µm), a manifestation of the no-slip condition on every surface. Thinner still (≈ 10–20 nm) and closer to the surface, lies the electrical double layer composed of physically highly structured water molecules and dissolved ions (electrostatic interaction with the substratum).

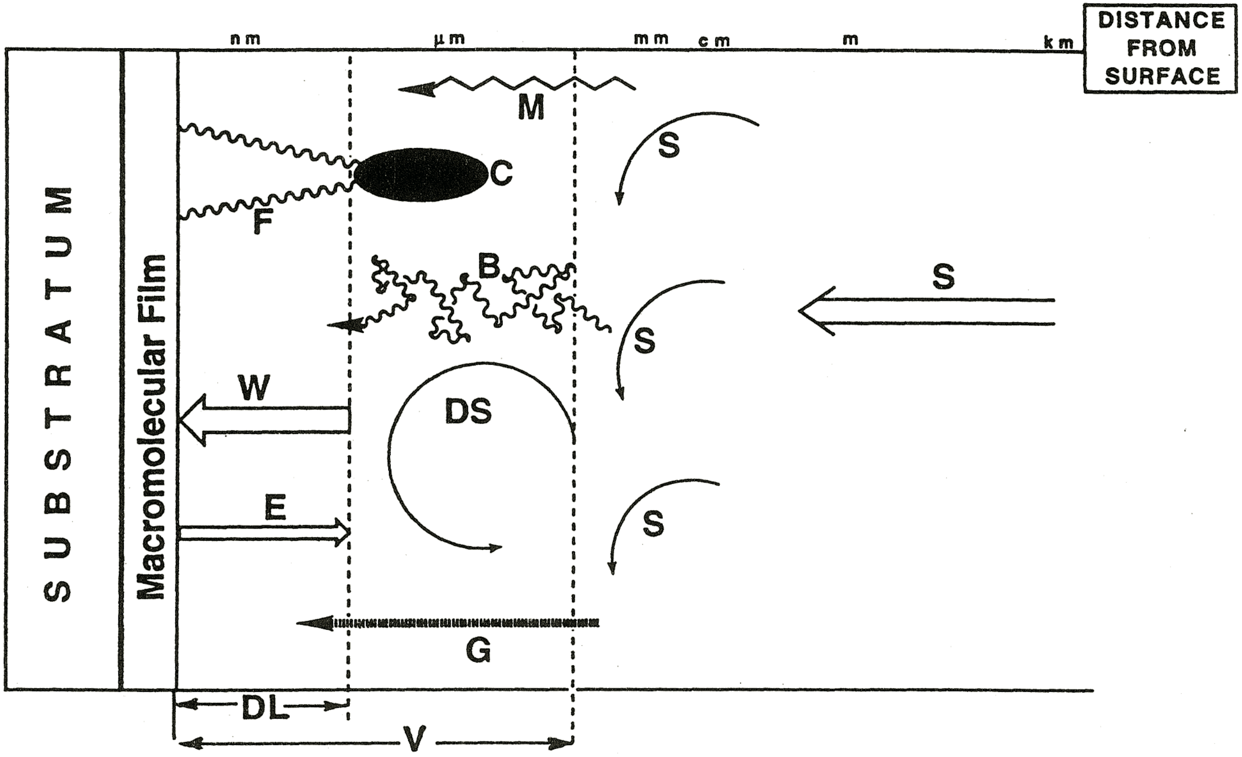

Figure 2. Forces involved during bacterial colonization as a function of distance (log-scale) from surface. **B** = Brownian motion, **C** = cell, **DL** = electrostatic double layer, **DS** = downsweeps, **E** = electrostatic repulsion, **F** = fibrils, **G** = gravity, **M** = bacterial motility, **S** = currents, **V** = viscous layer, **W** = Van der Waals attraction (modified Wahl 1989).

Long range transport of the cells up to the outer borders of the viscous layer will be governed by water currents mostly. Approach through the viscous layer is motored by cell motility (if present and if chemotactically attracted), by random Brownian motion or by microturbulences (downsweeps) that occasionally break through the viscous layer. Most cells and substrata are predominantly negatively charged. So, on further approach, the antagonistic forces of electrical repulsion and Van der Waal attraction between cell and substratum tend to immobilize the cell at a distance of 3–20 nm from the surface. Rearrangement of glycocalyx polymers (Schneider 1994) and/or production of fibrils, attachment of these, and subsequent enzymatic shortening (Fletcher and McEldowney 1984) may help to overcome the repulsion and pull the cell into contact with the surface. This last phase of settlement is facilitated by an opposite charge of cell and substratum, by a hydrophobic cell surface or by reduced cell diameter as in rod shaped bacteria (e.g., Absolom et al. 1983, Pringle and Fletcher 1983, Fattom and Shilo 1984). Firm attachment is achieved by covalent bonding between glycocalyx polysaccharides and binding sites on substratum or macromolecular film (often through divalent cations or lectins, e.g., Costerton et al. 1978). Subsequent, often copious production of exopolymers and continued bacterial settlement lead to the formation of a complexly structured biofilm: matrix compartments containing dead and living cells are separated and interconnected by a branching channel network in which nutrients and wastes circulate (Schneider 1994). The biofilm matrix not only serves as a mechanical support for the bacteria, but also enables these to create microhabitats suitable for their physiological demands. Within the biofilm, physicochemical conditions may locally be drastically different from bulk water with regard to solute concentrations, oxygen tension, pH, redox potential, etc. (e.g., Dexter 1993). During bacterial colonization, successional features have been suggested (e.g., Marshall et al. 1971, Corpe 1972), although in most studies bacteria are rarely identified to genus or even species level. Generally, rod-shaped bacteria seem to arrive first, followed by coccoid and, finally, stalked forms. Even during the subsequent phases of colonization, the biofilm community continues to evolve under the influence of recruitment, predation, competition, and disturbance (Little 1984).

Diatom and protozoan colonization : The settlement of eukaryote unicellulars typically begins within days to weeks after immersion of a new substratum. These cells are subjected to the same physical forces as bacteria. But due to larger cell size and higher motility (at least in the case of many ciliates), their contribution to the adsorption process relative to behavioral aspects should be smaller. After contacting the substratum, the cells attach with polysaccharide or protein glues to biofilm, conditioning film or substratum surface (e.g., Tosteson et al. 1983, Cooksey et al. 1984). Wettability and availability of suitable linkage sites are of relevance. The most common sessile protozoa are foraminiferans or ciliates, the latter mostly of the *Folliculina, Vorticella, Zoothamnion* or *Suctoria* type. Some aufwuchs diatom genera found around the world are *Coscinodiscus, Licmophora, Asterionella, Synedra, Achnanthes, Cocconeis, Navicula, Nitzschia, Amphora.* Diatoms usually dominate this third phase of colonization, but ciliates may reach peaks during spring (personal observation in the Western Baltic) or on specific substrata (e.g., certain crustacea: e.g., Precht 1935). This aufwuchs subcommunity, too, exhibits succession (O'Neill and Wilcox 1971, Ferreira and Seeliger 1985), and dynamic evolution.

Colonization by pluricellular eukaryotes: The settlement, succession and dynamic interactions of macrofoulers (animals and algae) is undoubtedly the most extensively studied phase of the aufwuchs sequence. Some key publications on this subject comprise Sutherland (1974), Jackson (1977), Osman (1977), Sutherland and Karlson (1977), Hadfield (1986), and Richmond and Seed (1991). While succession has been thoroughly investigated, predictability remains poor (Richmond and Seed 1991), and the existence of multiple stable points seems to be rather the rule than the exception (Sutherland 1974, Law and Morton 1993). This may equally hold true for bacterial, diatom, and protozoan colonization, but has not yet been demonstrated.

One important difference to the previous settlement phases should be mentioned. Settlement is done not by the adult life form or something similar in most respects, but by a "gene vehicle" (larva, spore, etc.). Typically, the latter differs from the adult it will grow into by almost any criterion: size, motility, biology, and physiology. The adult is larger by orders of magnitude and lives, and thus depends on stable substratum, for months to years. Furthermore, distal parts of the growing organism often leave the protective proximity of the substratum chosen by the settling form to encounter conditions quite different with regard to hydrodynamics, light, nutrient supply, and the like. To meet the challenge of choosing for a different life form, the adult, many larvae (and spores?) rely on a set of settlement cues, which with evolutionarily satisfying probability, indicate the "right" attachment site. Numerous such cues have already been described, including light levels, hydrodynamics, gravity, surface texture, roughness, color and wettability, surface chemistry, presence of certain other aufwuchs organisms or conspecifics, exuded secondary metabolites, etc. (Neumann 1979, Olson 1980, Todd and Doyle 1981, Kirchman and Mitchell 1983, Crisp 1984, Morse 1984, Rittschof et al. 1984, Burke 1986, Butman 1986, Wethey 1986, Chabot and Bourget 1986, Roberts et al. 1991, Morse 1992, Leitz and Wagner 1993). Negative cues may be as important as positive triggers. Persistent absence of positive cues may lead to a prolongation of larval phase, a lowering of the cueing threshold, metamorphosis without settlement and/or death of the larva.

While the four colonization phases described typically start sequentially, they coexist and intensely interact for the rest of the aufwuchs community's life span.

The above model is certainly a very simplified view of aufwuchs development. For a given location or season, single phases may be skipped, subsequent phases may start simultaneously or even in reverse order. But the presented sequence is by far the most commonly observed. This probably has a dual reason: availability of colonizers and facilitation:

- From macromolecules, over bacteria, diatoms and protozoa, to larvae and spores exists a decreasing gradient of presence (spatial and seasonal) and concentration in seawater. Thus, the encounter probability between newly immersed substratum and settling unit follows the same gradient. Furthermore, macromolecules and the physiologically very adaptive bacteria are less 'choosy' with regard to substratum properties than larvae, for instance.
- In addition, there are examples of facilitation in aufwuchs succession. Adsorbed macromolecules constitute a potential nutrient source for chemotactically attracted bacteria (e.g., Wardell et al. 1983). Also, the conditioning film often exhibits much less extreme surface-free energy values than the original substratum. Biofilms are known to neutralize adverse substratum properties by detoxification or masking (e.g., Saroyan 1968). Bacterial vitamin production (Lynch et al. 1979), N_2 production (Goering and Parker 1972) and provision of suitable linkage sites may facilitate subsequent colonization phases. Bacteria and diatoms may produce settlement cues for larvae (e.g., Crisp 1984, Kitamura and Hirayama 1987).

It seems reasonable that availability and facilitation concertedly constitute the causal basis for the usual sequential character of aufwuchs development.

Fouling

The rather anthropocentric term "fouling" originally described those aufwuchs communities that develop on man-made structures in the sea, and that usually interfere with human interests. Unfortunately, this term is often extended to any hard bottom community or, at least, its attached components. There certainly is nothing foul, dirty, disgusting or putrid (Webster synonyms) about kelp forests, mussel beds or gorgonian communities. On the other hand, sessile organisms settling on underwater structures man-designed for a specific use may indeed severely interfere with this function.

As mentioned before, fouling pressure of variable intensity is omnipresent in the sea. Generally, it decreases with latitude, distance from shore, distance from natural hard bottom communities, and depth (Richmond and Seed 1991). On undefended substrata a fouling sequence corresponding to the above model can be observed. On protected surfaces, however, the sequence may be substantially altered or truncated for a limited amount of time (see below). For convenience, marine engineers distinguished between:

- microfoulers (bacteria, cyanobacteria, diatoms, protozoa),
- soft foulers (without calcareous excretions: many algae, sponges, hydrozoa, sea anemones, soft corals, polychaetes, ascidians, etc.),
- hard foulers (with calcareous excretions: calcareous algae, stony hydrozoa and corals, bivalve molluscs, bryozoans, cirriped crustaceans, polychaetes, etc.), and
- borers (representatives of cyanobacteria, sponges, isopod crustaceans, bivalves, polychaetes, sea urchins, phorinids, etc.).

All types of surfaces may become fouled, while boring is restricted to mineral materials (stone, concrete), wood and, rarely, metals (some urchins, sulfate-reducing bacteria in the last case). The unwanted effects of fouling comprise the following aspects: destruction of material, insulation, accrual of mass, and increase of frictional drag.

Effects of Fouling

The destructive potential of fouling is known since man began using wooden boats. Especially, when ships became larger and could not be dragged ashore between uses, the danger of loosing vessel (and crew) to *Teredo*, *Spaeroma*, and other borers increased. In areas with high borer incidence like the Indian Ocean, every single one of 60 timber species tested was destroyed by borers within 12 months (Santhakumaran and Rao 1988). Evidently, not only ship hulls are attacked, but also any other wooden material immersed in the sea: rafts, pilings, live mangrove trees, etc. (Boyle 1988, Nagabushanam and Alam 1988, Rao et al. 1991). Besides wood, other materials, too, are subject to boring. Calcareous rock