Reprints

BARNACLES
The Biofoulers

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Ecology of Indian Barnacles

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An overview of the ecology of Indian tropical balanomorph and lepidomorph barnacles is presented. Findings relating to systematics, distribution, the role of primary film and its significance in barnacle settlement, breeding, seasonal and ecological succession, substratum preferences, growth, and biomass generation are discussed. Contributions relating to physical, chemical, and geographical factors such as salinity, temperature, waves, tides, currents, light, and color, nature, and texture of substrata are reviewed with particular reference to Indian tropical conditions. Some thrust areas to be dealt in greater detail in future work are also suggested.

Introduction

Cirripede crustaceans are a major group of fouling organisms because of their reproductive capacity, gregareousness, and settlement abundance compared to other fouling animals. Barnacles are studied in greater detail than other foulers due to their world-wide distribution and significant contribution to frictional drag in ships. Nearly 300 barnacle species are reported, of which 25 are represented in fouling (WHOI 1952). They are very common, hard shelled, and well distributed fouling animals. Three types of fouling barnacles are recognized, namely, lepadomorpha (goose barnacles), balanomorpha (acorn barnacles), and verrucomorpha (deep-water forms). They are found in diverse habitats such as intertidal shallow rocky shores, as commensals on turtles, whales, and sponges, and also as foulers on boats, navigational buoys, underwater acoustic systems, and mooring structures as well as in deep waters. This chapter reviews the literature on the ecology of Indian tropical barnacles.

Systematics and Distribution

A large collection of barnacles from the Indian peninsula was studied by different researchers with focus on their incidence and nature of their fouling. The 30 species, subspecies, varieties, and forms recorded are chiefly from the Bombay coast (Nilsson-Cantell 1938, Bhatt and Bal 1960, Karande and Palekar 1963, Karande 1967a); Ratnagiri (Alam et al. 1988); Cochin (Balasubramanyan and Menon 1963, John 1964, Nair 1967, Meenakumari and Nair 1984); Neendakara (Dharmaraj and Nair 1981); Tuticorin (Renganathan et al. 1982); Visakhapatnam (Ganapati et al. 1958); Kakinada (Rao and Balaji 1988); Porto Novo (Dhandapani and Fernando 1994); Madras (Paul 1942, Daniel 1952, 1953, 1954); and Andaman waters (Karande 1978). These studies, chiefly on the ecology of fouling, contain references on the distribution and systematics of the barnacles.

While studying the biology of fouling at different locations, Karande (1967a) was able to make a large collection of barnacles. He added 11 more species, subspecies, varieties, and forms to the 4 previous records from Bombay shores (Nilsson-Cantell 1938, Bhatt and Bal 1960, Karande and Palekar 1963).

It is evident that the cirripede fauna are very rich around Bombay. This may be due to the greater attention they received there compared to other locations in India. Barnacles such as *Balanus amphitrite variegatus, B. amphitrite communis, B. amaryllis euamaryllis,* and *B. tintinnabulum tintinnabulum* contribute chiefly to the fouling community on ship hulls in Bombay. Karande (1967a) also presented detailed comments on the inter-relationships among 15 varieties found in these waters, of which 7 were varieties of *B. amphitrite.* Of these, *B. amphitrite variegatus, B. amphitrite insignis, B. amphitrite venustus,* and *B. amphitrite denticulata* are essentially offshore species while *B. a. communis, B. amphitrite hawaiiensis,* and *B. amphitrite cochinensis* are intertidal forms. *Balanus a. communis,* though an intertidal form, is also found settling on ship hulls, mooring chains, buoys, and other structural materials. In Japanese waters, *B. a. communis,* together with *B. a. hawaiiensis,* are not found on intertidal rocks but only on ship hulls. Hiro (1939) classified barnacles according to their habits (Karande 1967a). He suggested that the varieties of *amphitrite* in Bombay can be grouped into intertidal and offshore.

Determining barnacle varieties, particularly of *amphitrite,* is difficult (Karande 1967a), but groupings of offshore varieties are comparatively easy as there are distinct differences in color, shape, size, and opercular valves. The intertidal varieties need careful study. Karande (1967a) presented figures of adult specimens, opercular valves, and the labrum, which are helpful in identifying the various *amphitrite* varieties. *Balanus* *a. denticulata* and *B. a. hawaiiensis* are synonyms according of Utinomi (1960) but the two varieties are separable from one another (Karande 1967a). The opercular values in var. *denticulata* are weaker than those of var. *communis.* The carinal margin at the apex of the tergum of var. *denticulata* distinguishes it from other varieties of the *amphitrite* series. The specimens of var. *communis* at Bombay possess 25 teeth on the labrum (Karande 1967a), while var. *denticulata* has only 8. Var. *communis* is also provided with a white strip along the tergal margin of the scutum, which is absent in var. *denticulata.* Var. *hawaiiensis* is easily distinguishable from others by a deep sinus suture between the opercular valves and the horizontal disposition of the latter in contrast to the inclined position in other varieties.

Karande (1967a) observed that the cirripede barnacles from the Bombay coast are primarily composed of Indo-Pacific forms with Malayan elements. Of the 15 barnacles, *B. a. cochinensis* and *B. a. insignis* were recorded from Sumatra and, subsequently, from Cochin (Meenakumari and Nair 1984). The chthamalid barnacles described by Karande (1967a, 1967b) were reported earlier from the Malay archipelago, Formosa, and Japan. *Balanus a. hawaiiensis, B. a. variegatus, B. amaryllis euamaryllis, Balanus amphitrite nivea,* and *Tetraclita purpurascens* have been recorded from the Indian Ocean. Utinomi (1960) found world-wide distribution of *B. a. hawaiiensis* and *B. a. denticulata* because of the synonymy between the two species. *Balanus a. communis, B. a. venustus,* and *B. t. tintinnabulum* recorded by Karande (1967a, 1967b) are also widely distributed and reported from the Malay archipelago, the Pacific Ocean, Mediterranean Sea, Atlantic Ocean, and the Indian Ocean.

Barnacles *Chthamalus* sp., *Balanus amphitrite, B. amaryllus,* and *B. tintinnabulum* are present in the Zuari Estuary, Goa (Anil and Wagh 1988).

In Ratnagiri waters (Alam et al. 1988), the dominant barnacles are *Chthamalus malayensis, Chthamalus* sp., *B. t. tintinnabulum, B. a. communis,* and *Balanus amphitrite stutsburi.*

Sundera Raj (1927) recorded five species of cirripedes from the Krusadai Islands. Daniel (1962) found *Balanus (Semibalanus) sinnurensis* at Porto Novo, Madras, and *B. (Semibalanus) madrasensis* n. sp. on fishing craft off Madras (Daniel 1958a). From Madras, he reported *B. tintinnabulum tintinnabulum, B. a. communis, B. a. variegatus, B. a. venustus, B. eburneus, B. amaryllis f. euamaryllis, Tetraclita purpurascens, Chthamalus stellatus stellatus, Lepas anatifera indica, Lepas anserifera, Lepas bengalensis, Lepas tenuivalvata, Lepas hilli indicus, Lepas pectinata longi tergata, Lepas pectinata diatata, Octolasmis clubii, and Conchoderma indicum* (Daniel 1952, 1953, 1956a). From Krusadi waters, *B. a.* var. *venustus* Darwin, *B. a.* var.

denticulata Broch, *B. tintinnabulum* Linn., *Chelonobia testudinaria* Linn., *L. anserifera* Linn. are reported (Kurian 1952).

In Visakhapatnam harbor waters, *B. a. communis, B. a. variegatus, B. tintinnabulum tintinnabulum* and *Chthamalus* sp. have been identified (Ganapati et al. 1958). At Kakinada Bay near this harbor, the barnacles identified were *B. amphitrite, B. patelliformis,* and *Megabalanus tintinnabulum* with *B. amphitrite* being most abundant and dominant (Rao and Balaji 1988).

Sessile barnacles of five species were reported from the Vellar Estuary, Porto Novo (Dhandapani and Fernando 1994). They are *B. a. amphitrite, B. variegatus, B. reticulatus, B. kondakovi,* and *C. malayensis.*

Cirripedia from the suboceanic islands of the Andamans were also noted by Karande (1978). As in the mainland waters, rich barnacle fauna were observed. The species identified by him (1978) from Port Blair were *B. t. tintinnabulum, B. amaryllis euamaryllis, B. a. amphitrite, B. kondakovi, B. variegatus, Tetraclita* sp., *C. malayensis, C. withersi* and *Lepadid* sp. Of these, *B. variegatus* was the most dominant followed by *B. a. amphitrite. Balanus a. amphitrite* together with chthamalid and tetraclitid barnacles occurred in large numbers in the near-shore waters of Port Blair because of their ability to grow in enclosed areas.

Primary Film and Barnacle Settlement

Any surface immersed in seawater becomes coated with adsorbed organic molecules. This is followed by settlement of bacteria, microalgae, and small protozoans. This slime film is further strengthened by depositions of inorganic salts, detritus, and accumulations of surface corrosion products. The metabolic products of microbial organisms, such as phospholipids ~~and~~ polysaccharides, also support and strengthen the initial conditioning film.

The formation of biofilm is influenced by several factors such as substrate composition, surface charge (Dexter et al. 1975), chemotaxis (Young and Mitchell 1972), and reactions of participating organisms and slimy exudates (Gerchakov et al. 1977) of bacteria and other microbial fauna. It is known that conditioning films play a critical role in the attachment of larvae of microfoulers, particularly barnacle cyprids, due to surface probes by barnacle larvae before final attachment by barnacle cement.

The gelatinous exudates of bacteria provide a physical surface/ nutritive source for the microfoulers, including barnacle cyprids. This primary layer is not an absolute necessity for barnacle larvae as they can settle on clean surfaces (Liberatore and Dyckman 1972, Nair and Pillai

1977). Many organisms prefer slimed surfaces (Wilson 1955, Doochin 1959, Crisp and Medows 1963), particularly barnacles, sedentary polychaetes (Knight-Jones (1951), and *Ophelia bicornis* (Wilson 1955).

Settling barnacle cyprids are capable of investigating the nature of a surface prior to settlement. Stimuli are from the water (current, presence of food) and the atmosphere (light flux, wind direction), especially in littoral and sublittoral species and from the surface itself (surface texture or rugophilic behavior) (Barnes 1956). Slime layers entrap cyprids by making it difficult for them to leave, by providing food and also by changing the color of the surface. They may also sorb various chemicals, helping in gregareousness, and act as barriers, preventing release of toxins from antifouling paints. These slime layers can affect the tenacity of attachments by surface free energy (Disalvo 1971). The bonding between surfaces and barnacles varies with different materials (Crisp and Medows 1963). Crisp (1965) observed a tactile chemical sense that recognizes specific molecular groups on a surface. These releaser chemicals help in the final metamorphosis of cyprids and their attachment. The releaser chemicals may be species specific anthropodins produced by other barnacles.

There are only a few studies on slime film and its role in settlement and metamorphosis from Indian tropical waters. Daniel (1955a) found that 48 hours were needed for the culmination of primary film in Madras harbor waters. He noted that the slime film was composed of 34 diatom species, 14 algal species, and a small proportion of bacteria. He was not able to establish the role of the various constituents of the film. In 1955 he noted the settlement of barnacle cyprids after 48 hours on slimed surfaces and found that slime film is an essential prerequisite for barnacle and serpulid settlement.

There are three stages in the development of a primary film, namely, bacterial slime, diatom flora, and attachment of higher animals. Kuriyan's observations (1952) of 10-day blocks of wood did not reveal any separate stages. He noted the formation of primary film consisting of bacteria and diatoms and the settlement of organisms, simultaneously or immediately. It is reasonable to assume that some fouling animals need such a film while others are capable of settling on clean or newly submerged surfaces. In some species, there is more settlement on filmed surfaces. Balasubramanyan and Menon (1963) recorded bacteria, diatoms, and protozoans as the foremost of all settling organisms on test panels exposed in the Port of Cochin; Ganapati et al. (1958) found bacteria, diatoms and protozoans as the primary settlers. Nair and Pillai (1977), while conducting studies on the role of slime film in marine fouling, found progressive increases in bacterial counts from 2 to 72 hours; 85% of the bacterial isolates were nitrate reducers and 5% sulfate reducers.

The majority were non-sporing Gram-negative, motile rods with flagella. A few genera of *Vibrio, Acromobactor,* and *Aeromonas* were also identified. In addition to bacteria, eight species of diatoms were recorded from the slime. Their study showed that a primary film is not an essential prerequisite for fouling by barnacles, but that slime facilitated their settlement.

There are variations in primary films formed during different times of the year. Nair and Ravindran (1994) studied the dynamics of bacterial colonization and barnacle settlement on surfaces treated with selected repellants and attractants. They tested several chemicals impregnated in porous ceramic plates to evaluate their effects on bacteria and barnacles. A distinct preference for rough surfaces over polished ones was found, with chemical preferences benzoic acid > amino acids > copper-chrome-arsenic composition > tannic acid > creosote > copper creosote > formalin > tributyltin oxide. Karande (1987) found that materials such as titanium, stainless steel, and copper-based alloys develop microbial films following immersion in seawater. In clean as well as polluted waters of the Bombay harbor, titanium and stainless steel gathered more film than copper-based alloys, particularly in polluted waters. The biofilms on the copper-based alloys, however, were more tenacious and firm and, therefore, difficult to remove. The films formed on metallic materials contained more inorganic components; the organic fibrilar mucilagenous secretion released by bacteria help to strengthen the film formation. Sulfate-reducing bacteria associated with microfilms also accelerate metallic corrosion. Meenakumari and Nair (1994) compared the ratio of settlement of cyprids to young barnacles on panels with and without slime films. The pattern and ratio of settlement varied significantly during different months and different exposure periods. However, preferential settlement of cyprids was found on the slimed panels.

Breeding and Settlement

Reproduction in Indian barnacles has been studied by Daniel (1954, 1958b), Pillai (1958), Karande and Palekar (1963), John (1964), Karande (1967a), Pillai and Nair (1972), Fernando and Ramamoorthi (1975, 1977), Rege et al. (1980), Matheswari and Fernando (1989), and Dhandapani and Fernando (1994).

At Madras harbor, Paul (1942) observed attachment of barnacles on experimental panels in large numbers, covering the surfaces to a great extent. Cement blocks immersed for 10–12 days also developed dense settlement of *B. amphitrite*: about 14 barnacles settled per square centimeter. Biweekly observation of the gonads of barnacles obtained from experimental objects and harbor structures revealed ripe eggs and developing nauplii throughout the year, suggesting no special breeding intensity. The uninterrupted temperature conditions and uniformly high salinity may be the causative factors for their continuous breeding in the harbor waters (Paul 1942). Daniel studied the settlement and succession of four species, namely, *B. a. variegatus, B. t. tintinnabulum, B. amphitrite,* and *B. a. communis.* He found breeding and continuous settlement in *B. a. communis* and *C. stellatus* in Madras. However, in *B. t. tintinnabulum,* he noted two sporadic occurrences from July to August and December to January. *Balanus a. variegatus* had a preference for still waters of the harbor area and was present throughout the year. Limited settlements were observed in *B. a. venustus, B. eburneus, B. amaryllus forma euamaryllis, Tetraclita purpurascens, Lepas anatifera indica,* and *L. anserifera.* Daniel (1954) and Paul (1942) found that relatively high temperature and a consequent high metabolic activity were responsible for rapid growth and attainment of sexual maturity at a surprisingly early age. Acceleration of the reproductive process and constant settling of generations of barnacles in a tropical harbor like Madras are also due to the prevalence of high temperature throughout the year. As observed by Paul (1942), in Madras waters, Antony Raja (1963) also found continuous breeding of *Mytilus striatulus, Bowerbankia* sp., and *Dasychone cingulata* throughout the year with different intensities during specific times.

Barnacle settlement is a complex process involving exploration of the substrata by cyprids and fixation (Crisp 1976). It is influenced by various factors including plankton abundance. Observations on daily settlement of barnacle cyprids at the intake of the condenser cooling system in Kalpakkam coastal waters showed two peaks, one in May–June and the other in October–November (Sasikumar et al. 1989). They noticed variations in settlement at the outfall and forebay of the cooling circuit. Low barnacle settlement during the operational period of this power plant was ascribed to altered water temperature, presence of chlorine, and high water velocity. While studying the biology of fouling in the Visakhapatnam harbor, Ganapati et al. (1958) found settlement of four species of barnacles: *B. a. communis, B. a. variegatus, B. t. tintinnabulum,* and *Chthamalus* sp. With the exception of the *Chthamalus* sp., all settled on test panels during the entire period of investigation. The peaks of abundance were in April, May, and August, correlating probably with local differences in hydrobiological and biological conditions.

From Kakinada Bay, Rao and Balaji (1988) reported dense encrustations of *B. amphitrite* during most of the year. Heaviest settlement was from March–August. In the low saline months of September and October, there was a slight decline.

Fecundity based on egg numbers and size of five species of barnacles from Porto Novo — *B. a. amphitrite* Darwin, *B. variegatis* Darwin, *B. reticulatus* Utinomi, *B. kondakovi* Tarazovi and Zevina, and *C. malayensis* Pilsbry — were studied by Dhandapani and Fernando (1994). They found that in all species the number of eggs increased with the size of animals, irrespective of species or stability of the substrata. Barnacles on unstable substrata attained maturity earlier than those on stable substrata.

At Karapad Creek in Tuticorin, peak barnacle settlement was found from July to August (Renganathan et al. 1982). Barnacles may have different breeding seasons governed by local hydrographical conditions. Their settlement also depends on many factors such as light intensity, substrate specificity, depth, nutrients, salinity, and temperature.

Peak abundance was in August and November on short-term panels at Neendakara (Dharmaraj and Nair 1981). They were absent in February due to salinity fluctuations resulting from the monsoon. John (1964) recorded a high rate of occurrence of *Balanus* from September to December and a much diminished but more uniform rate the rest of the year; there was no settlement in June. There were fully developed ova from November to April, indicating the breeding season. Nair (1967) recorded *B. amphitrite* as the most important fouling animal at Cochin harbor, occurring throughout the year. Barnacles were found settling in large numbers during the postmonsoon (September–December), in fair numbers premonsoon (January–April), and a few during the monsoon (May–August). The heaviest settlement of *B. amphitrite* was during November and December, when they contributed the major share of surface coverage. Settlement was controlled by salinity. *Balanus amphitrite* appears to be a continuous breeder in Cochin harbor (Nair 1967, Meenakumari 1989). Pillai and Nair (1972) found that *B. a. amphitrite* attained sexual maturity at a rostro-carinal diameter of 7.5 mm. They noticed a synchrony in the development of the ovary and testis and that, along with cross-fertilization, self-fertilization also took place. Even though they settled in all months, there was considerable fluctuation in intensity, which increased from August reaching a high in December. Salinity of the surface waters fluctuated between 19.7 and 26.5 ppt during the premonsoon (January–April) and declined to 0.93 ppt during the monsoon (May–August). The low saline conditions continued until November and then reached a maximum of 33.8 ppt in January. Observations by Balasubramanyan and Menon (1963), Nair (1967), and Meenakumari and Nair (1984) showed that the quality and quantity of fouling were least during the monsoon. Many barnacles were killed and sloughed off during the periods of very low salinity prevailing at that time. When normal conditions returned, areas left bare were recolonized by fresh planktonic larvae brought to the site by tidal currents and other movements of the medium (Nair 1967).

Nair and Nair (1987) made some fouling forecasts based on the settlement of the fouling organisms at Cochin harbor. Of the fouling groups studied, barnacles contributed the greatest intensity of settlement. Based on the intensity per unit area of a test surface, Nair and Nair predicted maximum fouling in December. The horizontal and vertical distributions of barnacles are considerably influenced by salinity distributions. Their maximum settlement was found near the bar mouth, and slowly reduced towards the upper reaches of the estuary (Meenakumari 1989). Wallershaus (1972) also studied salinity stratification in Cochin backwaters: an upper regime of low salinity and a high one in deeper waters. The barnacles survived in the deeper water even though they were eliminated in the upper strata during the monsoon.

Menon et al. (1977) at Mangalore harbor found peak barnacle settlements during March, May, November, and December. Here, barnacles settled throughout the year, interrupted by the monsoon, with a major peak of settlement in November–December and another one during March and May. At Bombay harbor, Karande (1967a) noticed restricted breeding of barnacles from July to September and opined that low salinity conditions were the causative factor. Rege et al. (1980) found that *B. a. amphitrite*, irrespective of habitat, attained sexual maturity in Bombay waters when reaching a basal diameter of 2–3 mm. For a given body weight, the number of eggs produced was lowest in the population inhabiting polluted waters, the fully grown adult barnacles had poor breeding potential. In Ratnagiri waters, barnacle settlement was intense from January to May and again from September to November and during the monsoon months. The percentage of fertilized individuals of *B. amphitrite* was low (Alam et al. 1988). Karande (1978) saw continuous settlement throughout the year in *B. variegatus* and *B. a. communis* inhabiting the suboceanic islands of the Andamans. Settlement of spat was particularly heavy during January to May with little or no fluctuations in abundance, unlike that in many mainland ports such as Bombay, Cochin, Visakhapatnam, and Madras.

While studing the breeding of animals of the Madras coast Paul (1942) observed the following: A single breeding period, not lasting the entire year (e.g., *Polycarpa* sp.). Continuous breeding all year with more active breeding during a specific time of the year (e.g., *Mytilus viridis*). Continuous breeding throughout the year without any special intensity during any part of the year (e.g., *B. amphitrite*). Discontinuous breeding related to phases of the moon (e.g., *Platynereis*).

This was also true in the open-sea condition as at Madras, but different in enclosed harbor waters such as Cochin, Neendakara, and Mangalore. Here, breeding of barnacles is continuous with variations in intensity depending upon the prevailing hydrographic conditions (Nair (1965, 1967; Menon et al. 1977; Dharmaraj and Nair 1981; Meenakumari and Nair 1984; Meenakumari 1989).

India, being tropical, epibenthic animals, including barnacles, breed continuously throughout the year. The constant settling of generations of organisms, production of several offsprings in an year, their rapid growth and attainment of sexual maturity at a surprisingly early stage are all brought about as a result of the constant high temperature throughout the year (Paul 1942, Nair 1965). The noted absence of seasonal succession (Daniel 1954) in tropical waters is due to temperature, which does not fluctuate as in higher latitudes. Salinity has been recognized as an important factor in the distribution of fouling organisms in several locations in India where water salinity is reduced by rainfall. Even though salinity fluctuations are insignificant in the open ocean, in estuaries and harbor areas fluctuations are pronounced due to land drainage consequent to precipitation. In barnacle settlement and succession in most Indian harbors, salinity acts as a 'master factor'.

Development and Biocoenosis

During the development of biofouling communities (biocoenosis), species composition and abundance are influenced by new recruits, physical and chemical disturbances, mortality of adults, predation, overgrowth, and several biological interactions; all, in turn, help in the development of climax species. Such a community is established as a result of true ecological succession (Coe and Allen 1937). Climax communities of balanids, mussels, and serpulids were recognized by Daniel (1954) and Ganapati et al. (1958). However, Antony Raja (1959) felt that the differences in the sequence of community development are not true, regular or definite and are modified by prevailing ecological conditions. Rao and Balaji (1994) noted the emergence of dominant species of barnacles and oysters. However, Rao and Balaji (1994) opined that dominance was not due to the discrete selection/presence of new surfaces by species or to biological succession. Rao and Balaji (1994) observed dominance of the exotic species *Mytilopsis sallei* within 30 days in polluted waters of Visakhapatnam and dominance of different species (spirorbis, bryozoans, barnacles, sponges, oysters) in cleaner waters that was not orderly or directional. They felt that this should be recognized as a 'multiple stable point' rather than a climax community.

In Ratnagiri waters, the spread of many slow growing organisms was inhibited by the fast breeders. Spreading of *Chthamalus* was controlled by intense settlement of bryozoans (Alam et al. 1988). Heavy mortality of barnacles was noticed at Kakinada Bay, possibly due to overcrowding and interspecific competitions. Barnacles were often suppressed by massive settlements of *Mercierella enigmatica* (Rao and Balaji 1988). Investigators dealing with fouling communities have often used the term 'climax community' to describe monopolies of successful species found on test panels. Such climax communities of balanids were identified in the Cochin harbor (Meenakumari 1989).

Succession of communities is an orderly and directional process leading to a physical modification of the environment by the community resulting in the establishment of a stable climax community (Odum 1969). Orderly biological interaction with a predictable outcome results in the bacterial biofilm — the precursor to macrofouling. It may trap cyprids, provide food for immature barnacles, change the color of the surface by making it more attractive, may sorb various chemicals helping in gregariousness, reduce the toxicity of antifouling paint surfaces, and affect the tenacity of attachment (Fischer et al. 1984). Development of some fouling communities is not orderly or directional but the orderly and directional process leading to succession of the constituents of the slime film is clearly discernible in the initial stages of fouling community development. However, the development of climax communities at the macrofouling level leading to a competitive hierarchy is still uncertain as is clear from the studies on fouling from Indian harbors.

The adhesive and compressive strengths of foulers play an important role in community maintenance, thereby, resisting dislocation. Studies on this are limited in India. Udayakumar and Karande (1986) determined that the adhesive strength of barnacles at Bombay was highest for *B. amphitrite*. It was 1.14×10^8 Nm^2 for *B. amphitrite* and 0.13×10^8 Nm^2 for *C. malayensis*.

Temperature is the most important factor limiting the geographical distribution of marine animals. The noted absence of seasonal succession (Daniel 1954) in tropical waters is due to temperature, which does not fluctuate as in higher latitudes. Few studies (Ganapati and Rao 1962; Rao 1975; Rao et al. 1981, 1988) were conducted on the effects of temperature on Indian barnacles. Those by Ganapati and Rao (1962) deal with respiratory movements (cirri beating) and temperature, and those by Rao et al. (1981) and Rao (1975) on the effects of temperature and oxygen consumption in *B. t. tintinnabulum* and *B. a. amphitrite*, respectively. They observed peaks in oxygen consumption and respiratory movements at higher temperatures. However Rao et al. (1988) found in *C. withersi* a slight shift in the peak towards 40°C compared to 30°C in *B. t. tintinnabulum* and *B. a. amphitrite.* They saw higher metabolic rates in tropical barnacles compared to the boreo-Arctic species *B. balanoides, B. balanus,* and *C. stellatus* (10–15°C) observed by Barnes and Barnes (1969). According to Rao et al. (1988), low Q_{10} values (the operation of homeostatic mechanisms at higher temperatures) and the shift in metabolism-temperature curves towards higher temperatures appear to be characteristics of tropical barnacles.

Barnacle settlement is also influenced by several complex factors, often interactive in nature, such as light, gregareousness, tides, and the nature, color and texture of substrata:

Light: Daniel (1963) found five times more settlement of *B. amphitrite* during the day than night. *Balanus tintinnabulum* attached mostly during day time, shaded from direct sunlight. Larvae of *C. stellatus* settled most abundantly in direct sunlight. All three species settled at night under artificial illuminiation. Daniel (1957) also observed that *B. tintinnabulum* abounds in the sublittoral fringe of rocky coasts 3 meters below mean sea level, on the shady sides of rocks where total depth is 6–7.5 meters. *Balanus amphitrite* occurred in harbor structures most abundantly 0.3 meters below the surface at low tide, where illumination was of moderate intensity, while *C. stellatus* was found in the supralittoral fringe of rocky coasts where they were regularly exposed to the sun during low tide. Kuriyan and Mahadevan (1953) found barnacle attachment chiefly on surfaces deeply submerged. Settlement in blocks near the surface was confined to its underside away from abundant light.

Gregarious Attraction: Barnacles exhibit gregarious attraction. The adults of *B. amphitrite, B. tintinnabulum,* and *C. stellatus* attract the larvae of their own and other species (Daniel 1955b). Gregareous attraction of a particular species is directly proportional to the number of barnacles already settled. Availability of shelters like edges and corners allow the larvae to settle in large numbers (rugotropism), which, in turn, attract more larvae.

Waves, Tides, and Currents: Waves, tides, and currents affect the dispersal and growth of barnacles. Water movement facilitates the existence of sessile animals as it transports additional food materials to them and also removes waste materials. Currents additionally play a very important role in the distribution of planktonic larvae of barnacles and prevent overcrowding in any particular substratum. Sometimes water movements are harmful when the larvae of littoral forms are swept far away to the open ocean where settlement is impossible (Nair 1967). The velocity of water currents on the surfaces of substrata is important since the larvae of many foulers select suitable substrata for settlement in relation to the velocity gradients of currents (Crisp 1974). The limiting velocity of *B. amphitrite* is 0.6 to 1.8 knots (Smith 1946). The attachment and survival of barnacles are chiefly influenced by water currents.

The tidal stage also affects barnacle cyprids although conflicting views are expressed by various workers. Daniel (1957, 1963) stated that the stage of tide influences the attachment of barnacles. He observed maximum attachment of *B. amphitrite* during low tide as did Weiss (1947) who found maximum settlement of *B. improvisus* cyprids. However, *B. tintinnabulum* and *C. stellatus* preferred to settle at high tides.

Substratum: Investigations support the hypothesis that for major classes of marine invertebrate colonizers on hard substrates, settlement and recruitment are highly substratum specific and that larval recognition of an environmental chemical cue is an obligatory requirement for the settlement induction of plankton and subsequent metamorphic development (Barnes 1956; Morse and Morse 1984, 1991; Morse 1988). Preferential settlements on wood and metals were observed by Sasikumar et al. (1989) Substantial settlement of barnacle cyprids was seen on all wooden panels in 24 hours except for *A. lebbeck* and *Tectona grandis*, which showed relatively lower numbers. When metal panels were used, highest settlement in 24 hours was found on mild steel. Settlement on aluminum was also relatively high. Copper coupons showed no settlement at all. Substratum preference was studied by Chandrasekharan and Gnanajothi (1988). They found the order of preference was molluscan shells, fixed pillar erections, large ships, catamarans, fishing boats, and rocks. The color of the substratum also influences settlement of barnacle cyprids (Kuriyan and Mahadevan 1953, Daniel 1956b). They found that red, black, and white attracted large numbers and blue, green, and gray fewer sedentary forms.

Growth

The tenacity with which barnacles attach to surfaces and their conical shape contribute to the drag of boats and ships. In ships, drag is directly proportional to growth and biomass accumulation. Even after the death of barnacles, their shells are found intact on ship hulls, contributing to increased drag.

Various workers have recorded the growth of barnacles from Indian harbors. (Paul 1942; Ganapati et al. 1958; Nair 1967; Balakrishnan 1975; 1977; Karande 1978; Meenakumari and Nair 1988). Paul (1942) studied the growth of *B. amphitrite* in Madras harbor, where they reach a rostro-carinal diameter of 8.8 mm in 16 days. This rapid growth of tropical species immediately following settlement is important in ship fouling because when settlement occurs within the first few days after a ship has arrived in port, the barnacles will be quite large before the ship leaves in two to three weeks. Smith (1946) showed that large barnacles are able to survive a sea passage that is fatal to smaller individuals. Thus, rapid growth is presumably an important factor affecting the persistence of fouling on hulls.

John (1964) recorded rapid growth in October, slower growth in July–August, and highest growth in January to April coinciding with higher salinities in harbor areas. Nair (1967) found rostro-carinal diameters of 12.1 mm in April in 36 days. Meenakumari and Nair (1988) showed *B. amphitrite communis* attained 16.5 and 22 mm after 90 and 165 days, respectively. They computed theoretical growth curves (following von Bertalanffy) and found that observed growth agreed well with the computed growth. Growth rate was faster in the initial stages and slower in older barnacles.

A comparison of 15-day growth showed maximum values of 8.8 mm at Madras (Paul 1942), 6.5 mm at Cochin (Meenakumari and Nair 1988), and 5.5 mm at Visakhapatnam (Ganapati et al. 1958). For the same period, Nair (1967) recorded 5.4 mm and Balakrishnan (1977) 5 mm at Cochin. The average maximum growth after 45 days at Madras was 12.6 mm (Paul 1942), 9.2 mm at Visakhapatnam (Ganapati et al. 1958), and 8.7 mm at Cochin (Nair 1967, Meenakumari and Nair 1988). The slower growth rate at Cochin was ascribed to estuarine conditions at the harbor versus typical marine conditions at Madras and Visakhapatnam. *Balanus amaryllis euamaryllis* attained a basal diameter of 25 mm and height 28 mm in the Andamans (Karande 1978).

Sasikumar et al. (1991) found that *B. variegatus* grew 12 mm in diameter after 200 days on nickel, stainless steel, and aluminum panels at Kalpakkam. On mild steel panels, a maximum of 8 mm was attained in 15 days (exfoliation caused termination of the study).

Biomass

Data on biomass accumulation on similar materials under identical conditions are not available for comparison. However, a cursory evaluation of fouling biomass accumulation at different locations shows higher generation of biomass at Cochin. De (1984) made a comparison of biomass generated at tropical harbors, namely, Bombay, Kalpakkam, Cochin, and Port Blair and found that these ports are 12-month fouling ports. He reported that studies conducted by the Naval Chemical and

Metallurgical Laboratory, Bombay, showed a fouling accumulation of 5–6 kg/m^2 at Bombay, 8 kg/m^2 at Kalpakkam, and 7–8 kg/m^2 at Port Blair, on nontoxic panels. Biomass accumulation at Kakinada Bay (Rao and Balaji 1988) indicated that fouling was moderate to moderately heavy, the maximum recorded being 9.43 kg/m^2 wet weight on glass panels and 8.26 kg/m^2 on timber panels. In the Zuary Estuary, Anil and Wagh (1988) saw depth differences in the settlement intensity of barnacles that, in turn, contributed to increased biomass. From the offshore waters of Bombay High (Raveendran and Wagh (1988), maximum biomass was 0.06 kg/m^2. At Cochin, Meenakumari (1989) recorded a fouling load of 12 kg/m^2, Balasubramanayan et al. (1973) 10–15 kg/m^2 on Al M575 sheathed fishing boat hulls, and Ravindran and Pillai (1984) 21.9 kg/m^2 on Al M575 panels exposed in harbor waters. While adverse conditions prevailing in the Cochin harbor waters during monsoons restrict breeding and settlement of many fouling organisms, barnacles have a natural tendency to overcome them and to grow to maturity within a very short time. The higher values of weight accumulation recorded by different workers (Balasubrâmanayan et al. 1972, Ravindran and Pillai 1984, Meenakumari 1989) may be due to this. Even though all species contribute to the fouling biomass, the major portion is from barnacles and bivalves.

Conclusions

In spite of numerous studies on the effects of various ecological factors on barnacles in Indian waters, there are several areas that require further elucidation. Except for taxonomy, the Indian lepidomorph barnacles have received scant attention. Fecundity of different barnacle species needs to be investigated, in detail, in different regions with emphasis on environmental factors and substrate specificity because fecundity is related to competition for settlement and to effects of adverse circumstances. The adhesive strength of barnacles, including the lepidomorphs, is another area to be explored in detail as it plays an important role in community maintenance by resisting dislocation. The techniques for rearing barnacle larvae under controlled conditions for bioassay studies need to be intensified. Nontoxic methods of biofouling control, particularly for barnacles, are gaining momentum as environment friendly replacements of toxic chemicals are now in use. In this context, the settlement preferences of barnacle cyprids, their rugophilic behavior, gregareousness, and substratum preferences should be thrust areas in the studies of barnacle ecology. Finally, the attachment mechanism of barnacle cyprids is another topic needing extensive investigation as it relates to site selection, temporary attachment, and permanent settlement.

LITERATURE CITED

Alam, S.M., A.K. Khan, and R. Nagabhushanam. 1988. Marine biofouling at Ratnagiri coast, India. Pages 539–550 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam, eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Anil, A.C., and A.B. Wagh. 1988. Aspects of biofouling community development in the Zuari Estuary, Goa, India. Pages 529–537 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Antony Raja, B.T. 1959. Studies on the distribution and succession of sedentary organisms of the Madras Harbour. *J. Mar. Biol. Assoc. India* 1: 180–197.

Antony Raja, B.T. 1963. Observations on the rate of growth, sexual maturity and breeding of four sedentary organisms from Madras Harbour. *J. Mar. Biol. Assoc. India* 5(1): 113–132.

Balakrishnan, K.P. 1975. *Studies on the Biology of Cirripedes of the West Coast of India.* Ph.D. Thesis, University of Cochin, India.

Balakrishnan, K.P. 1977. Growth rate of *Balanus amphitrite* in Cochin Harbour area. Pages 313–315 in *Proceedings Symposium on Protection of Materials in the Sea.* NCML, Bombay. Defence Research and Development Organisation, Government of India.

Balasubramanyan, R., and T.R. Menon. 1963. Destruction of boat building timbers by marine organisms in the port of Cochin. I. Raft tests. *J. Mar. Biol. Assoc. India* 5(2): 294–310.

Balasubramanyan, R., N.U. Nair, and A.G.G.K. Pillai. 1972. The problem of marine fouling in the coastal waters of India and its economic implications with special reference to fishing fleet management. Pages 674–681 in R.F. Acker, B.F. Brown, J.R. De Palma, and W.P. Iverson, eds. *3rd International Congress on Marine Corrosion and Fouling,* Evanston, Ill. Northwestern University Press, Evanston, Illinois.

Barnes, H. 1956. Surface roughness and the settlement of *Balanus balanoides* (L.). *Arch. Soc. Zool. Bot. Feun. Vanamo* 10: 164–168.

Barnes, H., and M. Barnes. 1969. Seasonal changes in the acutely determined oxygen consumption and effect of temperature for three common cirripedes, *Balanus balanoides, Balanus balanus and Chthamalus stellatus. J. Exp. Mar. Biol. Ecol.* 4: 36–50.

Bhatt, Y.M., and D.V. Bal. 1960. New records of barnacles from Bombay shores. *Curr. Sci.* 29: 439–440.

Chandrasekharan, P., and R.B.C. Gnanajothi. 1988. Effect of first antennule ablation of feeding and anchoring activities of *Balanus tintinnabulum tintinnabulum* (Linne.). Pages 433–437. in M.F. Thompson, R. Sarojini, and R. Nagabhushanam, eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Coe, W.R., and W.E. Allen. 1937. Growth of sedentary organisms on experimental blocks and plates for nine years at Scripps pier. *Bull. Scripps Inst. Oceanogr. Tech. Ser.* 4(4): 101–136.

Crisp, D.J. 1965. Surface chemistry, a factor in settlement of marine invertebrate larvae. *Botanica Gothroburgensia* 3: 51–65.

Crisp, D.J. 1974. Factors influencing the settlement of marine invertebrate larvae. Pages 177–265 in P.T. Grant and A.M. Mackie, eds. *Chemoreception in Marine Organisms.* Academic Press, New York.

Crisp, D.J. 1976. Settlement responses in marine organisms. Pages 83–124 in R.C. Newell, ed. *Adaptation to the Environment.* Butterworth, London.

Crisp, D.J., and P.S. Medows. 1963. Adsorbed layers: The stimulus to settlement in barnacles. *Proc. R. Soc. Lond. B.* 158: 364–372.

Daniel, A. 1952. A new barnacle *Lepas bengalensis* from Madras. *Ann. Mag. Nat. Hist. Ser.* 12(5): 400.

Daniel, A. 1953. Some new cirripedes from the Madras coast. *J. Madras Univ. B.* 23(3): 219–226.
Daniel, A. 1954. The seasonal variations and the succession of the fouling communities in the Madras Harbour waters. *J. Madras Univ. B.* 24(2): 189–212.
Daniel, A. 1955a. The primary film as a factor in settlement of marine foulers. *J. Madras Univ. B.* 25: 189.
Daniel, A. 1955b. Gregarious attraction as a factor influencing the settlement of barnacle cyprids. *J. Madras Univ.* B 25(1): 97–107.
Daniel, A. 1956a. The Cirripedia of Madras coast. *Bull. Madras Govt. Mus.* 6(2): 1–40.
Daniel, A. 1956b. Colour as a factor influencing the settlement of barnacles. *Curr. Sci.* 25: 21–22.
Daniel, A. 1957. Illumination and its effect on the settlement of barnacle cyprids. *Proc. Zool. Soc. Lond.* 129: 305.
Daniel, A. 1958a. A new barnacle *Balanus (Semibalanus) madrasensis* N. sp. from fishing craft off Madras. *Ann. Mag. Nat. Hist.* 13(1): 305.
Daniel, A. 1958b. The development and metamorphosis of three species of sessile barnacles. *J. Madras Univ.* 28B: 23–47.
Daniel, A. 1962. On a new species of operculate barnacle (Cirripedia: Crustacea) from the gastropod mollusc *Murex* sp. from Porto Novo, Madras State. *Ann. Mag. Nat. Hist.* 13(5): 193.
Daniel, A. 1963. Factors influencing the settlement of marine foulers and borers in tropical seas. Pages 363–382 in *Proceedings First Summer School of Zoology (Simla 1961)*. Government of India, New Delhi.
De, C.P. 1984. Present state of technology for control of marine corrosion and fouling in tropical Indian waters. Page 497 in *Proceedings 6th International Congress on Marine Corrosion and Fouling (Marine Biology)*. Athens, Greece.
Dexter, S.C., J.D. Sullivan, J. Williams, and S. Watson. 1975. Influence of substrate wettability on the attachment of marine bacteria to wetted surfaces. *Appl. Microbiol.* 30: 298–308.
Dharmaraj, K., and N.B. Nair 1981. Biology of fouling in Neendakara Port, a tropical estuary in the south west coast of India. *Fish. Technol.* 18(2): 79–94.
Dhandapani, K., and S.A. Fernando. 1994. Fecundity of some sessile barnacles with emphasis of fugitive forms from Porto Novo, south India. Pages 133–140 in M.F. Thompson, R. Nagabhushanam, R. Sarojini, and M. Fingerman, eds. *Recent Developments in Biofouling Control.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.
Disalvo, L.H. 1971. Evaluation of early steps in the fouling sequence in relation to control of wettable film: film formation on glass surfaces. *Interim Report 1–7, University of California.* U.S. Naval Biomedical Research Laboratory.
Doochin, H.D. 1959. On the morphology of *Balanus improvisus* Darwin and *Balanus amphitrite niveus* Darwin during initial attachment and metamorphosis. *Bull. Mar. Sci. Gulf Carrib.* 1: 15–39.
Edmondson, C.H. 1944. Studies of fouling organisms in Kaneohe Bay. *Hawaiian Acad. Sci. Proc.*: 21–22.
Fernando, S.A., and K. Ramamoorthy. 1975. Reproductive biology of barnacles. *Bull. Dept. Mar. Sci. Univ. Cochin* 7: 721–732.
Fernando, S.A., and K. Ramamoorthy. 1977. Breeding of *Chthamalus malayensis* Pilsbry from Tranquebar (southeast coast of India). In *Proceedings: Protection of Materials in the Sea.* R. and D.O. Ministry of Defence, N.C.M.L., Bombay.
Fischer, E.C., V.J. Castelli, S.D. Rodgers, and H.R. Bleile. 1984. Technology for control of marine biofouling. Pages 261–299 in J.D. Costlow and R.C. Tipper, eds. *Marine Biodeterioration — An Interdisciplinary Study.* E. & F.N. Spon. Ltd., London.
Ganapati, P.N., M.V. Lakshmana Rao, and R. Nagabhushanam. 1958. Biology of fouling in the Visakhapatnam harbour. *Andhra Univ. Mem. Oceanogr.* 62 II: 193–209.

Ganapati, P.N., and D.G.V.P. Rao. 1962. Studies on the respiration of barnacles. The temperature characteristics of the respiratory movements in *Balanus amphitrite communis* (Darwin). *J. Anim. Morph. Physiol.* 9: 72–78.

Gerchakov, S.M., F.J. Roth, B. Sallman, L.B. Udey, and D.S. Marszalek. 1977. Observations on microfouling applicable to OTEC systems. Pages 63–75 in *Proceedings Ocean Thermal Energy Conversion (OTEC) Biofouling and Corrosion Symposium.*, Seattle, Washington.

Hiro, F. 1939. Studies on cirripedian fauna of Japan. IV. Cirripedes of Formosa (Taiwan) with some geographical and ecological remarks on the littoral forms. *Mem. Coll. Sci. Kyoto, Ser. B.* 15(2): 245–284.

John, P.A. 1964. Biology of *Balanus amphitrite communis* in the Cochin Harbour waters. *Fish. Technol.* 1(2): 189–201.

Karande, A.A. 1967a. On cirripede crustaceans (barnacles), an important fouling group in Bombay waters. *Proceedings Symposium on Crustacea. Mar. Biol. Assoc. India* 2/4: 1245–1253.

Karande, A.A., 1967b. Field and laboratory investigations on some marine fouling and boring organisms in Bombay Harbour. *Proceedings: Symposium on the Indian Ocean. Bull. Nat. Inst. Sci. India* 38: 612–622.

Karande, A.A. 1978. Marine fouling and timber deterioration in sub-oceanic islands of Andamans. *Indian J. Mar. Sci.* 7(1): 39–43.

Karande, A.A. 1987. Fouling biofilm development in harbour waters. *Adv. Aquat. Biol. Fish.*: 105–116.

Karande, A.A., and V.C. Palekar. 1963. Observation on the breeding activities of the shore barnacle *Chthamalus malayensis* (Pilsbry) in Bombay Harbour. *Def. Sci. J.* 13: 130–137.

Knight-Jones, E.W. 1951. Gregariousness and some other aspects of the settling behaviour of *Spirorbis. J. Mar. Biol. Assoc. U.K.* 30: 201–212.

Kuriyan, E.W. 1952. Notes on the attachment of marine sedentary organisms on different surfaces. *J. Zool. Soc. India* 34 (4): 689–692.

Kuriyan, G.K., and S. Mahadevan. 1953. A note on the effect of light and colour of the substrata on the settlement of barnacles. *J. Bombay Nat. Hist. Soc.* 50: 522–524.

Liberatore, G.L., and E.J. Dyckman. 1972. Antislime coatings. Part III. Pre-conditioning value of slime for barnacle attachment. DTNSRDC Report 3597.

Matheswari, R. and S.A. Fernando. 1989. Fecundity of epizoic barnacles. *Indian J. Invert. Zool. Aquat. Biol.* 1: 31–33.

Meenakumari, B. 1989. *Ecobiology of Fouling in the Cochin Harbour.* Ph.D. Thesis, University of Kerala, Trivandrum.

Meenakumari, B., and N.B. Nair. 1984. Ecology of fouling in Cochin Harbour, India. Pages 159–171 in *Proceedings 6th International Congress on Marine Corrosion and Fouling, Marine Biology.* Athens, Greece.

Meenakumari, B., and N.B. Nair. 1988. Growth of the barnacle *Balanus amphitrite communis* (Darwin) in Cochin backwaters. Pages 109–121 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam. eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Meenakumari, B. and N.B. Nair. 1994. The effects of slime film on barnacle settlement. Pages 3–9 in M.F. Thompson, R. Nagabhushanam, R. Sarojini, and M. Fingerman, eds. *Recent Developments in Biofouling Control.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Menon, N.R., R.J. Katty, and H.P.C. Shetty. 1977. Biology of marine fouling in Mangalore waters. *Mar. Biol.* 41: 127–140.

Morse, D.E. 1988. Trigger and amplifier pathways: Sensory receptors, transducers, and molecular mechanisms controlling larval settlement, adhesion, and metamorphosis in response to environmental chemical signals. Pages 453–462 in M.F. Thompson,

R. Sarojini, and R. Nagabhushanam, eds. Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Morse, A.N.C., and D.E. Morse. 1984. Recruitment and metamorphosis of *Haliotis* larvae are induced by molecules uniquely available at the surfaces of crustose red algae. *J. Exp. Mar. Biol. Ecol.* 75: 191–215.

Morse, D. E., and A.N.C. Morse, 1991. Enzymatic characterization of the morphogen recognised by *Agaricia bumilis* (scleractinian coral) larvae. *Biol. Bull.* 181: 104–122.

Nair, N.U. 1965. Marine fouling in Indian waters *J. Sci. Indian Res.* 24(9): 483–488.

Nair, N.U. 1967. The settlement and growth of major fouling organisms in Cochin Harbour. *Hydrobiol.* 30 (3/4): 303–512.

Nair, N.U., and N.B. Nair, 1987. Marine fouling dynamics in and around the Cochin Harbour. *National Seminar on Estuarine Management*, 4–5 June 1987. State Committee on Science, Technology & Environment, Trivandrum, India.

Nair, N.U., and A.G.G.K. Pillai. 1977. Observation on the composition of slime film and its influence on the settlement of certain marine fouling organisms in Cochin Harbour. Pages in 284–289 in *Proceedings Symposium on Protection of Materials in the Sea.* Naval Chemical and Metallurgical Laboratory, Bombay.

Nair, N.U., and K. Ravindran. 1994. Studies on chemosensor induced surface modifications on the control of biofouling dynamics, Pages 313–319 in M.F. Thompson, R. Nagabhushanam, R. Sarojini, and M. Fingerman, eds. *Recent Developments in Biofouling Control.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Nilsson-Cantell, C.A. 1938. Cirripedes from Indian Ocean in the Collection of the Indian Museum, Calcutta. *Mem. Indian Mus.* :13.

Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164: 262–270.

Paul, M.D. 1942. Studies on the growth and breeding of certain sedentary organisms in the Madras Harbour. *Proc. Indian Acad. Sci. B* 15(1): 1–42.

Pillai, N.K. 1958. Development of *Balanus amphitrite* with a note of the early larvae of *Chelonibia testudinaria. Bull. Centre Res. Inst. Univ. Kerala* 6: 117–130.

Pillai, K.K., and N.B.K. Nair. 1972. Reproductive biology of the sessile barnacle *B. a. communis* (Darwin) of the southwest coast of India. *Indian J. Mar Sci.* 1: 8–16.

Rao, D.G.V.P. 1975. *Studies on Respiration of Barnacles.* Ph.D. Thesis, Andhra University, Waltair.

Rao, D.G.V.P., Y. Prabhakara Rao, and V. Linga Murthy. 1981. Oxygen consumption and metabolic rate in relation to temperature in *Balanus tintinnabulum tintinnabulum* (L): *Indian J. Mar. Sci.* 10: 387–389.

Rao, D.G.V.P., Y. Prabhakara Rao, and V. Umadevi. 1988. Temperature related metabolism in some tropical barnacles. Pages 123–133 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam, eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Rao, K.S., and M. Balaji. 1988. Biological fouling at Port Kakinada, Godavari Estuary, India. Pages 551–574 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam, eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Rao, K.S., and M. Balaji. 1994. Observations on the development of test block communities at an Indian harbor. Pages 75–96 in M.F. Thompson, R. Nagabhushanam, R. Sarojini, and M. Fingerman, eds. *Recent Developments in Biofouling Control.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Raveendran, T.V., and A. B. Wagh. 1988. Studies of wood-boring organisms in coastal and offshore waters of the western Indian coast: a comparative account. Pages 575–586 in M.F. Thompson, R. Sarojini, and R. Nagabhushanam, eds. *Marine Biodeterioration — Advanced Techniques Applicable to the Indian Ocean.* Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi.

Ravindran, K., and A.G.G.K. Pillai. 1984. Observations of the interrelation on marine corrosion and fouling in a tropical environment (India). Pages 369–384 in *Proceeding 6th International Congress on Marine Corrosion and Fouling* (*Marine Biology*), Athens, Greece.

Rege, M.S., S.S. Joshi, and A.A. Karande. 1980. Breeding in *Balanus amphitrite amphitrite* Darwin inhabiting polluted waters off Bombay coast. *India J. Mar. Sci.* 9: 15–18.

Renganathan, T.K., N.B.K. Nair, and K. Dharmaraj. 1982. Ecology of marine fouling organisms in Carapad creek, Tuticorin bay, south east coast of India. *Indian J. Mar. Sci.* 11(2): 132–137.

Sasikumar, N., S. Rajagopal, Jayapaul Azriah, and K.V.K. Nair. 1989. Condenser cooling using seawater, a case study in Kalpakkam coastal waters. In *Water 89. Water Decade and Beyond,* 13–16 December. Communication International Associates Pvt. Ltd., Singapore.

Sasikumar, N., K.V.K. Nair, and J. Azariah. 1991. Some observations on barnacle growth and corrosion of materials in seawater. *Corrosion Prevent. Control* 1991: 145–150.

Smith, F.G.W. 1946. The effects of water currents upon the attachment and growth of barnacles. *Biol. Bull.* (Woods Hole) 90(1): 51–70.

Sundera Raj, B. 1927. The littoral fauna of Krusadai Island in the Gulf of Mannar, 'Cirripedia'. *Bull. Madras Govt. Mus. (ns)* 1(1): 111–115.

Udayakumar, M., and A.A. Karande. 1986. Adhesive strengths of some biofouling organsims. *Curr. Sci.* 55(14): 656–658.

Utinomi, H. 1960. On the world-wide dispersal of Hawaiian barnacle *Balanus amphitrite hawaiiensis* Broch. *Pacific Sci.* 14(1): 43–50.

Wallershaus, S. 1972. On the hydrography of the Cochin backwater, a south Indian estuary. *J. Mar. Biol. Assoc. India* 14: 487–495.

Weiss, C.M. 1947. The effect of illumination and stage of tide on the attachment of barnacle cyprids. *Biol. Bull.* 93: 240–249.

WHOI. 1952. Pages 1–388 in *Marine Fouling and Its Prevention.* U.S. Naval Institute, Washington, D.C.

Wilson, O.P. 1955. The role of micro-organisms in the settlement of *Ophelia bicornis* Savigny. *J. Mar. Biol. Assoc. U.K.* 34: 531–543.

Young, L.Y., and R. Mitchell. 1972. The role of the chemotactic response in primary film formation. Pages 617–623 in *Proceedings Third International Congress on Marine Corrosion and Fouling.* Northwestern University Press, Evanston, Illinois.