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REVIEW

Biotechnological investigation for the prevention of biofouling. I. Biological and biochemical principles for the prevention of biofouling

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ABSTRACT· The most important biological and biochemical methods with potential for the prevention of biofouling are described. Among these methods, the isolation of biogenic agents produced by several species of micro- and macroalgae and marine invertebrates with antibacterial, antialgal, antiprotozoan and antimacrofouling properties may be the most promising and effective method for the prevention of biofouling. The isolated substances with the most potent antifoulant activity are fatty acids, terpenes, terpenoids, lipoproteins, glycolipids, phenols, lactons, peptides and steroids. The advantage of the utilization of micro- and macroalgae for the isolation of biogenic agents is that algae can be cultivated in a short time in mass culture, independent of season. Furthermore, they can be manipulated to a large extent in the direction of the 'production of biogenic agents' However, the cultivation of micro- and macroalgae is very expensive. Marine invertebrates must be collected in certain seasons. This collection of marine invertebrates could lead to an uncontrolled exploitation of marine organisms and to a change in the balance of marine ecosystems. Therefore, determination of the chemical structure and the subsequent synthesis of the determined biogenic agents is necessary if marine invertebrates are to be used as producers of biogenic agents. Antifouling systems must be both environmentally safe and effective for at least 3 yr when formulated as antifouling paints. There have been a few attempts at this, but no applicable successes have been reported to date.

KEY WORDS: Antifouling · Biofouling Growth inhibition Marine bioactive agents · Macrofoulers · Microfoulers · Settlement

INTRODUCTION

What is biofouling?

Biofouling is one of the most important problems currently facing marine technology. In the marine environment any solid surface will become fouled. Materials submerged in seawater experience a series of discrete physical, chemical and biological events which results in the formation of a complex layer of attached organisms known as biofouling.

Loeb & Neihof (1975), Baier (1984) and Lewin (1984) have shown that the first event is the accumulation of an organic 'conditioning' film consisting of chemical compounds (mostly protein, proteoglycans and polysaccharides) making the surface wettable (Dexter 1978). This process occurs in the first minutes of the biological settlement (Fig. 1). After approximately 1 to 2 h, the colonization of bacteria involving 2 distinct phases, a reversible approach phase ('adsorption') and a nonreversible attachment phase ('adhesion'), occurs (Marshall 1980, Wahl 1989) (Fig 1). The first, reversible adsorption, is an instantaneous attraction which holds bacteria near the surface. The bacterial adsorption is essentially governed by physical forces: Brownian motion, electrostatic interaction, gravity, and van-der-Waal forces (Fletcher & Loeb 1979, Walt et al. 1985). The phenomenon is termed reversible because the organisms can easily be removed before substantial contact of cell surface has been made. The second, irreversible attachment phase can be made by bacteria that produce extracellular bridging polymer (e.g. poly-

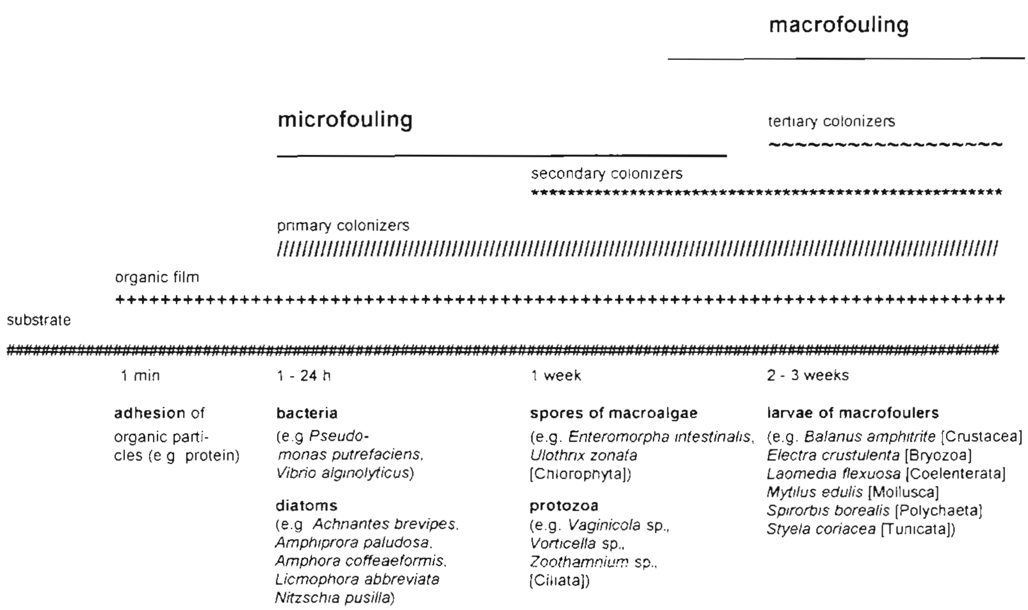

Fig. 1. Temporal structure of settlement

saccharide fibrils consisting mostly of glucose and fructose). It is known that these polysaccharide fibrils (slimes) are anchored to their chemical counterparts in the macromolecular film by lectins or divalent cations (Ca^{++}, Mg^{++}) (Costerton et al. 1978). With the establishment of covalent bonds between the bacterial glycocalix and the macromolecular film the adsorption phase blends into the adhesion phase (Wahl 1989). The growing bacterial lawn, composed of dead and living cells and their secreted 'slime', together with the macromolecular film, constitutes the so-called primary film (slime film) (Wahl 1989).

Diatoms, spores of macroalgae and protozoa appear after the development of the primary film (Fig. 1) with a clear quantitative dominance of the diatoms (Marshall et al. 1971, Caron & Sieburth 1981, Cuba & Blake 1983, Zahuranec 1991). Benthic diatoms are attached by mucus secretion (Cooksey et al. 1984, Ferreira & Seeliger 1985) and may densely cover wide substratum areas. While in the majority of observed events diatom colonization was always preceded by bacterial attachment (Little 1984), there may be exceptions (Sieburth & Tootle 1981, Maki et al. 1988). Attachment of spores of macroalgae is realized by species such as *Enteromorpha intestinalis* and *Ulothrix zonata*; protozoan colonizers belong mostly to the sessile or hemisessile forms (e.g. Ciliata) or are mobile predators of microorganisms, not being considered to be true epibionts.

Bacteria and diatoms represent the primary colonizers and spores of macroalgae and protozoa constitute the secondary colonizers in the process of microfouling (Fig. 1). A clear separation between microfouling and macrofouling is impossible because the spores of macroalgae belong to the macrofouling organisms (Von Oertzen et al. 1989), therefore there is an overlapping between micro- and macrofouling (Fig. 1). Larvae of macrofoulers (sessile marine organisms such as tunicates, coelenterates, bryozoans, barnacles, mussels, polychaetes), which are called tertiary colonizers, then attach to the microfouling film (Fig. 1) (Takazawa et al. 1992). Larvae of macrofoulers prefer to settle on surfaces coated with microbial and algal films (Colwell 1983).

According to micro- and macrofouling processes the following overlapping time sequence is observed: bacteria appear after approximately 1 to 2 h, diatoms after 24 h, spores of macroalgae and protozoa after 1 wk and larvae of macrofoulers after 2 to 3 wk (Von Oertzen et al. 1989). It seems that all micro- and macrofoulers produce adhesive substances necessary for their attachment to solid surfaces such as the hull of a ship (Cooksey et al. 1984). In the literature there are contradictory opinions on the question whether this sequence of events constitutes a real ecological succession or not (Little 1984).

The settlement of micro- and macrofoulers on the hulls of ships must be prevented for both economic and ecological reasons. The bacterial slime films and the large numbers of barnacles, mussels and tunicates which accumulate on ships increase drag forces and surface corrosion, thereby causing additional fuel, CO_2 emissions and maintenance costs (Gitlitz 1981).

Effect of the utilization of antifouling paints

In the efforts to avoid marine biofouling, antifouling paints are used, mostly with copper and tri-n-

butyltin (TBT) as very effective active agents (Willemsen & Ferrari 1993). The antifouling paints prevent biofouling by releasing effective biocides at a constant rate. Since the early 1970s, triaryltin and trialkyltin compounds have been increasingly used in antifouling paints because of their excellent ability to prevent marine organisms from becoming encrusted on ship bottoms and culturing nets (Suzuki et al. 1992).

TBT is used as a biocide in coatings in 3 different ways: in free association paints (biocide dispersed in a resinous matrix), in ablative paints (biocide is bonded in a less permeable matrix that gradually flakes off) and in self-polishing copolymers (SPC) (biocide is chemically bonded). Self-polishing organotin copolymer formulations have the best release rate characteristics of currently available antifouling paints and are capable of maintaining vessels free from macroscopic biofouling for periods of up to 5 yr (Christie & Dalley 1987). In use as an antifouling additive the use of marine paints containing the broad-spectrum poison TBT grew to an estimated 136 000 kg yr^{-1} by the late 1980s (Uhler et al. 1993). The worldwide application of TBT-based paints has caused a growing pollution of the environment and foods on a worldwide scale (Suzuki et al. 1992). TBT harms many forms of marine life other than fouling organisms, including economically important species like oysters. Thus, shell deformation of the Pacific oyster *Crassostrea gigas*, and little or no natural oyster larvae settlement on hard substrates, suggesting toxic effects in early life stages, were obseved in Arcachon Bay, France. More extreme deformations occur in the common dogwhelk *Nucella lapillus*, a species of thick-shelled snail found around the southwest peninsula of England. The occurrence of imposex (the development of male characteristics, notably a penis and a sperm duct, on females) was shown in centres of boating and shipping activities, which is a sign of decline (Oehlmann et al. 1993). Fewer females occur than would be expected, and juveniles and deposited egg capsules are scarce or absent, indicating a low reproductive capacity.

Due to risk in application of organotin antifouling coatings they have come under increasing governmental regulation in the United States and many western European countries (Price et al. 1992). This has initiated further development of TBT-free antifouling paints, containing herbicides, antibiotica, copper salts and other organic additives like amino-, azine- and thio-derivatives (Golchert 1993, Peterson et al. 1993). These TBT-free antifouling coatings are capable of maintaining ships free from biofouling for about 3 yr but none of these additives can compete with organotin containing SPCs (Golchert 1993).

Alternative methods for the prevention of biofouling

Due to present and expected future restrictive regulation on the use of TBT (Dalley 1987) and probably other polluting antifouling compounds there is a growing need for other methods of the prevention of biofouling. Several physical/mechanical, physical/chemical and biological/biochemical principles for the prevention of biofouling were used in the last 30 yr (Gerencser et al. 1962, Schulz & Subklev 1964, Kühl & Neumann 1969, Loeb & Neihof 1975, Characklis 1981, Dhar et al. 1981, Branscomb & Rittschof 1984, Fletcher & Baier 1984, Humphries et al. 1986).

It is the aim of the present work to describe and evaluate the most important biological/biochemical methods used for the prevention of settlement and to discuss the possibility of using biogenic agents produced by several marine organisms with antibacterial, antialgal, antiprotozoan and antimacrofouling properties for the prevention of biofouling.

BIOLOGICAL AND BIOCHEMICAL METHODS FOR THE PREVENTION OF BIOFOULING

Dissolution of adhesive substances by several enzymes

All biofouling organisms achieve their attachment by using adhesive substances, the chemical structure of which is quite similar for bacteria, diatoms, spores of macroalgae and macrofoulers (acid polysaccharides and glycoproteins) (Fletcher & Floodgate 1973, Haug 1976, Humphrey et al. 1979, Percival 1979, Daniel et al. 1987, Wigglesworth-Cooksey & Cooksey 1992). It is assumed that a dissolution of these substances would reduce the long-term attachment to solid surfaces (Christie et al. 1970, Dempsey 1981, Evans 1981, Cinti et al. 1987). Certain enzymes, like trypsin, chymotrypsin, pronase and α-amylase, are active in the weakening action on adhesion in the bacterium *Vibros proteolytica* and in zoospores of the green macroalga *Enteromorpha intestinalis* (Christie et al. 1970, Paul & Jeffrey 1985). Short-term exposure to the enzymes actinidin and pepsin can be used to separate the stalked epiphytic diatoms *Synedra tabulata* and *Licmophora* species from their brown or green algal hosts (Booth 1981). A variety of hydrolytic enzymes were tested for effects on barnacle settlement on solid surfaces (Rittschof et al. 1991). The majority of enzymes tested (cellulase, chitinase, collagenase, trypsin, chymotrypsin, carboxypeptidase A, B, Y) had little effect on settlement. But protease XI significantly inhibited the settlement of barnacles on polystyrene and glass surfaces, while papain had an inhibitory

effect on polystyrene surfaces only. The biotechnological production of these enzymes in large quantities is possible, but relatively expensive. Furthermore, the enzymes are not permanently stable and different enzymes are necessary to split the various adhesive substances. Therefore, the method of dissolution of adhesive substances is applied only partly in practice.

Intervention in the metabolism of fouling organisms

A well-balanced supply of calcium is necessary for a successful adhesion of bacteria, diatoms and spores of macroalgae (Marshall et al. 1971, Grant et al. 1973, Haug 1976, Fletcher 1979, Cooksey & Cooksey 1980, Cooksey 1981, Turakhia & Characklis 1989). The process of synthesis and secretion of adhesive substances leading to motility and adhesion in diatoms can be prevented by uncouplers of energy metabolism (CCCP, carbonyl cyanide 3-chlorophenyl hydrazone), protein synthesis inhibitors (cycloheximide), and compounds that interfere with Ca transport (D-600, α-isopropyl-α-[(N-methyl-N-homoveratryl)-γ-amino-propyl]-3,4-5-trimethoxy phenylacetonitrile) (Cooksey & Cooksey 1980, Cooksey 1981, Cooksey et al. 1984). The formation of sulfated polysaccharides responsible as gel for the attachment of the spores of green macroalgae can be blocked by the reduction of calcium and borate supply (Haug 1976). All these experiments, however, have been carried out only under laboratory conditions and without regard to antifouling aspects.

Competitive inhibition of receptors by offering specific lectin-like substances

It has been shown for many macrofouling organisms that special substances (e.g. insoluble protein-conjugates) can contact with corresponding receptors of the larvae and induce an attachment and a metamorphosis. By offering specific lectin-like substances, which have a stronger affinity to the receptors than the insoluble protein-conjugates, the attachment is affected (Morse 1984). It is also possible to inhibit adhesion processes by offering simple sugars to bacterial lectins (reversed process) (Corfield & Schauer 1982, Reuter et al. 1982, Imam et al. 1984, Sönnichsen 1993). These experiments have been performed only under laboratory conditions.

Negative chemotaxis

Numerous experimental results prove that special organic nontoxic substances (e.g acrylamide, benzoic, tannic and sialic acids) have a negative effect on the chemotaxis of bacteria, which results in an inhibition of bacterial attachment (Chet et al. 1975, Mitchell et al. 1975, Chet & Mitchell 1976). Chemotaxis acts as a form of gravity, holding motile bacteria close to biofouling surfaces (Mitchell & Kirchman 1984). The strong negative charged molecules of sialic acid are able to hold bacteria at distance, so that fixed association with the surface is blocked up (Corfield & Schauer 1982, Reuter et al. 1982, Sönnichsen 1993). Successful field experiments have not yet been carried out.

Biogenic agents

Many marine organisms produce biogenic agents with antibacterial, antialgal, antifungal, antiprotozoan and antimacrofouling properties to defend themselves against robbers and settlement in the marine environment. Therefore, the production and isolation of biogenic substances from marine organisms seem to be the most promising and effective methods for the prevention of biofouling.

BIOGENIC AGENTS AND THEIR EFFECTS ON FOULING ORGANISMS

Definition of biogenic agents

Numerous living organisms, including microorganisms, fungi, plants and animals, are able to synthesize biogenic agents. These biogenic agents are synthesized in the secondary metabolism of the producer and are not directly essential for its life. They serve animals as protection from enemies (e.g. robbers), plants as protection against feeding and microorganisms in the suppression of growth and reproduction of other microbes. Teuscher & Lindequist (1988) defined biogenic agents as follows: biogenic agents are chemical compounds which are synthesized by living organisms and which, if they exceed certain concentrations, cause temporary or permanent damage or even the death of other organisms by chemical or physicochemical effects. The concentration which causes damage and the extent of this damage are determined by the type of substance, the place and type of application, the duration of the effect, the individual sensitivity of the corresponding organism and other factors.

Marine organisms (especially micro- and macroalgae and marine invertebrates) were investigated in the last decade with growing intensity regarding chemistry and pharmacology of their active agents. The sub-

stances isolated in this connection belong, above all, to the groups of fatty acids, terpenes, terpenoids, lipoproteins, glycolipids, phenols, lactons, alkaloids and peptides. Depending on the screening methods used, the effects of the isolated potential drugs were mainly antibacterial, antiviral and antifungal. According to Ireland et al. (1993), ca 35% of these biogenic compounds are produced by micro- and macroalgae and ca 65% by marine invertebrates. The ability of marine organisms to produce biogenic substances with antibacterial, antialgal, antiprotozoan and antimacrofouler properties could be used in the prevention of biofouling.

Biogenic agents isolated from micro- and macroalgae

An immense number of substances with antibacterial, antiviral, antifungal and pharmacological properties have been isolated from micro- and macroalgae, analyzed, and tested for medical purposes in the last few years. Tables 1 to 5 give an overview of the existence of special biogenic compounds in micro- and macroalgae and their effect on the growth of several bacteria, algae, fungi, protozoa and macrofoulers. Several biogenic compounds, such as bromophenols, malyngolides, aponin, cyanobacterin, hapalindoles, fischerellin, galactosyldiacylglycerols, tjipanazoles and scytophycins, isolated from special species of Cyanophyceae that have either antibacterial, antialgal, antifungal or antiprotozoan effects, are given in Table 1. Macrofoulers were not tested. Tables 2 & 3 show bioactive substances (e.g. fatty acids, glycolipids/lipoproteins, terpenes/carbohydrates, goniodomin, chlorophyll *c* and α-linolenic acid) isolated from special species of Chrysophyceae, Dinophyceae and Chlorophyceae that have inhibitory effects on the growth of bacteria, algae, fungi and protozoa. Macroalgae like Phaeophyceae, Chlorophyceae, Conjugatophyceae and Charophyceae also produce biogenic substances with antibacterial, antialgal, antifungal, antiprotozoan and antimacrofouling effects (Tables 4 & 5). The special biogenic substances listed in the tables were isolated from micro- and macroalgae and tested predominantly with regard to antibacterial, antialgal and antifungal activities and not with regard to antifouling aspects. Effects on the growth of macrofoulers (e.g. polychaetes, mussels) were investigated only with some species of macroalgae (*Laminaria digitata*, *Costaria costatum*, *Undaria pinnatifida*; Tables 4 & 5). In contrast to micro- and macroalgae, higher plants are well documented as antifouling agents (Sawant et al. 1992, Sawant & Wagh 1994).

The cultivation of micro- and macroalgae as well as the extraction of biogenic agents is expensive. However, algae can be used very well as 'extraction organisms' because they can be cultivated in a short time in mass culture independent of season and can be manipulated to a large extent in the direction of 'production of biogenic agents'.

Table 1. Existence and effects of biogenic agents isolated from Cyanophyceae (microalgae)

Species	Biogenic agent	Effects				Source
		Anti-bacterial	Anti-algal	Anti-fungal	Anti-protozoan	
Calothrix brevissima	Bromophenols	×	×			Pedersen & Da Silva (1973)
Lyngbya majuscula	Malyngolide	×				Cardllina et al. (1979)
Gomphosphaeria aponina	Aponin		×			Eng-Wilmot et al. (1979)
Anabaena flos-aquae	?				×	Snell (1980)
Scytonema hofmanni	Cyanobacterin		×			Mason et al. (1982), Gleason & Paulson (1984), Gleason & Baxa (1986)
Fischerella muscicola	?		×			Flores & Wolk (1986)
Scytonema pseudohofmanni	Scytophycins			×		Ishibashi et al. (1986)
Hapalosiphon fontinalis	Hapalindoles		×	×		Moore et al. (1987)
Synechocystis leopoliensis	Methanolic extracts	×				Cannell et al. (1988)
Oscillatoria sp.	Ether extracts		×			Baghi et al. (1990)
Fischerella muscicola	Fischerellin		×			Gross et al. (1991)
Nostoc muscorum	Methanolic extracts			×		De Mule et al. (1991)
Nostoc muscorum	Aqueous extracts	×				Bloor & England (1991)
Nostoc linckia	Cyanobacterin LU-1		×			Gromov et al.(1991)
Phormidium tenue	Galactosyldiacylglycerols		×			Murakami et al. (1991)
Tolypothrix tjipanasensis	Tjipanazoles			×		Bonjouklian et al. (1991)
Scytonema ocellatum	Tolytoxin (scytophycin)			×		Patterson & Carmeli (1992)

Table 2. Existence and effects of biogenic agents isolated from Chrysophyceae and Dinophyceae (microalgae)

Species	Biogenic agent	Effects				Source
		Anti-bacterial	Anti-algal	Anti-fungal	Anti-protozoan	
Chrysophyceae						
Ochromonas dancia	Fatty acids?		×			Aaronson & Bensky (1967)
Prymnesium parvum	Glycolipid/lipoprotein				×	Paster (1973), Shilo (1979)
Dinophyceae						
Protogonyaulax tamarensis	Terpenes/carbohydrates	×				Burkholder et al. (1960)
Prorocentrum micans	Terpenes/carbohydrates	×				Burkholder et al. (1960)
Goniodoma sp.	Goniodomin	×				Sharma et al. (1968)
Peridinium bipes	Fatty acids, chlorophyll *c*	×	×			Uchida et al. (1988)
Prorocentrum lima	Polyether compounds			×		Nagai et al. (1990)
Dinophysis fortii	Polyether compounds			×		Nagai et al. (1990)
Gambierdiscus toxicus	Polyether compounds			×		Nagai et al. (1990)

Biogenic agents isolated from marine invertebrates

In recent years several comprehensive accounts of antifungal, antibacterial, antialgal, antiviral and pharmacological activities of biogenic substances isolated from several species of marine invertebrates have been published (Targett et al. 1983, Bakus & Kawaguchi 1984, Wahl 1987, Sears et al. 1990, Ireland et al. 1993). From 1977 to 1987, 1595 bioactive compounds were isolated from marine invertebrates worldwide, predominantly sponges, coelenterates, bryozoans and ascidians (Ireland et al. 1993). Tests for medical purposes were performed, for instance, with bryostatines from bryozoans with antitumoral properties, with didemnines from ascidians with antiviral and antitumoral activities and palytoxin from corals with neurotoxic effects (Ireland et al. 1993). Furthermore, a variety of sessile marine invertebrates contain secondary metabolites affecting the settlement of fouling organisms. It is known that representatives of Porifera, Cnidaria and Tunicata are rarely overgrown by epiphytic organisms. They frequently produce high concentrations of biogenic agents with potent antifoulant activities. Especially octocorals and sponges are a rich source of compounds that act as antifoulants (Willemsen & Ferrari 1993).

Targett et al. (1983) determined that *Leptogorgia virgulata* and *L. setacea* contain high concentrations of homarine, which inhibited growth of the biofouling diatom *Navicula salinicola*. Extracts of *L. virgulata* and *Neosimnia uniplicata*, a snail of *L. virgulata*, strongly inhibited the settlement of the barnacle *Balanus amphitrite*. Bioassay-directed purification of *L. virgulata* extracts led to the identification of 2 diterpenoid hydrocarbons, pukalide and epoxypukalide, as antifouling agents (Gerhart et al. 1988). Many investigations with new species of octocorals and sponges result in the discovery of new compounds, e.g. herbacin, a new furanosequiterpene from the marine sponge *Dysidea herbacea* (Sarma et al. 1986).

A series of chemical compounds, like lactons, fatty acids, bromopyrroles, homarine, herbacin, pukalides,

Table 3. Existence and effects of biogenic agents isolated from Chlorophyceae (microalgae)

Species	Biogenic agent	Effects		Source
		Antibacterial	Antialgal	
Stichococcus mirabilis	Fatty acids?	×		Harder & Oppermann (1953)
Protosiphon botryoides	Fatty acids?	×		Harder & Oppermann (1953)
Chlamydomonas reinhardii	Fatty acids		×	Proctor (1956)
Hydrodictyum reticulatum	Fatty acids	×		Olfers-Weber & Mihm (1978)
Dictyosphaerium pulchellum	Methanolic extracts	×		Cannell et al. (1988)
Klebsormidium crenulatum	Methanolic extracts	×		Cannell et al. (1988)
Chlorokybus atmophyticus	Acetone extracts	×		Cannell et al. (1988)
Pleurastrum terrestre	Methanolic extracts	×		Cannell et al. (1988)
Staurastrum gracile	Methanolic extracts	×		Cannell et al. (1988)
Chlorococcum sp.	Aqueous extract	×		Ohta et al. (1993)
Chlorococcum HS-101	α-Linolenic acid	×		Ohta et al. (1993)

Table 4. Existence and effects of biogenic agents isolated from Phaeophyceae (macroalgae). *S.*: *Spirorbis*; *M.*: *Mytilus*

Species	Biogenic agent	Effects: Anti-bacterial	Anti-algal	Anti-fungal	Antimacro-fouling on:	Source
Laminaria digitata	?	×			*S. inornatus*	Al-Ogily & Knight-Jones (1977)
Fucus vesiculosus	Phlorotannins	×				Glombitza & Lentz (1981)
Cytoseira balearica	Lipid extract	×		×		Caccamese et al. (1981)
Zanardinia prototypus	Lipid extract	×		×		Caccamese et al. (1981)
Pelvetia canaliculata	Phlorotannins	×				Glombitza & Klapperich (1985)
Laminaria saccharina	Unsaturated fatty acids	×				Rosell & Srivastava (1987)
Desmarestia ligulata	Unsaturated fatty acids	×				Rosell & Srivastava (1987)
Sargassum horneri	Mucilage extract		×			Tanaka & Asakawa (1988)
Costaria costatum	Glycerols				*M. edulis*	Katsuoka et al. (1990)
Fucus vesiculosus	Methanolic extract	×				Lustigman & Brown (1991)
Fucus endentatus	Methanolic extract	×				Lustigman & Brown (1991)
Fucus spiralis	Methanolic and chloroform extract	×				Lustigman & Brown (1991) Lustigmann et al. (1992)
Laminaria agardhii	Methanolic and chloroform extract	×				Lustigman et al. (1992)
Sargassum wightii	Chloroform extract	×				Sastry & Rao (1994)
Padina tetrastromatica	Chloroform extract	×				Sastry & Rao (1994)

peptides, steroids and saponins, isolated from several species of Porifera, Cnidaria, Tunicata and Mollusca with antibacterial, antialgal activities and activities preventing the settlement by macrofouling organisms are listed in Table 6. In some cases, the structure of the active agent has not yet been clarified (Standing et al. 1984, Ware 1984, Rittschof et al. 1985, Sears et al. 1990, Mary et al. 1991) (Table 6). Even the results of tests of 51 sponge extracts under field conditions for their ability to prevent biofouling showed the potential antifouling activity of most of the tested crude extracts (Willemsen & Ferrari 1983) containing compounds of unknown structure. It can be seen from Table 6 that antibacterial and antialgal effects (effects against microfouling) are predominantly observed for homarine, fatty acids, peptides and steroids from *Polysyncraton lacazei* (ascidian) and *Leptogorgia virgulata* (coral) (Targett et al. 1983, Wahl 1987).

Potent antimacrofouling activity against the blue mussel *Mytilus edulis* and the barnacle *Balanus amphitrite* and other macrofouling organisms was found in extracts of several sponges (*Lissodendoryx*

Table 5. Existence and effects of biogenic agents isolated from Rhodophyceae, Chlorophyceae, Conjugatophyceae and Charophyceae (macroalgae). *M.*: *Mytilus*

Species	Biogenic agent	Effects: Anti-bacterial	Anti-algal	Anti-fungal	Anti-protozoan	Antimacro-fouling on:	Source
Rhodophyceae							
Laurencia obtusa	Laurencienyne	×					Caccamese et al. (1981)
Centroceras clavulatum	Lipid extract	×		×			Caccamese et al. (1981)
Sphaerococcus coronopifolius	Lipid extract	×		×			Caccamese et al. (1981)
Gracilaria corticata	Chloroform extract	×					Sastry & Rao (1994)
Acanthophora delilei	Chloroform extract	×					Sastry & Rao (1994)
Chlorophyceae							
Codium coralloides	Lipid extract	×		×			Caccamese et al. (1981)
Caulerpa ashmeadii	Terpenoids	×					Paul et al. (1987)
Undaria pinnatifida	Glycerols					*M. edulis*	Katsuoka et al. (1990)
Enteromorpha linza	Methanolic extract	×					Lustigman & Brown (1991)
Conjugatophyceae							
Spirogyra sp.	Tannin?				×		Misra & Sinha (1979)
Charophyceae							
Chara globularis	Dithiolan, trithian		×				Wium-Andersen et al. (1982)

Table 6. Existence and effects of antifouling agents isolated from special species of marine invertebrates. Species: *Agaricia lamarcki, Balanus amphitrite, Bugula neritina, Hippoporina americana, Hydroides norvegica, Laomedia bistriata, Mytilus edulis, Serpula vermicularis*

Species	Biogenic agent	Effects: Anti-bacterial	Effects: Anti-algal	Effects: Antimacro-fouling on:	Source
Porifera					
Xestospongia halichondriodes	?			*B. neritina*	Ware (1984)
Placortis halichondroides	Lactons, phenols, cyclic peroxides			*A. lamarcki*	Porter & Targett (1988)
Lissodendoryx isodictyalis	Terpenoids?			*B. amphitrite*	Sears et al. (1990)
Agelas conifera	Bromopyrroles			*B. amphitrite*	Keifer et al.(1991)
Dysidea herbacea	Herbicin (furanosesquiterpene)			*L. bistriata* *H. americana* *H. norvegica* *S. vermicularis*	Sarma et al. (1991)
Phyllospongia papyracea	Fatty acids			*M. edulis* *B. amphitrite*	Goto et al. (1992)
Cnidaria (Anthozoa)					
Leptogorgia setacea	Homarine		×		Targett et al. (1983)
L. virgulata	Homarine		×		Targett et al. (1983)
L. virgulata	?			*B. amphitrite*	Standing et al. (1984)
L. virgulata	?			*B. amphitrite*	Rittschof et al. (1985)
Muricea fruticosa	Muricins (saponis)		×		Bandurraga & Fenical (1985)
Renilla reniformis	Diterpenes			*B. amphitrite*	Keifer et al. (1986)
Renilla reniformis	?			*B. amphitrite*	Rittschof et al. (1986)
L. virgulata	Pukalide, epoxypukalide (diterpenoids)			*B. amphitrite*	Gerhart et al. (1988)
Suberogorgia suberosa	?			*B. amphitrite*	Mary et al. (1991)
Spongodes sp.	?			*B. amphitrite*	Mary et al. (1991)
Solenocaulon tortuosum	?			*B. amphitrite*	Mary et al. (1991)
Echinogorgia complexa	?			*B. amphitrite*	Mary et al. (1991)
Juncella juncea	?			*B. amphitrite*	Mary et al. (1991)
Mollusca (Gastropoda)					
Neosimnia uniplicata	?			*B. amphitrite*	Gerhart et al.(1988)
Chordata (Ascidiacea)					
Polysyncraton lacazei	Fatty acids, peptides, steroids	×	×	Eggs of sea urchins	Wahl (1987)

isodictyalis, Phyllospongia papyracea, Agelas conifera, Dysidea herbacea) and corals (e.g. *Leptogorgia virgulata, L. setacea, Renilla reniformis, Suberogorgia suberosa, S. tortuosum* and others) (Table 6).

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Marine Productivity Division, Maurice-Lamontagne Institute, Dept of Fisheries and Oceans Canada, CP 1000, Mont-Joli, PQ, Canada G5H 3Z4
Early life history, growth and development in fishes; fish-zooplankton interactions

Bunt, J. S.
4/6 McDonald Street, Potts Point, NSW 2011, Australia
Mangrove systems; reef studies

Caron, D. A. Ⓢ
Biology Dept, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA
Microbial ecology; trophic relations between planktonic protozoans and other heterotrophic and photosynthetic organisms; pelagic detrital aggregates

Collos, Y. Ⓢ
Laboratoire d'Hydrobiologie, Université de Montpellier CC 093, F-34095 Montpellier Cedex 5, France
Nitrogen cycling and primary production

Conover, R. J.
Marine Ecology Laboratory, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2
Zooplankton biology

Cushing, D. H.
Ministry of Agriculture, Fisheries and Food, Fisheries Laboratory, Lowestoft, Suffolk NR33 OHT, England
Productivity of the sea; fish-population dynamics; biological oceanography

Deibel, D.
Ocean Sciences Center, Memorial Univ. of Newfoundland, St. John's, NF, Canada A1C 5S7
Zooplankton ecology/nutrition, gelatinous ecology/physiology

de Jonge, V.
National Institute for Coastal and Marine Management (RIKZ), PO Box 207, 9750 AE Haren, The Netherlands
Estuarine and coastal processes; microphytobenthos and eelgrass; process and impact of resuspension; eutrophication

Dolan, J.
Observatoire des Sciences de l'Univers, Université Paris VI-CNRS, Station Zoologique, BP 28, F-06230 Villefranche-sur-Mer, France
Microbial ecology, interactions of bacteria, protists and metazoa

Elliott, M. Ⓢ
Dept of Applied Biology, Institute of Estuarine and Coastal Studies, The University, Hull HU6 7RX, England
Structure and function of fish and benthic communities

Feller, R. J.
Biology and Marine Science, Belle W. Baruch Institute for Marine Biology and Coastal Research, Columbia, SC 29208, USA
Trophic dynamics and energetics of crustaceans; feeding and digestion of fishes; benthic ecology of meiofauna; ecological applications of immunology and serology

Fenchel, T. Ⓢ
Marine Biological Laboratory (Univ. of Copenhagen), DK-3000 Helsingør, Denmark
Population biology; microbial ecology

Field, J. G.
Univ. of Cape Town, Zool. Dept, Rondebosch 7700, Republic of South Africa
Dynamics of nearshore ecosystems

Floc'h, J. Y.
Université de Bretagne Occidentale, Lab. d'Ecophysiologie et de Biochimie des Algues Marines, Faculté des Sciences, 7 av. V. Le Gorgeu, BP 452, F-29275 Brest Cedex, France
Ecophysiology and biochemistry of macroalgae

Foster, M. S. Ⓢ
Moss Landing Marine Laboratories, California State Univ., PO Box 450, Moss Landing, CA 95039-0450, USA
Population and community ecology of macroalgae

Fowler, S. W. Ⓢ
International Atomic Energy Agency, Marine Environment Laboratory, 19, Ave des Castellans, BP 800, MC-98012 Monaco Cedex
Particle flux; biogeochemistry

Fuhrman, J. Ⓢ
Marine Biology Res. Section, Dept of Biological Sciences, Univ. of Southern California, Los Angeles, CA 90089-0371, USA
Planktonic microbial ecology. Productivity and growth of microorganisms, especially bacteria

Furness, R. W.
Dept of Zoology, The Univ. of Glasgow, Glasgow G12 8QQ, Scotland
Ecology of sea birds

Furuya, K.
Faculty of Bioresources, Mie Univ., 1515 Kamihama, Tsu 514, Japan
Phytoplankton ecology; community structure, dynamics

Gage, J. D. Ⓢ
Dunstaffnage Marine Research Laboratory, PO Box 3, Oban, Argyll PA34 4AD, Scotland
Benthos of deep sea and temperate coasts

Gray, J. Ⓢ
Institutt for Marinbiologi og Limnologi, Univ. Oslo, Postboks 1064, Blindern, Oslo 3, Norway
Soft-sediment ecology

Haedrich, R. L. Ⓢ
Memorial Univ. of Newfoundland, St. John's, NF, Canada A1B 3X9
Zoogeography; natural history of fish

Hansen, B.
Roskilde Univ., Institute I, Life Sciences & Chemistry, PO Box 250, DK-4000 Roskilde, Denmark
Laboratory and in situ studies on zooplankton; secondary production (grazing, growth, energetics, feeding behaviour)

Harding, G. C.
Marine Ecology Laboratory, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2
Crustacean ecology (incl. deep sea)

Heck, K. L., Jr Ⓢ
Marine Environmental Sciences Consortium, Dauphin Island Sea Lab., PO Box 369-370, Dauphin Island, AL 36528, USA
Benthic ecology, emphasis on seagrass ecosystems

Holm-Hansen, O. Ⓢ
Scripps Inst. of Oceanography, Univ. of California, La Jolla, CA 92093-0202, USA
Polar ecology; chemical oceanography; photosynthesis

Hoppe, H.-G.
Institut für Meereskunde, Univ. Kiel, Düsternbrooker Weg 20, D-24105 Kiel, Germany
Microbiology, including methods; microbial plantology

Hughes, R. N. Ⓢ
School of Animal Biology, Univ. College North Wales, Bangor, Gwynedd LL57 2UW, Wales
Ecological energetics (particularly feeding)

Karlson, R. H.
School of Life and Health Sciences Ecology Program, Univ. of Delaware, Newark, DE 19716, USA
Population and community ecology of benthic invertebrates

Kiørboe, T.
Danish Institute for Fisheries and Marine Res., Charlottenlund Castle, DK-2920 Charlottenlund, Denmark
Biological oceanography; physical and biological processes in the pelagial with emphasis on copepods and fish larvae

Klumpp, D.
Australian Institute of Marine Science, PMB No. 3, Townsville M.C., Q 4810, Australia
Trophodynamics; animal nutrition, energy and nutrient budgets; nutrient cycling; primary productivity; fish biology; seagrass, coral reef, kelp bed ecosystems

Kneib, R. T.
Marine Institute, The Univ. of Georgia, Sapelo Island, GA 31327, USA
Population and community dynamics of estuarine fishes and invertebrates; growth and mortality during early life of estuarine species; evaluation of coastal wetlands

Landry, M. R. Ⓢ
Dept of Oceanography, Univ. of Hawaii, Manoa, 1000 Pope Rd, Honolulu, HI 96822, USA
Food web interactions; zooplankton ecology

Lawrence, J. M. Ⓢ
Dept of Biology, Univ. of South Florida, Tampa, FL 33620, USA
Reproduction of invertebrates; nutrition

Levings, C. Ⓢ
West Vancouver Laboratory, 4160 Marine Drive, West Vancouver, BC, Canada V7V 1N6
Estuarine ecology of macrobenthos and fish

Lewis, J. B.
Dept of Biology, McGill Univ., Stewart Biology Bldg, 1205 Dr. Penfield, Montreal, PQ, Canada H3A 1B1
Coral-reef ecology; tropical marine biology

Lewis, M. R.
Dept of Oceanography, Dalhousie Univ., Halifax, NS, Canada B3H 4J1
Biological oceanography; phytoplankton physiology; modelling of physical and biological processes

Lobel, P. S.
Marine Biological Laboratory, Woods Hole, MA 02543, USA
Fish ecology, behavior, biogeography; coral reefs; fisheries and oceanography

Luoma, S. N.
US Dept of the Interior, Geological Survey, Water Resources Div., 345 Middlefield Rd, Menlo Park, CA 94025, USA
Feeding ecology of deposit feeders; geochemistry of trace elements in sediments

Marcus, N. H.
Dept of Oceanography, Florida State Univ., B-169, Tallahassee, FL 32306-3048, USA
Zooplankton ecology; biology and genetics of invertebrate populations; rhythms

Mauchline, J.
Scottish Marine Biological Ass., Dunstaffnage Marine Research Laboratory, PO Box 3, Oban, Argyll PA34 4AD, Scotland
Deep-sea ecology; radioactive pollution

Nelson, D. M.
College of Oceanography, Oregon State Univ., Oceanography Admin. Bldg 104, Corvallis, OR 97331, USA
Phytoplankton ecology; nutrient cycling

Newell, S. Y. Ⓢ
The Univ. of Georgia, Marine Institute, Sapelo Island, GA 31327, USA
Ecology of fungi and bacteria; decomposition

Nybakken, J.
Moss Landing Marine Laboratories, California State Univ., PO Box 450, Moss Landing, CA 95039-0450, USA
Ecology of molluscs; community structure of soft-sediment invertebrates

Oviatt, C. A.
Graduate School of Oceanography, Univ. of Rhode Island, Narragansett, RI 02882-1197, USA
Systems ecology; primary production; nutrient and carbon cycling; role of higher trophic levels; impact of pollutants on coastal systems

Pawlik, J.
The Univ. of North Carolina at Wilmington, Wilmington, NC 28403-3297, USA
Ecology and biology of invertebrate larvae; settlement; recruitment; life histories; dispersal; natural products

Peterson, C. H. Ⓢ
Institute of Marine Science, Univ. of N. Carolina at Chapel Hill, 3407 Arendell Street, Morehead City, NC 28557, USA
Marine benthic ecology; population biology

Platt, T.
Marine Ecology Laboratory, Bedford Institute of Oceanography, PO Box 1006, Dartmouth, NS, Canada B2Y 4A2
Phytoplankton ecology; primary production

Purcell, J. E. Ⓢ
The Univ. of Maryland Systems, Center for Environmental and Estuarine Studies, PO Box 775, Cambridge, MD 21613, USA
Zooplankton ecology and behavior; trophic dynamics; prey selection. Competition for space among benthic invertebrates

Rassoulzadegan, F. Ⓢ
Observatoire des Sciences de l'Univers, Université Paris VI-CNRS, Station Zoologique, BP 28, F-06230 Villefranche-sur-Mer, France
Microbial ecology (food webs, microbial loop); pico- and nanoplankton; planktonic flagellates and ciliates; carbon flux

Reise, K.
Biologische Anstalt Helgoland, D-25992 List/Sylt, Germany
Benthos ecology

Rivkin, R. B.
Ocean Sciences Centre, Univ. of Newfoundland, St. John's, NF, Canada A1C 5S7
Microbial ecology; polar planktonic processes; lower food web dynamics

Savidge, G.
The Queen's Univ. of Belfast, Marine Biology Station, The Strand, Portaferry, Co. Down, Northern Ireland
Phytoplankton ecology; primary production; photosynthesis

Schneider, D. C. Ⓢ
Newfoundland Institute for Cold Ocean Science, Memorial Univ. of Newfoundland, St. John's, NF, Canada A1B 3X7
Dynamics of large organisms; ecology of sea birds

Sherr, B. & E. Ⓢ
College of Oceanography, Oregon State Univ., Oceanography Admin. Bldg 104, Corvallis, OR 97331, USA
Microbial food webs; trophic roles of phagotrophic protozoans

Southward, A. J.
Plymouth Marine Laboratory, Citadel Hill, Plymouth PL1 2PB, England
Rocky-coast ecosystems; deep-sea ecosystems

Stoecker, D. K. Ⓢ
Horn Point Environmental Laboratories, PO Box 775, Cambridge, MD 21613, USA
Microzooplankton particularly ciliates; secondary production

Stoner, A. W.
Caribbean Marine Research Center, 805 East 46th Place, Vero Beach, FL 32963, USA
Shallow-water benthic ecology; associations between marine macrofauna and macrophytes; predator-prey relations

Tenore, K. R. Ⓢ
Chesapeake Biological Laboratory, PO Box 38, Solomons, MD 20688-0038, USA
Benthic ecology and bioenergetics; production; food chains of detritus-based systems

Thayer, G. W. Ⓢ
Ecosystem Structure Branch, Southeast Fisheries Center, Beaufort, NC 28516-9722, USA
Wetlands ecology, incl. submerged seagrasses and emergent marshes; production and utilization of detritus

Underwood, A. J. Ⓢ
School of Biol. Sci., Univ. Sydney, Zoology Building, Sydney, NSW 2006, Australia
Experimental intertidal and subtidal ecology; behavior; life cycles of sessile invertebrates

Wangersky, P. J. Ⓢ
SEOS, Univ. of Victoria, PO Box 1700, Victoria, BC, Canada V8W 2Y2
Organic matter in sea water; theoretical population dynamics; geochemistry; chemical oceanography

Warwick, R. M.
Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, England
Structure and functioning of benthic communities; meiofaunal ecology; energy flow

West, J. A.
School of Botany, Univ. of Melbourne, Parkville, VIC 3052, Australia
Reproductive dynamics of red algae; fine structure and parasites of algae

Williams, R.
Plymouth Marine Laboratory, Prospect Place, West Hoe, Plymouth PL1 3DH, England
Plankton ecology; community structure, population dynamics

Wu, B. L.
First Institute of Oceanography, State Oceanic Administration, PO Box 98, Qingdao, People's Republic of China
Ecology and morphology of coelenterates, echinoderms and polychaetes. Development and reproduction of polychaetes and phoronids

OCEAN MANAGEMENT

Ahmed, S. I.
School of Oceanography, WB-10, Univ. of Washington, Seattle, WA 98195, USA
Biofouling; application of biotechnology to marine systems

Bernhard, M.
ENEA, PO Box 316, I-19100 La Spezia, Italy
Radioactive and conventional pollution

Brown, B. E.
Dept of Biology, The University, Newcastle-upon-Tyne NE1 7RU, England
Effects of man-made and natural disturbances on coral reefs

Eisler, R.
US Dept of the Interior, Fish and Wildlife Service, Laurel, MD 20708, USA
Toxicology and pollution

Elliott, M. Ⓢ
Dept of Applied Biology, Institute of Estuarine and Coastal Studies, The University, Hull HU6 7RX, England
Marine pollution assessment and control

Fisher, N. S.
Marine Sciences Research Center, State Univ. of New York, Stony Brook, NY 11794-5000, USA
Pollutant effects on plankton; radioecology

Fowler, S. W. Ⓢ
International Atomic Energy Agency, Marine Environment Laboratory, 19, Ave des Castellans, BP 800, MC-98012 Monaco Cedex
Pollution effects on zooplankton; radioecology

Gray, J. Ⓢ
Institutt for Marinbiologi og Limnologi, Univ. Oslo, Postboks 1064, Blindern, Oslo 3, Norway
Pollution effects on benthos animals

Luoma, S. N.
US Dept of the Interior, Geological Survey, Water Resources Div., 345 Middlefield Rd, Menlo Park, CA 94025, USA
Bioaccumulation of trace contaminants (principally trace elements and radionuclide waste products)

Mauchline, J.
Scottish Marine Biological Ass., Dunstaffnage Marine Research Laboratory, PO Box 3, Oban, Argyll PA34 4AD, Scotland
Radioactive pollution

McLusky, D. S. Ⓢ
Dept of Biological Sciences, Univ. of Stirling, Stirling FK9 4LA, Scotland
Biological effects of pollutants (petro-, chemical, organic enrichment)

Peterson, C. H. Ⓢ
Institute of Marine Science, Univ. of N. Carolina at Chapel Hill, 3407 Arendell Street, Morehead City, NC 28557, USA
Fisheries management and ecology

Polikarpov, G. G.
Institute of Biology of South Seas, Academy of Sciences Uk. SSR, 2, Nahimov St., Sevastopol 335000, Ukraine
Chemical ecology, radioecology, radiotracers, pollution; protection of sea life

Sherman, K. Ⓢ
US Dept of Commerce, NOAA, Northeast Fisheries Center, 28 Tarzwell Dr., Narragansett, RI 02882, USA
Fisheries ecology; fishery resources; zooplankton

Wu, B. L.
First Institute of Oceanography, State Oceanic Administration, PO Box 98, Qingdao, People's Republic of China
Effects of pollutants on benthic organisms