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CHEMICAL ECOLOGY AND CHEMORECEPTION
 IN THE MARINE ENVIRONMENT

by

A.M. MACKIE and A.I. MITCHELL
 Natural Environment Research Council,
 Institute of Marine Biochemistry, St. Fittick's Road,
 Aberdeen AB1 3RA, Scotland, U.K.

R E S U M E

- On considère les principes de l'écologie chimique et de la chemoréception et on donne des exemples de substances composées qui possèdent des activités biologiques, surtout dans le contrôle de l'alimentation. On a isolé et caractérisé beaucoup de produits naturels marins, mais on n'a déterminé qu'en peu de cas leurs rôles biologiques ou écologiques. D'autre part, on a décrit un assortiment de réactions produites chimiquement dans lesquelles le médiateur chimique ne s'est pas identifié. —

Entre les substances composées qu'on a déjà identifiées, beaucoup sont des produits du métabolisme secondaire, lesquels par leur caractère même se sont révélés comme très intéressants pour le chimiste organique. Pourtant il y a d'autres cas qui impliquent des composés simples du métabolisme primaire. Les phagostimulants pour le turbot, Scophthalmus maximus, par exemple, sont l'inosine et l'inosine 5'-monophosphate; pour le Dover sole, Solea solea, le phagostimulant est le glycine bétaine.

A B S T R A C T

- The basic principles of chemical ecology and chemoreception will be discussed and examples given of compounds known to possess biological activity, particularly in the control of feeding behaviour. Many hundreds of marine natural products have been isolated and characterized, but in only a few instances have their biological or ecological roles been determined. Conversely, a wide variety of chemically mediated behavioural responses have been described where the chemical mediator remains unidentified. —

Of the compounds which have so far been identified, many are products of secondary metabolism which, by their very nature, have proved the most interesting to the organic chemist. However, in other instances rather simple compounds of primary metabolism are involved. Inosine and inosine 5-monophosphate, for example, are the feeding stimulants for the turbot, Scophthalmus maximus while glycine betaine is the feeding stimulant for the Dover sole, Solea solea.

M O T S - C L E S : Ecologie chimique, Chemoréception, Télémédiateurs chimiques.

K E Y W O R D S : Chemical ecology, Chemoreception, Semiochemicals.

INTRODUCTION

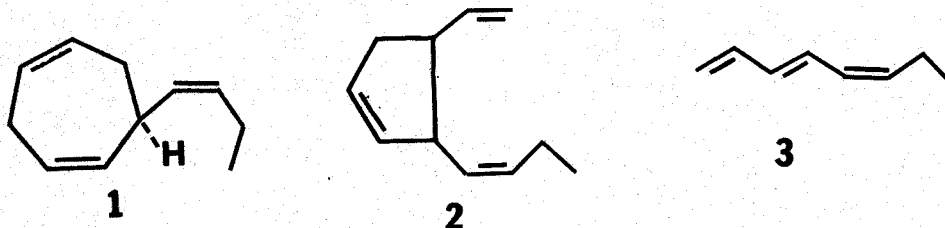
The term chemical ecology is used to describe chemical interactions between organisms while the term chemoreception is restricted to those interactions involving primary or secondary chemosensory cells in the receiving organism. The chemical signals have been termed semiochemicals (Regnier, 1971) or chemical telemediators (Aubert, 1971) and can be divided into two groups; pheromones, where the releasing and receiving individuals belong to the same species (Karlson & Luscher, 1959); and allelochemicals, where the two individuals are of different species (Whittaker & Feeny, 1971). The allelochemicals are further divided into allomones, which give an adaptive advantage to the releasing species, and kairomones which give an adaptive advantage to the receiving species (Whittaker & Feeny, 1971).

Many natural products have been isolated from marine plants and animals, but in only a few instances have their ecological roles been ascertained (for a recent review, see Daloz *et al.*, 1980). Two approaches to the study of marine natural products are possible. One, favoured by organic chemists, involves the isolation and characterization of marine natural products, perhaps followed by the study of their biological activities. The second more logical approach starts with a known biological activity or behavioural response, followed by the subsequent purification of the active material. In this article, the signals will be grouped according to their ethological effects.

1. PHEROMONES IN REPRODUCTION

1.1. Gamete attractants

The male gametes of marine algae are attracted by substances released by eggs of the same species. All the gamete attractants so far characterized have been polyunsaturated linear or cyclic hydrocarbons-ectocarpene (1) from Ectocarpus siliculosus, multifidene (2) from Cutleria multifida and fucoserratenene (3) from Fucus serratus (Muller, 1977).



1.2. Spawning-inducing pheromones

There is a considerable amount of evidence for the involvement of

spawning-inducing pheromones in marine invertebrates that undergo epidemic spawning. In the crown-of-thorns starfish Acanthaster planci, gamete release by one individual induces other ripe starfish to spawn, and a cell-free fraction was obtained from extracts of gametes which induced spawning (Beach et al., 1975). The active material was dialysable and heat stable, but no further information is available concerning its chemical nature.

1.3. Sex attractants

Once again little is known of the chemical nature of sex attractants although observations in the aquarium and in the sea indicate that these are widespread throughout the crustaceans and molluscs. Ryan (1966) demonstrated that the pre-moult female of the swimming crab Portunus sanguinolentus secretes a sex pheromone in her urine that attracts adult males. Kittredge et al., (1971) have studied the courtship and mating behaviour of three brachyuran crabs, and found that pre-moult females of all species elicited courtship from males. Further studies indicated that the moulting hormone crustecdysone is the sex pheromone in these species.

1.4. Sex-determining pheromones

In snails of the genus Crepidula the female releases a substance which attracts the sexually undifferentiated young into her vicinity, and which subsequently prolongs the initial male phase (Coe, 1953). Larvae of the echiuran Bonellia fulginosa develop into females if they settle on an inert substrate, but develop into smaller, parasitic males if they settle on a female of the same species (Nigrelli et al., 1967). A photodynamically-active pigment, bonellin identified as a chlorin of unusual structure, was isolated from Bonellia, (Pelter et al., 1976). This pigment in the presence of light lysed erythrocytes, destroyed echinoid gamete function and arrested the development of Bonellia eggs (Agius et al., 1979). However, it remains to be determined whether this chlorin is the pheromone responsible for growth inhibition and masculinization.

1.5. Spawning migration

Perhaps the most spectacular example of chemoreception is to be found in the spawning migration of salmon. Mid-ocean navigation would appear to be by means of the detection of the earth's magnetic field (Rommell & McCleave, 1973) but when the fishes reach the estuary, chemoreception is used to find their way to the home stream or tributary (Hasler, 1971). The electrical responses of the olfactory system of adult spawning chum salmon, Oncorhynchus keta, were found to vary on stimulation with different stream waters (Kaji et al., 1975).

Nordeng (1971) has proposed that the homing of the char, Salvelinus alpinus, in Norway was influenced by pheromones secreted in the skin mucus of fry and descending smolts of the same population. Behavioural (Selset & Døving, 1980) and electrophysiological (Døving et al., 1980) investigations indicate, however, that these "pheromones" may originate from sources other than the skin mucus.

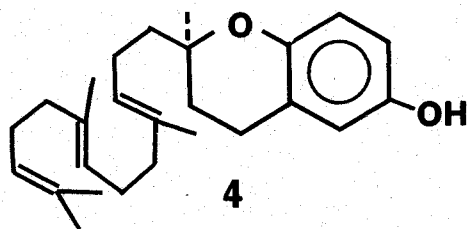
2. FACTORS CONTROLLING SETTLEMENT AND SITE SELECTION

2.1. Settlement of larvae

The larvae of many marine invertebrates must settle upon a suitable

substrate before they can metamorphose into the adult form, and the choice of settlement site is chemically controlled (Crisp, 1974). Experiment with the barnacle Balanus balanoides indicated that the settlement response is due to a substance originating in adult barnacles and adsorbed to the rock surrounding them. Fractionation of an extract of barnacles yielded two components active in promoting settlement (Gabbott & Larman, 1971). One component was a protein, associated with a nucleic acid fraction, while the other was probably a polysaccharide-protein complex.

The larvae of the hydroid Coryne uchidae settle on the alga Sargassum rotile, and two compounds, δ -tocotrienol (4) and its 2,3-epoxide are active in inducing settlement (Kakinuma et al., 1977). In the case of the association of the abalone Haliotis rufescens and certain red algae, settlement is induced by γ -aminobutyric acid and phycoerythrobilin, both covalently bound to proteins in the intact algae (Morse et al., 1979). As in the case of the barnacles, direct contact with the "adsorbed" settlement factor is necessary under natural conditions in the sea.



2.2. Symbiosis and commensalism

Many symbiotic or commensal associations have been documented, and there is evidence for a chemical attraction of the symbiont towards the host organism (Dimock & Davenport, 1971). In one case at least, the host starfish was attracted to its symbiotic worm, indicating that the association is mutualistic (Wagner et al., 1979).

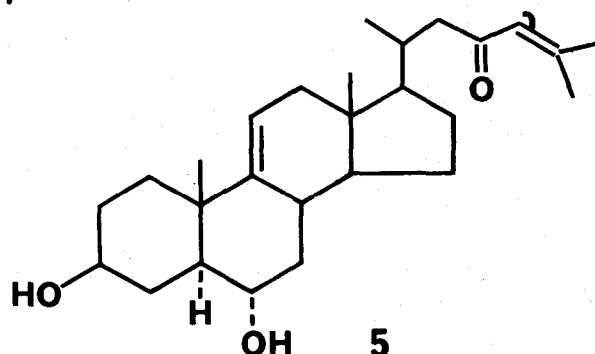
Stewart (1970) has studied the chemotactic response of the polychaete Ophiodromus pugettensis towards its host, the starfish Patiria miniata. Two low-molecular weight components were required for activity, the components normally being bound to a larger carrier molecule. One component, with a molecular weight of approximately 180, caused an increase in the non-directional locomotory activity of the polychaete, while the other component, molecular weight approximately 280, elicited the chemotactic response.

3. PREY-PREDATOR INTERACTIONS AND FEEDING

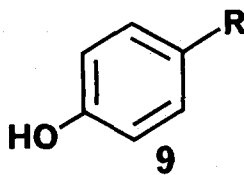
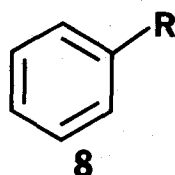
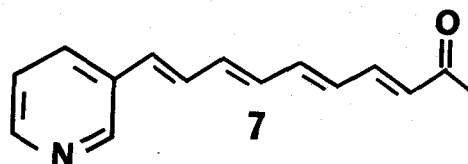
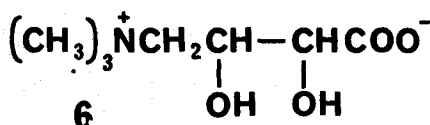
3.1. Escape responses

Predatory starfish induce avoidance or escape responses in many potential prey organisms. Most of the responding animals are molluscs, but sensitive echinoderms and coelenterates have also been reported. The response can be induced at a distance, but the most violent reactions are observed following contact with the starfish. Extracts of the starfish are also effective, and the active material present in the starfish Marthasterias glacialis which induces escape reactions in the whelk Buccinum undatum, the scallop Chlamys opercularis and the brittle star Ophiothrix fragilis is a mixture of saponins (Mackie et al., 1968; Mackie, 1970). Acid hydrolysis of the saponin yielded the parent steroids, marthasterone (5) and its 24,25-dihydro derivative (Turner et al., 1971; Smith et al., 1973).

Saponins are also responsible for the escape response of the snail Melagraphia aethiops to the starfish Coscinasterias calamera (Laurenson, 1970). Escape reactions by molluscs have been observed in the presence of predatory gastropods and Laurenson (1970) has shown that the escape response of M. aethiops to the thaid Haustrum haustorium is caused by urocanylcholine, originating in the hypobranchial gland.



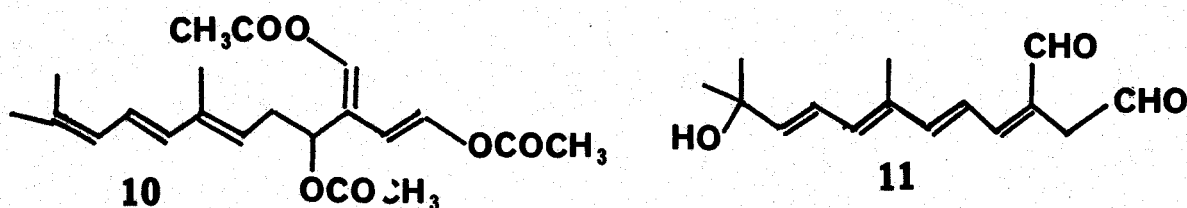
Alarm pheromones are employed by several marine organisms. When an individual of the colonial sea-anemone Anthopleura elegantissima is injured, a substance is released which causes other members of the species to contract (Howe & Sheikh, 1975). The active material, anthopleurine (6), has been shown to be a betaine, closely related to carnitine.



The carnivorous sea-slug Navanax inermis follows mucus trails laid down by individuals of its own species and by numerous prey opisthobranchs. If an individual is injured or attacked, a gland deposits a yellow secretion onto the mucus trail which has the effect of inducing immediate trail-breaking by other members of the species. The yellow secretion has been shown to contain three active methylketones, navenones A, (7), B (8) and C (9) (Sleper & Fenical, 1977).

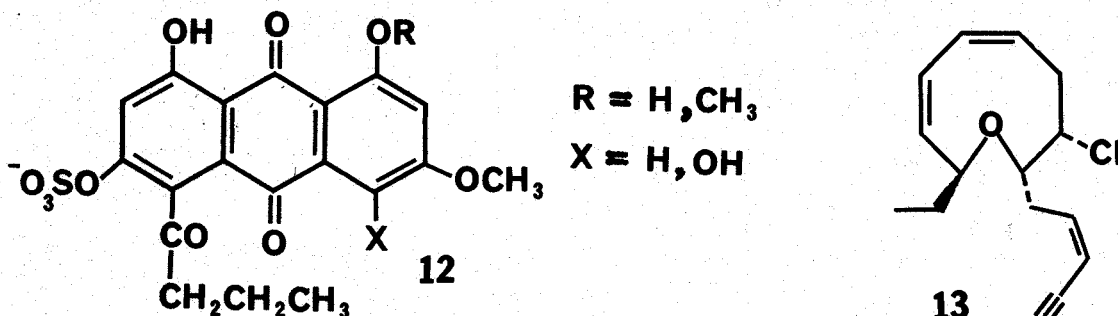
3.2. Defensive secretions

Many marine plants and animals produce compounds which render them unpalatable to herbivores and carnivores. Saponins present in the eggs and larvae of the crown-of-thorns starfish Acanthaster planci make them unpalatable to planktivorous fishes (Lucas et al., 1979) and the saponins of Coscinasterias tenuispina act as feeding deterrents for the Dover sole, Solea solea (Mackie & Mitchell, in preparation). Herbivorous Caribbean fishes do not eat the green alga Rhypocephalus phoenix and the feeding deterrents have been identified as two linear sesquiterpenoids, rhipocephalin (10) and rhipocephenal (11) (Sun & Fenical, 1979).



Crinoids or sea fans are in general avoided by fish and other predators, and polyketide sulphates (12) have been isolated from comatulid crinoids which act as feeding deterrents for several species of fish (Rideout *et al.*, 1979). These polyketides have an anthraquinone structure and Rideout *et al.*, (1979) reported that anthraquinone 2-sulphonate itself acted as a feeding deterrent. Anthraquinones such as carminic acid and the dyes Alizarin Red S and Acid Blue 45 also served as feeding deterrents for the Dover sole (Mackie & Mitchell, in preparation).

A medium ring haloether, brasilenyne (13), has been isolated from the opisthobranch, *Aplysia brasiliiana* and this compound acts as a feeding deterrent against several species of fish (Kinnel *et al.*, 1979).



3.3. Food attractants and feeding stimulants

The chemical control of feeding behaviour has been studied in considerable detail in the coelenterates. Chemicals present in the body fluids of the prey organism and released by penetration of nematocysts stimulate ingestion of the food. Proline and the tripeptide reduced glutathione are the commonest feeding activators, although certain coelenterates are stimulated by valine or glutamine (Lenhoff & Lindstedt, 1974).

In higher animals, feeding behaviour may be controlled by several chemical factors: attractants, incitants (biting factors) and stimulants (swallowing factors). Visual feeders are, by definition, attracted to their food by sight and long-range chemical attraction is not involved. However, in animals such as the lobster, *Homarus gammarus*, the chemical senses are used to detect food, and mixtures of chemicals serve as the attractant (Mackie, 1973). The eel, *Anguilla japonica*, is attracted by mixtures of L-amino-acids, although these mixtures were not as effective as the extract of short-necked clam upon which they were based (Konosu *et al.*, 1968). On contrast, two specific food attractants for Caribbean reef fish have been isolated from molluscs by Sangster *et al.*, (1975). Arcamine (14) was obtained from the mussel *Arca zebra* and strombine (15) from the conch *Strombus gigas*.

Table 1. Composition of chemical mixture, based upon the analysis of an extract of squid muscle (Mackie, 1973).

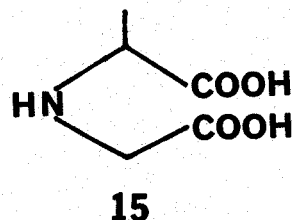
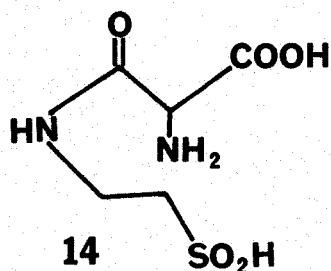
	g		g
taurine	0.370	L-arginine	0.250
L-aspartic acid	0.020	L-lysine HCl	0.032
L-glutamic acid	0.058	L-histidine HCl	0.016
L-proline	1.610	L-tyrosine	0.024
glycine	0.980	L-phenylalanine	0.032
L-alanine	0.300	betaine HCl	1.000
L-threonine	0.048	TMAO HCl	1.250
L-serine	0.036	TMA HCl	0.100
L-valine	0.040	hypoxanthine	0.052
L-methionine	0.040	inosine	0.028
L-isoleucine	0.032	AMP	0.044
L-leucine	0.060	L-(+)-lactic acid	0.100

The components of the mixture were dissolved in 40 ml distilled water, adjusted to pH 6.5 by the addition of NaHCO_3 and made to a final volume of 60 ml.

Table 2. Sea bass, Dicentrarchus labrax, mean weight 15g. Feeding stimulant activity of chemical mixture and constituents.

Test fraction	Moist diet eaten/100g/day (g) Mean \pm S.E.M.
Complete chemical mixture	6.62 \pm 0.34
Amino-acid mixture	5.50 \pm 0.32
Non-amino-acid components	0
Aromatic and basic amino-acids	0
Neutral and acidic amino-acids	5.05 \pm 0.70
Neutral amino-acids	4.20 \pm 0.76
Neutral amino-acids (D-forms)	0.27 \pm 0.18
Proline + glycine	0.67 \pm 0.40
Neutral amino-acids minus proline, glycine	0

The dry diet was prepared by mixing the following ingredients: vitamin-free casein, 55g; dextrin, 10g; -cellulose, 12.7g; D-glucose, 5g; cod-liver oil, 3g; capelin oil, 6g; binder (Edifas B, ICI, Glasgow), 5g; vitamin mixture (Cowe *et al.*, 1972), 0.5g; food dye (Sunset Yellow, ICI, Manchester), 0.1g, 30 ml of the solution of feeding stimulant mixture (Table 1) and 140 ml distilled water was added and thoroughly mixed.



Mixtures of L-amino-acids are the feeding stimulants for the rainbow trout, Salmo gairdneri (Adron & Mackie, 1978) and for the plaice, Pleuronectes platessa, and dab, Limanda limanda, although in the latter two species other chemicals enhanced the activity (Mackie, 1981). Inosine and inosine 5'-monophosphate are the specific feeding stimulants for the turbot, Scophthalmus maximus, other nucleosides and nucleotides tested being ineffective (Mackie & Adron, 1978). All these fish are primarily sight-feeders, while the Dover sole, Solea solea, detects its food at a distance, by means of smell or taste, and glycine betaine in this case acts as attractant and feeding stimulant for the adult animal (Mackie et al., 1980). In the juvenile, amino-acids are required in addition to glycine betaine.

The puffer fish, Fugu pardalis, is also stimulated to ingest food by the presence of glycine betaine plus amino-acids (Ohsugi et al., 1978) and this mixture has been implicated in the feeding behaviour of the pigfish, Orthopristis chrysopterus (Carr et al., 1977), the red sea bream, Chrysophrys major (Goh & Tamura, 1980) and the shrimp, Palaemonetes pugio (Carr, 1978).

The chemical nature of the feeding stimulant of sea bass, Dicentrarchus labrax, a sight-feeder, has also been studied using the same diets and chemical mixtures as with the Dover sole (Table 1). Essentially all the feeding stimulant activity resided in the L-amino-acid fraction, the non-amino-acid components being completely inactive (Table 2). Subdivision of the amino-acids showed that the mixture of neutral L-amino-acids was highly active, while the corresponding D-amino-acids were inactive. However, the two major neutral amino-acids, proline and glycine, were together essentially inactive, as were the remaining neutral amino-acids, indicating synergistic effects (Table 2).

4. ALLELOPATHIC EFFECTS

Rather less obvious, but still an aspect of chemical ecology, are various chemicals produced by phytoplankton and micro-organisms which influence the metabolism, growth or behaviour of other organisms. Lucas (1947) proposed the term ectocrine for the external metabolites of phytoplankton which control competition and integration in aquatic ecosystems. The filtration rate of Daphnia is slowed by substances released by dense senescent cultures of Chlorella and other algae, and this might be an explanation for the observed reduction in the density of zooplankton in high densities of phytoplankton in the sea and lakes (Lucas, 1947; Ryther, 1954). Hardy (1936) was the first to report that there was a "patchiness" in the distribution of plankton in the sea and this finding could indicate the involvement of chemical telemediators, but there is no direct evidence for this.

Many other chemically mediated interactions between bacteria, algae and animals have been reported and the interested reader is referred to a recent review by Gauthier and Aubert (1981).

5. CHEMOSENSORY MECHANISMS

The first step in chemoreception is thought to involve the reversible binding of the chemical stimulus to the receptor surface, which results in the production of a nerve impulse. Cagan and his co-workers have studied the "binding" of ^{14}C -labelled amino-acids to fractions obtained from the olfactory epithelium of the rainbow trout Salmo gairdneri (Cagan & Zeiger, 1978), and from the barbels of the catfish, Ictalurus punctatus (Krueger & Cagan, 1976; Zelson & Cagan, 1979). In the rainbow trout system, there was a reasonable correlation between extent of binding of the labelled amino-acids and their reported relative stimulatory effectiveness measured electrophysiologically.

However, Brown & Hara (1981) have also studied the "accumulation" of ^{14}C -labelled amino-acids by a fraction from olfactory epithelium of S. gairdneri and they have concluded that, while saturability, reversibility and affinity were reasonably consistent with receptor criteria, the kinetics of the association were not.

Tissue from areas of the turbot (Scophthalmus maximus) buccal cavity rich in taste buds reversibly "bind" ^{14}C -labelled inosine, the feeding stimulant for this fish. There was a highly significant correlation between feeding stimulant activity and the ability to compete with ^{14}C -inosine for a series of fifteen nucleosides and nucleotides (Mitchell, in preparation). It is hoped to study the kinetics of binding of this system.

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