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MARINE ECOLOGY AND NATURAL PRODUCTS

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Abstract - Marine natural products are grouped according to their functions. Products involved in the interactions between organisms are divided into those whose function is based either on their physical properties or on their chemical properties. The latter group are considered in detail and particular emphasis is given to the role of chemical communication in the marine environment.

INTRODUCTION

Marine natural products have been classified according to their chemical structure (1) or according to the organisms from which they have been obtained (2). An alternative approach is to group them according to their functions, on which depend their importance in marine ecology. Compounds of ecological significance may be conveniently, if not absolutely, divided into those whose functions relate solely to their producers and those whose functions are dependent upon the interaction of two or more organisms. Compounds of the first type include all the normal metabolic equipment of the organism and such products as blood and photosynthetic pigments, vitamins, cytochromes, buoyancy, insulation and anti-freeze materials and energy storage compounds. These marine products generally differ little from those present in, or produced by, organisms in other environments. It is the second type of compound, whose function depends upon the interaction with another organism, that I shall consider. These compounds function by virtue either of their physical properties (e.g. as reflectors and pigments) or their chemical properties (e.g. as food attractants and pheromones). It is the latter group with which I shall be particularly concerned.

FUNCTIONS DEPENDENT UPON PHYSICAL PROPERTIES

Acoustic functions

The production and reception of sounds by many marine animals is still poorly understood. The only situation in which natural products appear to play a significant role (apart from purely mechanical effects) is in the head structures of whales and dolphins, where heterogeneous lipid structures, some of which are unusually rich in the branched chain fatty acid iso-valeric acid, are postulated to act as acoustic lenses and windows in the transmission and reception of ultrasonic pulses. In these processes the detailed role of the branched and straight chain low molecular weight lipids has not yet been resolved (3,4,5).

Photic functions

The absorption, perception, reflection and emission of light by marine organisms depends upon the various natural products functioning as pigments, reflecting materials and luciferins. The light environment in the sea is dependant not only upon the physical characteristics of pure sea water but also upon the properties of substances dissolved in it. The most important material in this respect is 'Gelbstoff', a generic name given to material of high ultraviolet absorbance whose major origin is probably the metabolic products of phytoplankton (especially polyphenols) including humic and fulvic acids (6). Gelbstoff, together with the effects of suspended material, is largely responsible for the greenish colour of coastal and highly productive oceanic areas and has obvious consequences for the visibility and vision of organisms in such waters.

Reflective materials produced by marine organisms depend for their effectiveness on their refractive indices and arrangement (7-9). In fishes the material most commonly utilised in specular reflectors is the purine guanine, in crystalline form. This provides the iridescent silvering of the surface of so many epi- and mesopelagic species, the purpose of the silvering almost invariably being camouflage (10). Reflectors are also present in the eyes of many marine organisms in the form of *tapeta lucida* whose function is to increase the sensitivity of the eye in low light levels. The tapeta may also be composed of guanine, as in the scallop *Pecten* (11) and many elasmobranchs (12), but where diffuse rather than specular reflectance is concerned lipid spheres are also frequently employed (13). The

lipids used are generally triglycerides, in the sandtrout largely glyceryl tridocosahexaenoate (14). Tapetal spheres of an unidentified non-lipid and non-purine material occur in some other fishes (13). Cephalopods utilise chitin as their reflecting material both in the epidermis and the eyes (8) though its identity has not been conclusively demonstrated. Reflecting materials present in the iridophores (and eyes) of many fishes and crustaceans may be of more varied composition including pterins (15), xanthine, hypoxanthine and uric acid (16). Reflectors in the photophores of many marine animals are generally formed of guanine or chitin and their function may include alteration of the spectral composition of emitted light (17).

The function of many marine animal pigments is the spectral modification of reflected light by the differential absorption of incident light, though a function in terms of selective advantage has been demonstrated for very few of the coloured natural products present in marine organisms. The main groups of natural products utilised for pigmentary purposes by marine organisms are the quinones, melanins, ommochromes, carotenoids and tetrapyrroles (18, 19).

Quinonoid pigments are largely restricted to the echinoderms (an evolutionary quirk of metabolism that remains unexplained) though their recent identification in polychaetes (20, 21) may be indicative of a wider, as yet unrecognised, distribution. The quinones of all five recent classes of echinoderms have been examined by several groups of workers (1, 22) but it should be noted that the ecological value of these pigments has not been convincingly demonstrated though their function as "cryptic odours" has been suggested (123). The pigments may also accumulate in the calcareous tissues of specific predators e.g. the sea otter and horned shark (19).

Melanins are common in marine animals of almost all groups, though particularly so among the deep-sea fishes, providing a protective colouration closely equivalent in effect to black velvet. The visible pigment density in species of the fish Cyclothone closely parallels their depth distribution; the deeper the species the darker is its colour, leaving little doubt as to its function. Dense accumulation of melanin in fish stomachs and peritoneum may prevent luminous food revealing the presence of the predator to other animals. Melanin deposits control the directionality of light emission both in light organs utilising symbiotic luminous bacteria and in many simple fish photophores which lack reflectors. Cephalopod ink is based on melanin and may act as both a visual and olfactory distraction (see 123). Other dark brown and purple pigments, particularly in cephalopods and crustaceans (23) may be ommochromes whose name derives from their discovery in insect (and crustacean) eyes. They undoubtedly play important roles in colour responses (especially in cephalopod chromatophores) and in the optics of the arthropod and molluscan eye but whether their redox capabilities serve any other physiological purpose (e.g. in Urechis eggs) is not known (18, 24).

The use of tetrapyrroles as pigmentary materials is not widespread, nor are there any known cases of their presence within chromatophores. Linear tetrapyrroles (or bile pigments) probably serve a camouflage function in the Portuguese man o' war Physalia, where they are present as a biliprotein complex (25), and have a functional role in the skin of several wrasses and parrot fishes in which biliverdin IXα forms a blue biliprotein complex (26, 27). Bile pigments are present in many other marine animals particularly fishes and molluscs, often as biliproteins (28-30) but in many cases probably adventitiously. The purple ink of Aplysia contain a bilin (31) which is derived from the algal phycoerythrobilin (32) and may also be an adventitious product. A similar ink in Janthina may perhaps be derived from the Physalia biliprotein in its diet. Cyclic tetrapyrroles derived from chlorophyll are not known to serve any pigmentary purpose though they are occasionally present in marine animals (33). Other porphyrins are more common, especially in the calcareous shells of molluscs but are probably accidental deposits. Free porphyrins are rarely utilised as pigments, largely due to their photosensitising effects, but protoporphryin IX is present in large amounts in deep-sea medusae (34, 35) where it may hide the luminescence of prey in the stomach as well as provide cryptic colouration.

Probably the most widely distributed pigments in marine organisms are the carotenoid pigments. They are abundant in algae as secondary photosynthetic pigments and in invertebrates (36, 37) particularly the Crustacea (38). Their functional significance in animals as pigmentary effectors is implied by their deposition in chromatophores and by the adaptive colour changes observed in many species. Although many coastal fishes have carotenoid colouration (39) deep-sea fishes in general do not (but see 40) despite the fact that many feed on crustaceans containing high levels of carotenoids. A great number of carotenoids have been identified in marine organisms (36, 37), some with unusual structures, but many are probably metabolites with no adaptive significance. Carotenoids are only synthesised in toto by photosynthetic organisms, not by the zooplankton. Thus all the various carotenoids present in such abundance, and at all depths, in the marine environment are derived from the surface layers. The transfer of these pigments through the food web is a remarkable example of chemical conservation in the marine fauna, though the biochemical modifications of the carotenoid groups show an equally remarkable metabolic diversity. Algal carotenoids are not usually abundant in marine animals; fucoxanthin is arguably the most abundant algal carotenoid yet astaxanthin is probably the dominant animal carotenoid. The preponderance of astaxanthin as a pigmentary effector may perhaps be related to its relative stability and the readiness with which it bonds to chitin, calcareous material and proteins, thereby further increasing its stability (41-43). The bonding to proteins of

astaxanthin (and some other carotenoids) provides a much greater range of potential colours; the blue pigments of the marine neuston provide examples of adaptive colouration utilising such carotenoproteins (43). Recently evidence has been obtained that carotenoid pigments may not only provide adaptive colouration for planktonic animals but also provide some degree of photoprotection (44).

The light emitting abilities of many marine organisms are of very great importance in the ecology of the marine environment and the uses to which they are put are numerous (45), one of the most widespread being that of camouflage (46). The structure of the luciferins of several groups of animal have now been identified. Coelenterates, the decapod shrimps Oplophorus and Heterocarpus, the mysid Gnathophausia, the fish Neoscopelus and the squid Watasenia all have a single type of luciferin (coelenterate-type luciferin or coelenterazine) (47 and references therein). A second closely related luciferin occurs in the ostracod Cypridina and the fishes Apogon, Parapriacanthus and Porichthys (47). This has an imidazopyrazine nucleus similar to that in coelenterate-type luciferin and biosynthesis is probably through cyclisation of the three amino acids tryptamine arginine and iso-leucine. Thus the luciferins of all marine animals in which they have so far been characterised have a common chemical skeleton. There is now considerable evidence that in at least some populations of the fish Porichthys the animal's luciferin is derived from a diet of either Cypridina or other zooplankton with the same luciferin (48). A similar situation may well apply to Apogon and Parapriacanthus (49).

A different reaction system is found in luminous bacteria (50). The function of bacterial light is in some doubt, except in symbiotic associations; the luminescence is stimulated by an unidentified metabolite, or inducer, which is produced by the bacteria and accumulates in the surrounding medium. At a critical concentration this initiates the synthesis of the luminescence system (51).

The spectral quality of the light emitted by many marine animals is modified by the presence of filter pigments in the optical path of the photophores (17). These pigments have not been identified definitively, but despite similar spectral transmission characteristics (46) several different types of compounds are involved, including porphyrins, carotenoproteins and proteins with unidentified prosthetic groups.

FUNCTIONS DEPENDENT UPON CHEMICAL PROPERTIES

Toxins

A large number of venoms and toxins have been recognised and isolated from marine organisms (1,2, 52-56). The ecological significance of naturally injected venoms of such animals as weever fish, sea snakes, cones, cephalopods and the nematocyst-bearing coelenterates is obvious, but the ecological role of many toxins is less clearly defined. It is not always clear that extracted compounds which are toxic when ingested by (or injected into) experimental animals (usually mammals) provide any adaptive advantage in normal prey-predator relationships in the sea. Thus ciguatoxin does not affect most marine animals (57) and saxitoxin apparently has no effect on clams and other bivalves. Most naturally injected toxins (or venoms) appear to be mixtures of high molecular weight compounds including enzymes (e.g. 54) whereas toxins extracted from other organisms are probably more often single or a few defined compounds. Compounds such as tetrodotoxin, though highly toxic to both vertebrate and invertebrate nerve preparations, may not perhaps be so effective when ingested by a predator. Nevertheless the presence of tetrodotoxin in such unrelated animals as puffer fishes, gobies, newts and frogs (58) suggests that it has a defensive function while its role in the blue-ringed octopus (59) is probably more offensive. Other toxins may also be of use to their producer in prey capture, while the ecological value of others, particularly those from superficial tissues (e.g. pahutoxin), may simply be to render the animal distasteful. The accumulation or production of toxins from the food has little direct value in cases such as ciguatoxin or saxitoxin accumulated by fish or molluscs, but the aplysin and aplysiatoxins of sea hares (2, 60) are derived from similar compounds in the molluscs algal diet (61) and undoubtedly confer upon the animal immunity from most predators. No doubt the ecological value of many marine toxins, particularly those of sessile or slow-moving animals such as sponges and echinoderms, is considerable though not yet clearly demonstrated. In many other cases however, even products of considerable biomedical interest may have no inherent value to their producer, to whom they may be merely metabolic by-products (as perhaps is nereistoxin (140)).

From a more general ecological point of view saxitoxin (from Gonyaulax) and other different dinoflagellate toxins (56) are of dramatic importance in 'red tide' conditions (55). The local effects of these toxins are probably more acute than those of any other marine natural products. Surprisingly few data are available on the effects of saxitoxin and other 'red tide' toxins on the local zooplankton. There is even some doubt as to whether the mortality of fishes under these conditions is entirely due to the toxins or is to some extent exacerbated by suffocation through the density of the dinoflagellate populations. If the toxins have more effect upon the fish than upon the zooplankton the net effect will be an increase in grazing pressure due to a reduction in the predation of zooplankton. The effects on the dynamics of the dinoflagellate bloom will therefore depend very much upon their relative toxicity to different organisms. If the structure and toxicity of other dinoflagellate toxins are very different to those of saxitoxin, the species composition of the

red tide will have a considerable effect on its subsequent dynamics, in which grazing plays an important part (62).

Extracellular products

Natural products which are secreted (or diffuse) into the surrounding sea water, like saxitoxin, may have a profound effect on ecological relationships. The potent antimicrobials and fungicides that have been extracted from many sessile organisms, particularly algae, sponges and coelenterates (2) may play an important role in preventing these organisms from being overwhelmed by epibionts. The freedom from epibionts of gorgonians, for example, has been attributed to toxic terpenoids produced by their symbiotic zooxanthellae (63). Algal polyphenols or tannins, present particularly in young growing tissues, inhibit the growth not only of bacteria but also of some larval zooplankton (63). A classic example of dietary transfer of antimicrobial agents is that of the alga Phaeocystis in the Antarctic. It produces allyl sulphides which hydrolyse to acrylic acid. The alga is grazed by krill and the krill eaten by penguins. As a result the penguins have a near-sterile alimentary tract (63 and references therein). Some woodboring marine crustaceans have been found to have an unexpected absence of gut micro-organisms (64); perhaps a similar antibiotic may be responsible.

The excretion or diffusion of antibiotics is of local importance in the ecology of these organisms, but other excretory products may be of more general significance. Many marine phytoplankton organisms secrete large proportions of their fixed carbon as extracellular products (65,66) though the evidence for this has recently been questioned (67). In general glycolic acid and polypeptides are among the major components; older cultures may produce more carbohydrate while nitrogenous products are particularly important in the blue-green algae (66, 68, 69). The products may be of considerable importance as energy sources for other organisms in the environment, particularly bacteria and algal heterotrophs (70). The significance of the products is not easy to quantify in the open sea (66) but is obviously of great importance in the energy balance of symbiotic associations of zooxanthellae and zoochlorellae (71-73). The minor products of algal extracellular material, namely growth promoters, inhibitors and others (66), may have greater ecological impact than their quantity might suggest. Chelating substances are present in algal extracellular products, and iron chelation by blue-green algae has been regarded as one reason for their dominance of certain phytoplankton associations (74). Chelation has also been implicated in the population dynamics of upwelling regions (75). The chelation of heavy metals (e.g. Cu^{++}) is likely to be of importance in polluted conditions (76). Various vitamins are among the excreted products and laboratory experiments have shown how active exchange of needed metabolites (e.g. B_{12}) can occur between syntrophic pairs of species (77). The extension of this concept to natural phytoplankton successions has some support from the observed species successions and nutritional requirements (78). Extracellular vitamin B_{12}-binding factors are produced by some algae and Droop (77) has considered how these might enable a dominant species to maintain its dominance by rendering B_{12} unavailable to its competitors. The potential ramifications of such relationships between algae and/or bacteria are obviously extensive (79). Provasoli (78) has extended these concepts to the zooplankton by demonstrating the varying nutritional requirements of different species. The fertility of the zooplankton may depend upon the nutritional value of the algal species which in turn may be affected by the extracellular metabolites of other algal species. Though the importance of algal excretory products has long been a matter for speculation (80) the intricacies of the relationships are only just beginning to emerge.

Chemoreception

Extracellular products released either by accident or by design from marine organisms play a vital ecological role. The perception of these products requires highly specific chemosensory mechanisms and the behavioural responses often induced by them are no less complex. The field of chemoreception and chemical communication in marine animals (81-86) is at an early stage in its development by comparison with terrestrial animals, particularly insects. The specific products eliciting the observed responses are still almost entirely unidentified, but recognition of the importance of chemoreception in the marine environment is now widespread.

The responses involved may be divided into three groups. 1. Feeding and avoidance of predators. 2. Homing and settlement. 3. Intraspecific communication (e.g. pheromones).

1. Feeding and predator avoidance

Many investigations have shown that feeding responses in marine animals can be elicited by prey extracts. The distinction between gustatory and olfactory responses and receptors in aquatic invertebrates is largely academic and is one of threshold not of kind. In fishes, however, taste buds occur all over the body including fins and barbels, whereas the olfactory organs comprise one or two sacs containing the sensory lamellae on the fore part of the head (87, 88). Kapoor et al. (89) regard the gustatory system of fishes primarily as a final discriminatory sense for food after its recognition by other senses. In the invertebrates no such distinction is practicable, and chemosensory organs are present at

many different locations in different groups.

It is not always clear which particular fraction (or fractions) of the prey extract is involved in the sensory pathways. In fishes, both teleosts and elasmobranchs, amino-acids, including some novel types (94), appear to be potent agents in eliciting feeding responses (90-94) and in herring larvae the olfactory system is responsible (93). Similar responses have been obtained in various invertebrates, particularly crustaceans (95-104, 119). Both stereospecificity of receptors and the need for simultaneous stimulation of several different types of receptor have been demonstrated (105, 106). Electrophysiological responses of specific chemoreceptors to amino-acids and other compounds have been identified (98, 107) and in Panulirus specific receptors have been shown to be responsive either to taurine or to amino acids (95, 96, 108). The identification of a taurine receptor which is insensitive to α-amino acids provides the possibility of sensory discrimination against a chemical 'white noise' background caused by free α-amino acids in the sea; taurine is an almost universal constituent of marine invertebrate tissues (109). Other compounds such as trimethylamine oxide and betaine are frequently stimulatory; in general, responses are stronger to mixtures of compounds than to individual ones. The role of higher molecular weight compounds, especially proteins, has been demonstrated (110-113) with response thresholds as low as 10^{-10}M in the snail Nassarius. Thresholds for behavioural responses to individual amino acids are as low as 10^{-12}M in Gnathophausia (100) and 10^{-15} g/l of whole clam extracts in the crab Callinectes (114). Chemosensory food discrimination has been demonstrated experimentally in grazing copepods (115). The response thresholds in the mollusc Diaulula are affected by its nutritional state and by the presence of other prey species (116). The interaction of chemosensory, visual and statocyst responses to prey have been investigated in the nudibranch Hermissenda (117) and the lobster (118). Integrated responses of this type have more direct relevance to the normal in vivo situation.

The situation in coelenterates is rather different as the feeding response of many species is elicited by the single tripeptide reduced glutathione, at concentrations of 10^{-9}-10^{-7}M (119). Other coelenterates respond singly to proline, valine, glutamine or leucine, and in the freshwater Hydra glutathione has additional behavioural effects (119).

The complementary chemosensory ability of potential prey to recognise predators has been noted particularly in echinoderm/mollusc relationships. The active principle eliciting escape responses to Marthasterias and Asterias by both gastropods and lamellibranchs is a glycoside of the steroid marthasterone (120, 121). The snail Melagraphia has an escape response to the predatory gastropod Haustrum which is initiated by uranylcholine (122). The identities of other specific compounds remain undetermined though Kittredge et al. (123) suggest that dopachrome (from octopus ink) may be recognised by its crayfish prey, just as the ink is also recognised by the octopus' predator the moray eel. Similar recognition of one species by another is essential for the establishment of symbiotic (124) or parasitic relationships and has been demonstrated in e.g. the symbiotic prawn Betaeus (107, 125), a polychaete (126) a parasitic platyhelminth (127) and the fish Carapus (128).

2. Homing and site recognition

Homing in migratory fishes appears to involve chemosensory cues, though the sources of the compounds involved are not fully resolved. Migrating salmon respond to water from the spawning ground, and it has been possible to imprint salmon smolt with artifical substances to which the animals will return (129, 130). Metabolic products of other individuals (131) or pheromones, perhaps in the skin mucus (132), may be responsible and damage to the olfactory system greatly impairs the homing ability of minnows (133-135).

Site selection by invertebrate larvae presents similar problems to the organisms. It is quite clear that many larvae respond to natural products from algae on which they preferentially settle (136-138) while work on barnacles has demonstrated that a cuticular protein 'arthropodin' is the recognised settlement factor. This response appears to involve a "chemotactile" sense rather than a response to soluble factors and may thus differ considerably from other chemosensory systems (139 and references therein).

3. Intraspecific communication

Intraspecific chemical cues are used in a wide variety of social communication contexts. They may be used in the recognition of single individuals, sexes, families or populations, or to indicate the physiological condition of individuals of one or both sexes. The components used in this type of communication (or pheromones) are almost entirely unidentified in aquatic animals (140-142), though many have been characterised in insects and other terrestrial organisms.

The firmest evidence for pheromones in the ecology of marine organisms concerns sexual attractants. Gamete attractants have been postulated in a number of species, particularly algae (143-145) and the sperm attractrants of species of Ectocarpus, Fucus and Cutleria have been identified. All three are unsaturated volatile hydrocarbons, hardly soluble in water and hence presenting a steep concentration gradient. The Fucus gamete attractant is stimulatory at 10^{-6}M, is not species-specific and isomers are much less active (144). Sexual determination in the echiuroid worm Bonellia is under pheromone control. Adult females have a greenish pigment which causes larvae settling upon them to become dwarf males. Other larvae develop into females. The pigment has been identified as a

chlorin (146).

Other sexual pheromones have been postulated on the basis of behavioural responses; in other words they are believed to induce the observed courtship or copulatory behaviour patterns. Most of the work on the effects of these substances has been done on crustaceans. A species-specific urinary sex attractant is produced by premoult female crabs of the genera Portunus, Carcinus and Macropipus (147, 148) and some preliminary investigations into the chemical nature of that in Portunus have been made (149). Work on three other crabs demonstrated little or no species-specificity in the attraction of premoult females to males, and the moulting hormone crustecdysone mimicked the action of the pheromone, though at markedly different thresholds in each species (10^{-8}-10^{-13}M) (150). These results led to a general theory of moulting hormones as sexual pheromones in decapod crustaceans and other arthropods (151). Work on lobsters failed however to show similar effects of crustecdysone or its metabolites (152, 153) though there is behavioural evidence for sexual pheromones in these animals (154, 155). 5-Hydroxytryptamine has been claimed to be the sexual pheromone in other crabs (156). Evidence for chemical transfer of sexual information has also been obtained in amphipods (157-159). Behavioural evidence for sexual pheromones in the copepods Eurytemora, Calanus and Pseudocalanus has been described (160, 161); in the latter two genera sexual dimorphism of chemosensory structures was noted, and uptake of tritium labelled material from females was greatest in the region of these structures.

Sexual pheromones affecting and produced by both sexes of nereid worms have been investigated (162-164). Special chemoreceptor complexes are developed and it is suggested that the pheromone is a polypeptide. In syllid worms which engage in sexual swarming a pheromone from the female stimulates the swimming activity of males (165). Pheromones may also be implicated in the sexual differentiation of the slipper limpet Crepidula and in the sexual behaviour of a number of other molluscs (166, 167 and references therein).

Trail following is a common pheromone controlled response in insects; it may also apply in the cases of certain marine molluscs (168, 169) and be important in the aggregation of some species (170-172).

Other aspects of the behaviour of marine animals which are suspected to involve pheromones are the 'epidemic spawning' of many marine invertebrates, particularly molluscs and echinoderms (82, 141) and the alarm responses so well demonstrated in certain fishes (see below) and apparently also effective in the echinoid Diadema (173) and the anthozoan Anthopleura (174).

Elaborate chemical communicatory repertoires may be involved in the complex parental and social relationships of fishes. Most of the experimental work on pheromones in fishes has utilised freshwater species, but pheromones are probably no less important in marine species (83, 134, 175-177 and references therein). Alarm substances are produced by many fish from epidermal glands and that of the minnow has been identified as a pterin. In the order Cypriniformes the alarm substances are not species specific though interfamilial responses are weak. The difficulties of behavioural identification are highlighted by the conflicting results in the case of the top smelt Atherinops (178,179).

Skin slime has been shown to be the source of individual recognition substances in some fishes (180) and these substances are probably responsible for both parental (181) and territorial behaviour and the complex social hierarchies present in some species, as well as the maintenance of schools in certain situations (182). Sexual pheromones have been implicated in the behaviour of several fishes both marine and freshwater but the direct evidence is less conclusive than that for invertebrates.

There is considerable circumstantial evidence for the effects of chemical mediators in the marine environment. Sexual dimorphism of the olfactory organs of deep-sea fishes is not uncommon (88, 183). Males of ceratioid anglerfishes become macrosmatic on metamorphosis, whereas the females have minute olfactory systems. The males are often parasitic and presumably use chemical cues to find the females, to which they then attach. The occasional 'mistake' when a male attaches to the 'wrong' species of female (184) suggests that the specific (?) pheromones may not be very dissimilar. It is also likely that the onset of pheromone release by females occurs before sexual maturity in some species (185). Similar sexual dimorphism of the olfactory system occurs in some species of the mesopelagic and bathypelagic fishes Cyclothone and Gonostoma. In these cases, too, males are smaller than the females but have much enlarged olfactory organs and associated regions of the forebrain. Recent data (186) show that immature male Gonostoma bathyphilum usually undergo a sex reversal but that some continue to grow and become large mature males with enlarged olfactory systems. In contrast Cyclothone microdon is an habitual protandrous hermaphrodite. The males have enlarged olfactory systems which regress in intersexes and females. The determination of sexuality in these animals is not known but it is tempting to speculate that parallels to the chemical determination of maleness in the shallow fish Anthias (187) may also apply in the deep sea. In this environment, where animals are not very abundant, there are obvious evolutionary advantages to the development of a sexual plasticity whose outcome can be determined by local conditions, particularly the presence of mature individuals of the same species. Sexual dimorphism of chemosensory structures has been noted earlier in some crustaceans (142) and probably occurs in other deep sea species. The widespread distribution of dwarf males in many different phyla (188) suggests the possibility of sexual pheromones similar to that in Bonellia. In fishes sexual dimorphism occurs in the luminous organs of some, the sound-producing organs of others, and the olfactory organs of still others (182, 189). All are examples of different modes of

sexual communication.

The greatly reduced olfactory systems of whales and dolphins imply that chemosensory mechanisms play a much less important role in their ecology than in that of most other marine animals.

The interrelationships between prey and predator in the darkness of the deep sea invite speculation on the widespread use of chemosensory rather than visual stimuli, but there is no direct evidence. The rapid aggregation of animals of all types, from crustaceans to fishes, round cans of inanimate bait placed on the sea floor at great depths certainly suggests that food packages, be they natural or artificial, are rapidly perceived and approached (190). Unfortunately behavioural observations are difficult to obtain, indeed are often impossible with present catching techniques. Molecular diffusion rates in water are 10^4 to 10^5 times slower than in air, but the size range of molecules that might be utilised as pheromones is much greater than is possible in air. Theoretical calculations of potential distances over which chemical communication might take place, given certain assumptions about the molecular weight of the compounds involved and their rate of release (191), are only very broadly applicable to natural conditions in the sea. Molecular diffusion in this environment has much less consequence for the spread of material than does eddy diffusion. Trails of relatively high molecular weight pheromones (or food substances) are likely to persist for long periods in relatively still conditions and the demonstrated potential abilities of the shrimp Acetes to follow food trails for 10-20m (100) can be readily extrapolated to support extensive trail-following, for whatever purpose, in the deep sea. The ocean is highly structured in that in non-turbulent conditions it consists of a very large number of layers stratified by virtue of their density differences and often moving relative to one another. The identity of these layers may persist for long periods. These considerations, and the daily vertical migrations of many oceanic animals, provide the opportunity for 'searching' the many layers through which they pass and hence increase the profitability of pheromone trails laid in particular layers. This will apply particularly where the vertical distributions of the two sexes of a species are disparate, or where the distribution of one sex is highly layered compared to the other.

A particularly important feature of chemoreceptive mechanisms is the ease with which they can be disrupted by alterations in the chemical environment of the organism concerned. The effects of pollutants of all types are often mediated first through the chemosensory system (84). Feeding responses and substrate selection abilities are soon lost by many animals in conditions of oil pollution or in the presence of dispersants (192-195). Exposure to heavy metals reduces the chemosensory responses of lobsters (196) and the effects of pollutants at 10^{-4}-10^{-5} times the lethal threshold have been discussed (197). Synthetic surfactants induce responses in molluscs similar to those of starfish glycosides (121). Recent work (159) has demonstrated that the sexual behaviour of male amphipods which is normally induced by females is blocked by surfactants, as well as the sensitivity of dactylopodite chemoreceptors to food extracts. By affecting the delicately poised chemosensory relationships of marine organsims pollutants may exert an effect upon the marine ecosystem out of all proportion to their apparent toxicity.

The roles of marine natural products are clearly vital factors in the ecology of marine organisms; it is equally clear that the roles are only partially recognised. The most obvious discrepancy in the chemistry of marine ecological interactions is the lack of information on chemical mediators, particularly pheromones. Behavioural assays are not easy, and in practice have to be limited to a very few experimental animals (198). Nevertheless recognition of the role of chemical mediators, and identification of their structures, must be a goal for all who work in the field of marine chemistry. The work on insects has for technical and biological reasons outstripped that in the marine environment. No doubt along with the uses of natural products discussed above other organisms have evolved equally effective chemical methods of blocking or mimicking chemical mediators. The biochemical ingenuity inherent in products such as cryptic odours (199, 123) and pheromones involved in agressive mimicry (200) is almost certain to have been developed in marine organisms. No doubt many will be found to have utilised or modified food products for behavioural purposes, as already shown in many insects (201) and in such marine examples as the Aplysia toxins, the carotenoid pigments and Porichthys luciferin.

An attempt has been made to classify marine natural products according to their ecological functions. The limitations of such an approach are all too apparent, but do at least expose the gap that still exists between the chemical and functional approaches. It is the task of both biologists and chemists to bridge this gap.

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