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Review

Genomes and Extracellular Organic Substances in the Ocean

Ian R. Jenkinson

Agency for Consultation and Research in Oceanography, Lavergne, 19320 La Roche Canillac, France; ian.jenkinson@ocean-expert.org or ian.jenknson1@gmail.com; Tel.: +33-608-89-13-62

Abstract: Dissolved organic matter (DOM) in the ocean represents about 662 billion tonnes of C, 200 times more than the living biomass. It is produced mainly by microbial primary production. The largest fraction of this DOM is old (>weeks to months) and both chemically and biologically recalcitrant. The remainder is young (seconds to weeks), more labile and surface active. It also changes the rheological properties in the bulk phase of the water and at interfaces including the sea surface microlayer (SML). In order of abundance, this DOM consists of sugars, amino acids, fatty acids and nucleic acids, often incorporated into complex polymers. The DOM molecules are produced by microbial genes, and are further modified by enzymes themselves produced by genes. The properties of ocean water and its interfaces as well as biogeochemical fluxes may thus be modified by ocean microbial genes. These fluxes influence ocean and atmospheric climate, which in return acts on the biota. Therefore the ocean microbial genomes and the fluxes and climates they influence may be subject to Darwinian-type selection. Research programmes need to integrate ocean ecology, rheology, biogeochemistry and genomics, to find the associations among them. Discovery of commercial bioactive molecules may be a bonus.

Keywords: ocean; phytoplankton; bacteria; biogeochemistry; rheology; genomics

1. Introduction

At 662 billion tonnes of carbon, marine dissolved organic matter (DOM) holds > 200 times as much organic matter (OM) as the living marine biomass and around 100 times more than the dead particulate organic carbon (1) (Hansell et al., 2009). Marine (DOM) contains as much carbon as the Earth's atmosphere, and represents a critical component of the global carbon cycle (2) (McCarren et al. 2010). In the ocean, this DOM is primarily produced by eukaryotic and prokaryotic phytoplankton, with some macroalgae, that reduce CO_2 to OM, using sunlight as energy source. The molecular characteristics of the proteins produced are controlled by the organisms' genes. Further proteins, and other OM, are then manufactured using enzymes, which also are proteins. This OM consists of particulate matter (POM), mainly the solid parts plankton organisms, and DOM that is secreted by phytoplankton and lost from cells during lysis. This paper is not concerned with the POM, treating only the DOM as well as mucus consisting of exopolymeric substances (EPS). Ocean DOM can be usefully characterized in two ways.

The first way to categorize DOM is by chemical composition. The most abundant primary component of DOM is sugars, followed in decreasing order by amino acids, fatty acids and nucleic acid bases, which correspond for EPS to polysaccharides, proteins, lipids and nucleic acids (DNA and RNA). Much of the EPS consists of polymer molecules bearing a variety of functional groups, which determine their physicochemical properties and roles in the ecosystem.

The first way to categorize DOM is by age. The largest fraction of DOM is weeks to hundreds or thousands of years old and has the highest proportion of DOM recalcitrant to biological breakdown (1) (3) (Hansell et al., 2009; Jiao et al., 2010), as well as showing little surfactant or rheological activity (4) (Jenkinson et al., 2015, JPR). The second, smaller, fraction of DOM is seconds to days or weeks old. It is thus biologically and chemically labile. Some of it is highly surface-active (hydrophilic, amphiphilic or hydrophobic) and some of it adds viscoelastic properties to the water, thus thickening it (4) (Jenkinson et al., 2015 JPR). This category of DOM is relatively the most abundant in the photic zone, particularly in certain harmful algae blooms and mucus events (4) (Jenkinson, 2015 JPR). It also includes most of the signalling, pheromone and toxin molecules (5) (Brown et al., 2019), that may modulate ecosystem structure (6) (Yamasaki et al., 2009) and bidirectional vertical fluxes, of OM within the water column (7) (Mari et al., 2017) and of matter and energy across the ocean-atmosphere interface (8) (9) (Wurl et al., 2017; Jenkinson et al., 2021).

Given that the allochthonous ocean OM is produced by marine organisms' genes, and that some of this OM changes the physical properties of bulk ocean water, as well as its interfaces and fluxes across them, it follows that these properties and fluxes are partly under genetic control, and thus subject to natural selection and evolution (10) (11) (Darwin, 2003; Dawkins, 2016).

Rapid progress is being made cataloguing the genes of the pelagic ecosystem, as well as discovering both their roles in producing proteins, and ultimately, via enzymes, of polysaccharides and lipids. Progress is also being made in categorizing the rheological properties of ocean waters and soft polymeric structures, as well as how these properties and structures modulate processes and fluxes. The terrestrial/atmospheric and submarine climates are currently changing (12) (IPCC, 2021), which is stressing and altering the biota, including humans. The first aim of this paper, therefore, is to suggest some of the possible roles of genomes in promoting biorheological changes that influence biogeochemical processes. The second aim is to promote bridging of the gap between ocean science and rheology, and to suggest how collaborative research programmes including genomics, ocean rheology, ocean ecology and flux studies can be set up to understand how genes control internal ocean processes, and their interaction with the atmosphere. As an added bonus such studies are likely to throw up commercially exploitable new natural bioactive products.

A sketch of these ideas is shown in Figure 1.

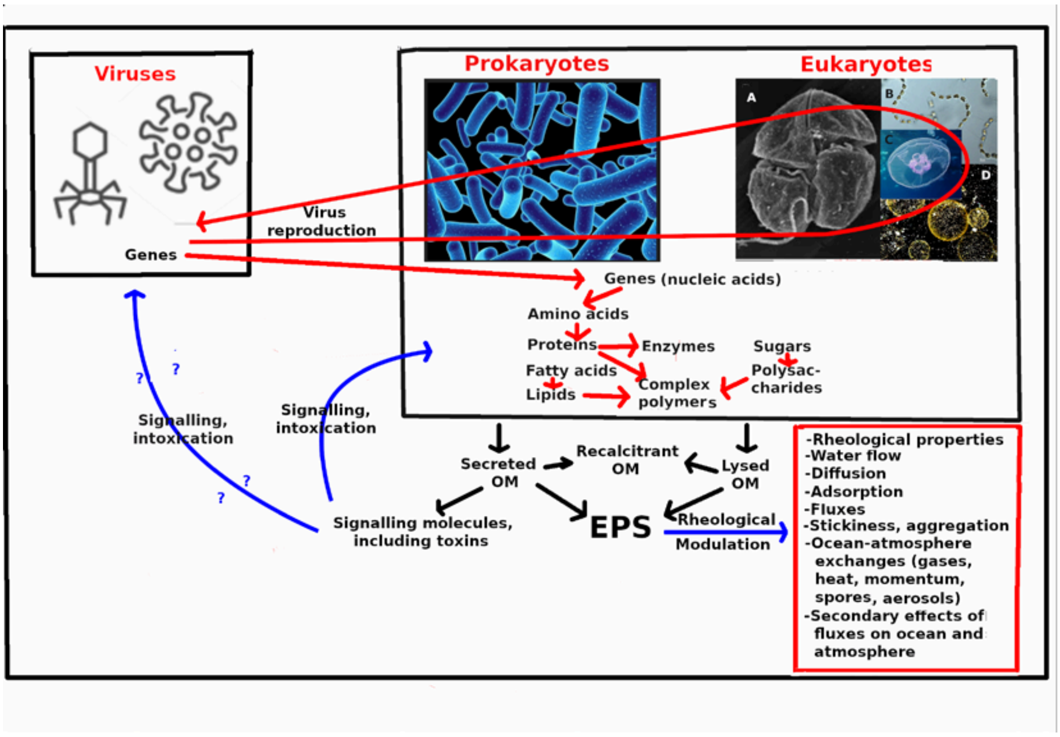

Figure 1. Three categories of gene-bearing ("living") organisms are presented, viruses, prokaryotes and eukaryotes. Prokaryotes and eukaryotes are shown in the same compartment, as generally they both have an independent machinery to form amino acids and proteins (including enzymes) from "instructions" in their genes. Enzymes modulate (catalyse) intracellular molecular transformations (modulation pathways not shown). Viruses are placed in a separate box as they need to introduce their genes into prokaryotic or eukaryotic cells, taking some control of these cells in order to reproduce their genes and outer casing. Red arrows represent the pathways of viral reproduction, and transfer of viral genes to replace or modulate prokaryotic or eukaryotic genes (13) (Rosenwasser et al., 2016). Red arrows are used also to represent transfers between the major types of organic molecules inside

cells. Black arrows represent transformations between the major suggested extracellular pools of organic matter (OM). Blue arrows represent modulation by extracellular polymeric substances (EPS) on physical and physicochemical processes in the ocean and at the ocean-atmosphere interface, as well as secondary effects in the ocean and the atmosphere (inside red box). Blue arrows also represent signalling and intoxication pathways by signalling molecules and toxins, respectively. Eukaryotic plankton is represented by: A - a dinoflagellate; B - a diatom; C - a jellyfish medusa; D - a raphidophyte. This is not a sketch of trophic or energy pathways.

2. Inorganic matter (IM) and organic matter (OM) in the oceans

2.1. Sources of available N and Fe

Estimated annual sources and sinks of organic nitrogen (ON), fixed inorganic nitrogen (IN) and Fe for the global coastal ocean (depth ≤200 m) the offshore ocean (>200 m) and the whole ocean (14) (Liu et al., 2021) are summarized in Table 1.

Table 1. Global coastal ocean nitrogen, N, and iron, Fe, budget terms (Tg y^{-1}) (estimated annual means).

	Coastal Ocean (1) (14)	**Whole ocean (15) (16) (2,3)**	**Open ocean (16) (3)**
Inorganic N (IN)			
Atmospheric deposition (DIN)	+ 4.5		
River input (DIN)	+20.4	+23 (16) (3)	+17(a)(16) (3)
Denitrification (water + sediments) (DIN)	-51.9		
Coastward net influx from offshore (DIN)	+47.4		
Total Δ TIN	**+20.4**		
Organic N (ON)			
Sedimentary burial (TON)	-12.3		
River input (TON)	+ 27.1		
River input (DON)		+11(a) (16) (3)	>0 to <11(a) (16) (3)
N_2 fixation (TON)	+15.4	164 (16) (3)	0 (16) (3)
Oceanward net outflux to offshore (TON)	-50.2		
Total Δ TON	**-20.0**		
Discrepancy (ΔTIN – ΔTON)	**+0.4**		
Net community production (DIN + TON)	**35.5**		
Atmospheric N deposition		39(b) (16) (3)	>30(b) (16) (3)
Atmosphere-ocean Fe budget			
Fe emissions from fires (<20 µm)		1.1 (15) (2)	
Soluble Fe flux to the ocean (from dust)		0.19 to 0.28 (15) (2)	
Soluble Fe flux to the ocean (from fires)		0.035 to 0.063 (15) (2)	
Soluble Fe flux to the ocean (anthropogenic)		0.016 to 0.034 (15) (2)	
Soluble Fe flux to the ocean (**Total**)		**0.24 to 0.38 (15) (2)**	
Soluble P flux to the ocean (from dust)		0.031 to 0.094 (15) (2)	
Soluble P flux to the ocean (from fires)		0.005 (15) (2)	

Soluble P flux to the ocean (anthropogenic)	0.0094 to 0.11(15) (2)
Soluble P flux to the ocean (**Total**)	**0.045 to 0.21 (15) (2)**

1 – Ref. (14) Liu et al. (2021); 2 – Ref. (15) Hamilton et al. (2022); 3 - Ref. (16) Jickells et al. (2017).
a – 75% of riverine input escapes beyond the shelf break; b – 75% of atmospheric input deposited outside the shelf break.

2.2. Origins and classes of allochthonous IM and OM

The main origins of dissolved IM (DIM) are soluble salts associated with: riverine and terrestrial diffuse sources. They include nutrient salts, notably nitrate, nitrite, ammonia and urea, dissolved inorganic phosphate and dissolved silicate. Anthropogenic sources have increased, not only of nitrogenous nutrients and phosphate, but also of silicate due to disruption of soils and coastal development. The current estimated annual global budget in for coastal waters (depth ≤200 m) (14) (Liu et al., 2021) is shown in Table 1 for marine reactive N.

Important sources and sinks of OC and reactive N in the ocean are atmospheric deposition, sedimentary burial (15) (Hamilton et al., 2022).

2.3. Origins and classes of autochthonous OM

Most OM in the ocean is produced autochthonously. Ocean Phytoplankton and bacteria *sensu lato* produce a wide variety of organic molecules. They result from direct extracellular secretion by living cells, as well as leakage from lysed and predated cells as dissolved OM (DOM), normally defined as that passing through a 0.2-µm filter, as well as particulate OM (POM), which is retained by a 0.5µm filter (17) (Shen and Benner, 2019). Between these extremes lies colloidal OM (COM). In order of abundance the DOM and COM comprise sugars, amino-acids, fatty acids and nucleic acid bases, polymerized to varying degrees into carbohydrates, proteins, lipids and nucleic acids, respectively, along with complex molecules bearing different radical groups.

2.4. Autochthonous particulate organic matter (POM)

POM produced within the pelagic ocean ecosystem consists principally of living cells and dead remains of cells. These particles act as mechanically solid surfaces allowing colonization by bacteria and protists such as ciliates. These particles also become included in marine aggregates, together with living bacteria and protists, within the more-or-less gluey polymeric matrix of COM. POM is believed to be negatively buoyant in general, and to act, together with autochthonous and allochthonous PIM to ballast marine organic aggregates, thus increasing downward organic flux (7) (Mari et al., 2017). More work is required on the functional density and sinking behaviour of marine POM.

The relationships between composition, measured density and sinking/rising rates of both non-living and living POM has subject to much research (18) (19) (20) (7) (Bienfang et al., 1977; Bienfang, 1980; Wakeham et al., 1984; Mari et al., 2017), this has given rise to varied and confusing results. Largely this may arise from the Derjaguin-Landau-Verwey-Overbeek assumption (DLVO), taught almost universally in engineering textbooks during the 20th century, of the quasi-universal non-stick non-slip interface between water and solid surfaces. Recent research on fluid dynamics at sub-mm and particularly sub-µm length scales, has shown very considerable departure from DLVO between even Newtonian liquids, such as water, and solid surfaces of different qualities, such as rough, smooth, hydrophobic or hydrophilic (21) (22) (23) (Rothstein, 2010; Conlisk, 2013; Jenkinson, 2014). Moreover, the surfaces of POM and even PIM adsorb a covering of OM, which may show varied and complex surface properties. Furthermore, living cells, including those in aggregates and biofilms, manage their surface properties through electric fields, partly by means of glycocalyxes.

2.5. *Autochthonous dissolved organic matter (DOM)*

Old DOM is mostly refractory (rDOM), while DOM newly produced by phytoplankton (pDOM) tends to be highly reactive and labile

Most DOM in surface, mesopelagic and deep waters is old rDOM. In laboratory studies, Shen and Benner(17) (2019) found that, over a time scale of 180 days, about 6-7% of DOM in surface water (50 and 100 m), 1-3% in mesopelagic water (300 m and 750 m) and 0% in deep pelagic water (1500 m) was removed by microbial degradation. The authors found that the amount of degradation depended on the depth origin of the OM, not on that of the microbial community.

pDOM was sampled by filtering (0.7 µm) an in-situ bloom was found to be utilized 50-75% within 7 d, and 76-94% within 180 d. By contrast, microbial utilization of DOM from 1500 m was not measurable even after 180 d: it consisted all of rDOM. Spectrophotometry at wavelengths from 250 to 750 nm of both pDOM and rDOM revealed that pDOM showed two absorbance shoulders, at 250-265 nm and at 300-350 nm due to chromophore molecules or groups, but rDOM did not. These two wavelength ranges correspond to labile compounds, including amino-acids and mycosporine-like amino-acids, respectively. Furthermore, elemental analysis revealed that while pDOM had a C/N value, 6.2, similar to the Redfield ration, the corresponding value for rDOM was 36.2, confirming that microbes utilized N-rich DOM referentially, and thus caused the remaining DOM to become depleted in N (17) (Shen and Benner, 2019), and thus probably in protein.

3. DOM with signalling and allelopathic functions

Many algal and protist species produce allelopathic compounds. The raphidophyte, Heterosigma akashiwo, produces high-molecular mass (>1 MDa) allelopathic polysaccharide-protein complexes that inhibit its competitor, the diatom Skeletonema costatum (now S. marinoi), by binding to the latter's cell surface. The authors suggested that viscoelastic, colloidal and/or selectively adhesive of these and other allelopathic polysaccharide-protein complexes (APPCs). The Skeletonema in turn were found to produce several fractions (separated by solid phase extraction) that allelopathically inhibited the Heterosigma in a dose-related manner (6) (Yamasaki et al., 2009).

At bloom concentrations the diatoms, Skeletonema costatum, Chaetoceros danicus and Thalassiosira decipiens, all slowed the swimming of the dinoflagellate, Cochlodinium (now Margalefidinium) polykrikoides(24) (Lim, A.S. et al., 2014), and the authors suggested that this might have impaired vertical migration of the latter and hence its ability to form blooms. The nature of the allelopathic agent(s), however, was not determined.

Axenically cultured Margalefidinium polykrikoides was found to produce copious mucus, giving average yields of crude polysaccharide of 26 mg/L of culture medium., which on hydrolysis yielded mannose, galactose, glucose and uronic acid together with sulphate groups (7-8% w/w S). The purified polysaccharide inhibited 11 virus strains out of 15 tested at concentrations of 0.8 to 25 mg/L. This abundant occurrence of sulphur-rich molecules is compatible with mucous gel formation by inter-group disulphide links (25) (Hasui et al., 1995).

The first diatom pheromone was identified by Gillard et al. (26) (2012), Pheromones are defined as molecules involved in intraspecific signalling, notably facilitating sexual encounter, while those used for interspecific communication are allelochemicals(27) (Frenket al.2014).

Many algal pheromones are organic acids or alcohols, while some are also proteins or glycoproteins (27) (Frenket al., 2014). For example, in the freshwater colonial heterothallic alga, Volvox carteri f. nagariensis, that survives drying out as dormant zygotes, the end of drought induces male colonies to secrete a pheromone inducer that is a large-molecular-mass glycoprotein, and that affects both male and female colonies. This pheromone inducer acts at a concentration of only10^{-16} M. It is produced by somatic cells, but initiates gametogenesis by male and female cells. The gene that encodes the pheromone has been discovered (28) (Tschochner et al., 1987) and the corresponding protein contains 208 amino acids with a molecular mass of 22 kDa (29) (27) (Mages et al., 1988; Frenkel et al., 2014).

Much laboratory work has been carried out on the influence of bacteria on phytoplankton biosynthesis of natural products (5) (Brown et al., 2019). The results obtained may give general clues to the production and effects of signalling compounds in the ocean, as well as the roles of these compounds in structuring ecosystems.

Particularly since the 2010s, the emphasis of work has evolved from allelopathic interactions to intraspecific signalling (30) (Schwartz et al., 2016). Recent work has also targeted phytoplankton chemical defences, particularly where the molecules involved, e.g. paralytic shellfish toxins (PSTs) or amnesiac shellfish toxins (ASTs), can impact human health (17) (Shen and Benner , 2019). The use of –omics (metabolomics, proteomics and transcriptomics) are revealing mechanisms of biological response to many chemical signals and cues. Outside the area of compounds showing potential for medical or commercial innovation, characterization of the multitude of often unstable and very dilute compounds responsible for chemical mediation of pelagic interactions may remain impracticable (5) (Brown et al., 2019). Studies of molecules that modify turbulence, diffusion and binding processes, notably those produced in harmful algal blooms (31) (32) (Jenkinson and Sun, 2010; Gobler et al, 2017), in organic aggregates (33) (Karlusich et al., 2022), in biofilms and interaction of such molecules with pollutants (34) (Santschi et al., 2021) may also benefit from investigation using–omics. (See section **17.**)

A study by Poulson-Ellestad et al. (35) (2014a-JPR) of the allelopathic effects of the toxic dinoflagellate, Karenia breve, on 9 species of planktonic diatoms typically present in the areas where K. breve blooms in the Gulf of Mexico, showed only weak stimulatory or inhibitory effects on the diatoms, leading the authors to suggest that allelopathic effects could not have been useful to K. breve at the start of the bloom, but could be useful in maintaining blooms once they were established. A second study by Poulson-Ellestad et al. (36) (2014b-PNAS) on the allelopathic effects of K. breve on two different diatoms, one of the species, Thalassiosira pseudonana, turned out to be the more susceptible. That K. breve affected nutrient limitation of T. pseudonana was considered unlikely as concentrations were non-limiting. Metabolomic and proteomic investigation using gene ontology categories for a long suite of proteins associated with metabolic pathways and functions in T. pseudonana revealed that many processes, including those involved in cellular carbohydrate metabolism, were strongly stimulated when exposed to K. breve, while others, including photosynthesis and chromatin assembly, were strongly inhibited. That T. pseudonana was susceptible to K. breve may be associated with the finding that the two species do not co-occur in nature. Although K. breve produces the toxin, brevetoxin, it is not known if this was an allelopathic agent acting against T. pseudonana.

In a study from the Baltic, Hakenen et al. (37) (2014) tested 10-µm filtrate of cultures of 10 local strains of a recurring dinoflagellate, Alexandrium ostenfeldii on different flagellates. At characteristic bloom concentrations, all the strains caused allelopathic effects on the cryptophyte, Rhodomonas salina and the dinoflagellates, Kryptoperidinium foliaceum, Levanderina fissa and Heterocapsa triquetra. All the strains of A. ostenfeldii showed allelopathic effects on all the target species. K. foliaceum reacted by encysting, but excysted again within 24 h, a proportion of the L. fissa cells lysed, and H. triquetra shed their thecae and became immotile, but within 24 hours they had mostly recovered. The chemical nature of the allelopathic agent was not investigated.

4. Molecules in intraspecific and interspecific signalling

Pheromones, secreted by copepods such as Temora longicornis and Eurytemora affinis, change the swimming behaviour of conspecifics of the opposite sex (both males and females). This is consistent with evolved use of pheromones to optimize encounters which may lead to mating (38) (Seuront and Stanley, 2014).

Another use of intraspecific signalling is for communication in biofilms. Bacteria, Vibrio cholerae, cooperate to protect themselves and each other against predatory amoebae, Acanthamoeba casalanii, using vibriopolysaccharide, an extracellular matrix of proteins, nucleic acids, and sugars (39) (Yildiz et al., 2014), which are in part controlled by the quorum sensing (QS) regulator, HapR (40) (Sun et al., 2013). The genes, vpsR and vpsT, were shown to confer enhanced resistance to amoeboid grazing, since grazing was enhanced in knockdown mutants. Further reduction in grazing resistance occurred when QS was interrupted by knocking out the hapR regulator(40) (Sun et al., 2013).

As well as signalling by DMS (See section **5**), selection of bacterial prey by the ascidian tunicate, Microcosmus exasperatus, may depend on surface molecules of the bacteria more than on their shape or size. Marine picocyanobacteria, notably Synecococcus and Prochorococcus, have sticky, hydrophobic coatings, and are retained with relatively high efficiency by the feeding nets of the ascidian. In contrast, Pelagibacter ubique, and other species of the SAR11 guild have a non-sticky, non-hydrophobic coatings, which allows them to slip through the mucous feeding nets and thus show low retention by this tunicate. While such a coating may reduce adhesion to nutrient-rich organic particles, it may confer resistance to grazing by mucous-net suspension feeders(41) (Dadon-Pilosof et al., 2017).

Rosa et al.(42) (2017) carried out a study on feeding selection by two lamellibranch molluscs, Mytilus edulis and Crassostrea virginica, of 10 species of nanoflagellates. The selection and sorting structures in these molluscs are complex and dynamic, but like in ascidians, mucus is heavily involved. Amongst the nanoflagellates studied, only Pavlova lutheri had a wettable, hydrophilic surface, and its retention by the molluscs was also the least. The wettability (hydrophilicity) and surface charge of surface of many cells is largely modulated by lectins in the glycolcalyx. Lectins are widely distributed glycoproteins, with important functions in molecular recognition.

5. Dimethylsulphide (DMS) in signalling and structuring consortia

DMS is responsible for the characteristic smell of algae culture rooms. It is secreted by most dinoflagellates, including the hosts of the parasitic dinoflagellate, Parvilucifera sinerae. Garcés et al. (43) (2013) found that concentrations of 270-300 nM DMS end dormancy in P. sinerae. Correspondingly, all dinoflagellate species that produce DMS in sufficient concentration cause P. sinerae to wake up, but only some of these species get parasitized. Garcés et al. (43) (2013) suggested that this was a rare demonstrated example of the now classical idea of “watery arms race[s]” in the ocean(44) (Smetacek, 2001). Are watery arms races so rare, however? Schwartz et al. (30) (2016) review many examples of models as well as laboratory and field studies supporting complex dynamics between competing species, where one or more species deploys allelopathic compounds to inhibit or even lethally poison competitors. (See Sections **3, 4** and **7**.) Outcomes can be the elimination of one competitor or else co-existence, depending on environmental conditions such as nutrient concentrations or even allelopathically influenced nutrient uptake dynamics.

Signalling molecules are not all aggressive, but may be mutually helpful. Studies of mutualism in the sea have long been concentrated on bitrophic interactions and it was widely assumed that more complex mutualistic systems in the ocean were rare (30) (Schwartz et al., 2016). Recently, however, Savoca and Nevitt (45) (2014) produced evidence for tritrophic mutualism in the Southern Ocean, where phytoplankton are grazed by crustaceans. This phytoplankton releases copious DMS, which in turn attracts procelliiform seabirds that feed on these primary consumers, thereby reducing grazing pressure on the phytoplankton. In a similar vein, Amo et al. (46) (2013) found experimentally that the nestlings of the krill-eating chinstrap penguin, Pygoscelis antarctica, are attracted to the scent of DMS. Thus it is likely that DMS released by zooplankton grazing acts as a signalling molecule via the penguins within a consortium at length scales at least up to 100s of m. In this consortium cohesion was achieved by the penguins’ behavioural attraction to DMS.

6. Consortia structured by rheological properties, including stickiness, of polymers

In many other consortia, such as biofilms (47) (48) (49) (Kerfahi et al., 2022; Imai et al., 2021; Karn et al., 2020), lake and marine organic aggregates(50) (51) (Qin et al., 2021; McManus et al., 2021), however, cohesion is achieved by physical processes such as stickiness (52) (Santschi et al., 2020), gelling (53) (Duan et al., 2022) or increased viscosity (54) (Guadayol et al., 2020) mediated by exopolymeric substances (EPS). Schwartz et al. (30) (2016) suggested that consortia with more elements than 3 are likely to exist, but that the number of degrees of freedom would make their existence difficult to prove.

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Aron et al. (55) (2020) have introduced Global Natural Product Social Molecular Networking (GNPS) as a tool for analysing the infrastructure of molecular datasets. and curating the data in a public database in the style of *GenBase.* GNPS may have the potential for investigating diverse marine consortia and other biotopes, and ultimately the whole ocean. It may desirable to accompany such a molecular database with another on associated measured rheological properties in the ocean environment at different scales.

7. Prey-capture and predator-avoidance

Chemical cues exuded by prey or occurring on their surface can be used by predators to locate and choose their prey. The copepod, Temora longicornis, feeds on sinking marine snow (MDS) particles, which leave a chemical trail behind them (56) (Lombard et al., 2012). The detection of tunicate exoskeletons (as an experimental proxy for MS) produced doubling of swimming velocity towards the falling particle; the authors suggested that detection must have been chemical, as distances were too great for hydromechanical methods. They also drew parallels with how pheromones secreted by the copepods, T. longicornis and Eurytemora affinis, change the swimming behaviour of the opposite sex (38) (Seuront & Stanley, 2014). (See Section **4**.)

8. Predator-prey interactions

Schwartz et al. (30) (2016) reviewed the effects of chemical signalling in protist-protist and copepod-protist pairs. Many different reactions have been reported, both on predator-prey reactions and on the swimming behaviour of both prey and predators. Brown et al. (5) (2019) also reviewed the effects of signalling molecules on predator-prey pairs, particularly invoking the effects of phytoplankton toxins, acting either to harm potential predators or as aids in capturing prey.

Ianora and Miralto(57) (2009) review the short-chain polyunsaturated aldehydes (PUAs), secreted when copepods such as Calanus finmarchicus, or Temora longicornis graze on diatoms such as Thalassiosira rotula, T. pseudonana, Phaeodactylum tricornutum, Skeletonema marinoi, Chaetoceros affinis, C. decipiens or C. socialis, and as a result produce deformed and thus unviable larvae. Some species of the planktonic diatom genus, Pseudo-nitzschia, such as P. seriata, internally produce and partially release a nerve toxin that produce Amnesic Shellfish Poisoning (ASP) in humans, as well as behavioural changes in marine vertebrates and some invertebrates. Tammilehto et al. (58) (2015) found that P. seriata releases the secondary metabolite, domoic acid (DA), when damaged through grazing by copepods, such as C. hyperboreus and C. finmarchicus. The same copepods, however, were highly resistant to the DA (59) (Harðardóttir et al., 2015), which suggested to Brown et al. (5) (2019) that some populations of copepods may have evolved resistance to DA.

Prince et al. (60) (2013) showed that, as well as acting as a neurotoxin, DA, produced by Pseudo-nitzschia delicatissima, inhibits growth of another diatom, S. marinoi, only slightly under low (perhaps limiting) concentrations of Fe, (0.18 μmol L^{-1}), but much more strongly when Fe was replete (~18 μmol L^{-1}) for diatom growth. DA also inhibited growth of S. marinoi, while slightly stimulating growth by P. delicatissima. In the experimental work of Prince et al. (60) (2013), it was not clear whether P. delicatissima actually produced DA, like its congener, P. seriata. If it does, the DA might then play two roles: firstly, favouring diatoms that produce it; secondly, inhibiting competing phytoplankton possibly by scavenging Fe, and by poisoning potential predatory zooplankton.

9. Mucus trophic structures ("mucus traps").

Rather like terrestrial web-weaving spiders, many marine organisms feed using structures of polymeric mucus that entrap passing prey by more or less sticky polymers that in some cases are toxic as well, killing, or just immobilizing the prey.

Some multi-cellular zooplankters release mucus to the environment, and appear to provide manure and "garden" their prey before eating it. The harpacticoid copepod, *Diarthrodes nobilis,* secretes mucus fibres through vents in its carapace. It then weaves these fibres to produce an enmeshing capsule, to which adds its own faeces. This allows prokaryotes to multiply on the capsules, which are then ingested by the copepod (61) (Hicks & Grahame, 1979). While it is unclear how much of the mucus remains in the environment, the authors suggest this "gardening", on "mucus-traps" is analogous to procedures previously described in marine nematodes (62) (Riemann & Schrage, 1978).

Mucus traps produced by protists are structured in different ways. For example, the dinoflagellate genus, *Dinophysis*, produces various toxins, including okadaic acid, pectenotoxin (PTX2) and dinophysistoxin 1b (DTX1b) but from calculations of amount secreted extracellularly, Nielsen et al. (63) (2013) calculated that field concentrations would have been too low to support the idea that these toxins act as allelopathic agents. Instead, the dinoflagellate, *Dinophysis acuminata,* uses "mucus threads" to trap its prey, the ciliate, *Mesodinium rubrum,* which is an obligate part of its mixotrophic life cycle (64) (65) (Ojamäe et al., 2016; Jiang et al., 2018).

Ostreopsis cf. *ovata* cells produce collective benthic webs of sticky mucous fibrils associated with the toxins, ovatoxin-a, -b, -c, -d/e and putative palytoxin(66) (Honsell et al., 2013). Organisms that get stuck or entangled on the webs are then attacked, often by several cells collectively, and devoured.

The planktonic dinoflagellate, *Alexandrium pseudogonyaulax*, secretes transparent spheroidal mucous traps, which are sticky and entrap small flagellates. The trap often remains attached to the dinoflagellate by its trailing flagellum, then the dinoflagellate engulfs these prey individually, finally abandoning the spent mucus trap (67) (Blossom et al., 2012).

In gradients of viscosity significant at the length scale of cell size, motile cells are expected to be slowed more on their side in the more viscous water, thus being turned to swim into the more viscous region. Zones of high viscosity may this act as traps for swimming cells. Such "viscous traps" are sometimes used by heterotrophic and mixotrophic protists to catch prey, and in some cases the protists even lace the high-viscosity zones with lytic toxins (68) (Blossom & Hansen, 2020). Stehnach et al. (69) (2021), however, observed that in gradients of viscosity the chlorophyte, *Chlamydomonas,* uses viscophobic turning to actually steer their swimming away from zones of higher viscosity. This behaviour would allow these flagellates to avoid such viscous traps. It also implies that they are able to sense viscosity and the direction of viscosity gradients, a capability reminiscent of that of diatoms that detect and react to turbulence fields (70) (Falciatore et al., 2000). (See section 13.)

10. Mucus as a retention tool

At the ecosystem scale, endosymbiotic algae in the coral polyps, the zooxanthellae, account for most of the reef's primary production (PP). In the Great Barrier Reef, for example, half of this PP is exuded by the polyps as mucus. This mucus traps organic matter from the water column, settles and carries energy and organic matter to the reef sediments. Dissolved mucus (~50-80% of the total mucus) is filtered through the lagoon sands, where it is quickly (~7%/h) degraded. Undissolved mucus aggregates trap particles, increasing their organic C and organic N by 2 orders of magnitude within 2 h. Currents concentrate these aggregates into the lagoon. Coral mucus thus provides light energy, harvested by the zooxanthellae and trapped particles to the heterotrophic benthic community of the reef (71) (Wild et al., 2004). Filtration of DOM and POM by reef sponges may significantly add to the reef-scale trapping of OM (72) (de Goeij et al., 2013). This constitutes a recycling loop that retains energy and nutrients within reef ecosystems, known for their outstandingly high biodiversity and productivity. Evolutionary processes and structures within the community-scale genome of coral reefs deserve investigation.

11. The roles of cross-linked gels, rheological changes and reactive oxygen species in toxicity to fish

The sulphated amino acid, cysteine and its derivative acetyl-*N*-L-cysteine (NAC) are mucolytic and antioxidant. In human medicine, the mucolytic effect of NAC is based on the presence of the free sulphydryl group (—SH), that opens up disulphide bonds (S—S) of the high-molecular-weight glycoproteins of human mucus, thus reducing the viscosity and elasticity of the mucus. NAC can also lyse DNA in sputum. NAC is also a direct and indirect antioxidant. The direct effect is produced by the free sulphydryl group, which is a source of electron donors that inactivate (i.e. scavenge) reactive oxygen species (ROS). NAC scavenges $^{\bullet}NO_2$, $CO_3^{\bullet-}$, and thiol radicals quickly, but $O_2^{\bullet-}$, H_2O_2 and peroxynitrite only slowly and O_2 or NO not at all (73) (74) (Samuni et al., 2013; Calzetta et al., 2018).

Yang and Albright (75) (1994) sought treatment for coho salmon, *Oncorhynchus kisutch*, killed by blooms of the diatom, *Chaetoceros concavicornis*. This species bears sharp, pointed spines that are believed to irritate the gills and induce them to produce excess mucus. This mucus is a proteinaceous material which consists mainly of mucopolysaccharides, with the long, interconnected, fibrous molecules occurring within a gel. The physical properties of mucous secretions are largely determined by the high molecular weight glycoproteins which consist of a protein backbone with many oligosaccharide side chains, often called mucin. The peptide chain of mucin contains some non-glycosylated regions, which contain many cysteine residues. Many mucous glycoproteins are composed of polymerized glycoprotein subunits through the formation of disulphide bonds in the non-glycosylated region of each protein core, probably involving interaction between adjacent cysteine residues which results in a network of matted molecules. Yang and Albright found that salmon administered L-cysteine ethyl ester (LCEE) in their feed showed increased survival. Since cysteine and its derivatives, NAC and cysteine L-cysteine ethyl ester (LCEE) can break S=S bonds and thus fluidify mucus, including mucus secreted by gills (76) (Powell et al., 2007), Yang and Albright concluded that this effect was responsible for reducing mortality. NAC, also included in feed, was additionally found to reduce the toxic effect to fish of cylindrospermopsin, a toxin produced by several harmful cyanobacteria (77) (Gutiérrez-Praena et al., 2014).

After finding that gas bubbles were preventing from rising in a bloom of the fish- and invertebrate-killing dinoflagellate, *Karenia mikimotoi* (also then known as "*Gyrodinium aureolum*" or *Gymnodinium nagasakiense*) (78) (Jenkinson & Connors,1980), and measuring the viscoelasticity of cultures of the different species of phytoplankton (79) (Jenkinson, 1986), Jenkinson(80) (81) (1989) modelled that *K. mikimotoi* could slow flow and thus reduce O_2 supply, thereby suffocating the fish when present in sufficient concentration. Jenkinson & Arzul (82) (80) (1998, 2002)) found that found that cultures of *K. mikimotoi*, and the fish-killing raphidophyte, *Heterosigma akashiwo*, flowed through fish gills more slowly than culture of the harmless haptophyte, *Pavlova lutheri*, which itself did not slow flow relative to that of pure culture medium. *H. akashiwo* showed more variable results than either *K. mikimotoi* or *P. lutheri,* suggesting that the EPS it produced was more heterogeneous. The relationship between flow rate and hydrostatic pressure difference over the gills suggested that *K. mikimotoi* and *H. akashiwo* added significant amounts of gel-like EPS to their ambient milieu, but that *P. lutheri* did not. In addition, however, *K. mikimotoi* was found to produce reactive oxygen species (ROS) (82) (80) that contribute haemolytic toxicity(83) (Gentien et al., 2007), that is assayed by measuring the toxin's lysis of red blood cells. *K. mikimotoi* isolated from European waters (France and Ireland) may be more active rheologically than that from East Asian waters. The term, "rheotoxity" was used by Jenkinson & Arzul (82) (2002) to mean "toxicity" (i.e. harm) done to organisms by increased viscoelasticity. An allied meaning is local increase the concentration of chemical toxins again by increases in viscoelasticity thus reducing dispersal (79).

Harmful algae other than *Karenia mikimotoi* that produce conspicuous amounts of observed mucus, measured increases in viscosity and/or foam include blooms of *Karenia* species, mainly *K. selliformis (84)* (Orlova et al., 2022), the dinoflagellates, *Margalefidinium* (= *Cochlodinium*) *polykrikoides* (85) (Kim & Oda, 2010) *Ostreopsis* cf. *ovata* (86) (Berdalet et al., 2017) and the haptophytes, *Phaeocystis globosa* (87) (88) (Seuront & Vincent, 2008; Kang et al., 2020), *P. pouchetii* (89) (Balkis-Özdelice et al., 2021) and *P. antarctica (90)* (Seuront et al., 2010).

In July 1985, at Caño Island, close to the Pacific coast of Costa Rica, massive mortality of corals occurred, along with that of many species of fish (including scarids, acanthurids, pomacentrids, tetradontids and balistids), crabs and gastropods (91) (Guzman et al., 1990). The plankton contained 8.3×10^5 live cells and $>3 \times 10^6$ cells in total. The dinoflagellates, *Margalefidinium catenatum* comprised 97% and *Gonyaulax monilata* (=*Alexandrium monilatum*) 1%. In October and November 1985 at Uva Island, close to the Pacific coast of Panama, about 300 km SE of Caño Island, a red-brown bloom of dinoflagellates lasted several days. Dinoflagellates and viscous foam co-occurred, suggesting to the authors that the former had produced the latter. Pocilliporid corals were found bleached. The authors concluded that the mortality of the reef organisms at Caño and Uva Islands was most likely caused by adhering of the mucus and, in the case of polyps, interference with their expansion, although chemical toxicity and oxygen depletion may also have contributed (91) (Guzman et al., 1990).

Kim et al. (92) (2002) investigated toxicity in *M. polykrikoides* and in the raphidophyte, *Chattonella marina*, using human epithelial carcinoma (HeLa) cells as target. In culture, growth of both species was at first exponential, reaching a plateau phase. After 12 days, cultures of *M. polykrikoides* and *C. marina* the polysaccharide contents increased to reach respective concentrations of 47 and only 4 µg/ml glucose equivalent. The *M. polykrikoides* cultures became noticeably more viscous, but the *C. marina* cultures did not. Nevertheless, as antiviral activity had been previously reported in *M. polykrikoides* mucus (25) (Hasui et al., 1995). Kim t al. (92) ((2002) proposed that cytotoxic agents may have contributed to ichthyotoxicity by *M. polykrikoides.*

During extensive blooms of *M. polykrikoides* around Oman and Muscat, associated with the deaths of hundreds of tons of fish and shellfish, Al Gheilani et al. (93) (2012) reported that while strong odours occurred, thought to be caused by methyl sulphide, no toxicity was detected in mouse tests. Scanning electron microscopy, however, showed mucus proliferation, which might have clogged gills, and fish gills also appeared damaged.

Working on *M. polykrikoides* from South Korea, Lee et al.(94) (1996) conversely showed haemolytic activity in both the water-soluble and chloroform-soluble fractions isolated from methanol extracts of *M. polykrikoides*. Yet C.S. Kim et al.(95) (1999) found that *M. polykrikoides*, also isolated from South Korea, produced high quantities of reactive oxygen species (ROS), which they suggested was the primary cause of fish mortality, through damage to gills. Kim and Oda (85) (2010) investigated the fish-killing mechanisms of *Chattonella marina* and *M. polykrikoides* from the Yatsusiro Sea, Japan. Their results suggested that *C. marina* has an NADPH-dependent superoxide generation system in its glycocalyx. Their results also suggested that *C. marina* continuously releases H_2O_2 into the medium during culture, whereas *M. polykrikoides* may not release H_2O_2, at least under normal physiological conditions. Their results suggest that continuous accumulation of discharged glycocalyx on the gill surface occurs during *C. marina* exposure, which may be responsible for the ROS-mediated severe gill tissue damage leading to fish death. Compared to *C. marina*, the levels of O_2^- and H_2O_2 detected in *Margalefidinium polykrikoides* were only trace amounts. Both lectins and mucus prepared from fish skin and gills of yellowtail from *C. marina*, but not from *M. polykrikoides*, when administered separately, produced markedly increased levels of O_2^- in *C. marina*, but not in *M. polykrikoides.* Further results suggested that the O_2^- generation system of *C. marina* is located on the cell surface, whereas only slight evidence of cell-surface generation was shown in *M. polykrikoides*. Evidence was shown, however, for the production of H_2O_2 in both species. Cell-free aqueous solutions prepared from both *C. marina* and *M. polykrikoides* were tested on HeLa cells as target. After 24h treatment with 10% final concentration of each extract in α-minimal essential medium containing 10% fetal bovine serum, cytological changes took place on the HeLa cells and colony formation was reduced, whereas corresponding extract from *C. marina* produced almost no effect. Kim & Oda (85) (2010) suggested that the difference between Lee et al.'s (94) (1996) findings and their own could have reflected differences in strain characteristics.

Flores-Leñero et al. (96) (2022), studying ichthyotoxicity induced by the raphidophyte, *Heterosigma akashiwo*, in Patagonian fords, found that ROS and polyunsaturated fatty acid (PUFA) was too weak to explain the fish kills that occurred, and the authors suggested that further studies should explore other fish-killing mechanisms, such as the production o mucus or extracellular polymeric substances (EPS). These results may reflect the conclusions of Yamasaki et al. (97) (2010) that the role of PUFAs and ROS in *H. akashiwo* blooms may be rather part of a suite of non-lethal signalling molecules controlling marine microbial community structure and function. (See sections 1 and 3).

Blooms with the presence of either of the dinoflagellates, *Gonyaulax fragilis* or *G. hyalina,* have been associated with viscous/slimy water and foam, frequently associated with mass mortality of marine organisms. Such phenomena have been recorded from: Sea of Marmara, Turkey (*G. fragilis* - foamy mucilage) (89) (Balkis-Özdelice, et al., 2021); Tasman Bay, New Zealand (98) (MacKenzie et al., 2002); Northern Adriatic (*G. fragilis* - mucilaginous masses) (99) (100) (Honsell et al., 1992; Pompei et al., 2003). *G. fragilis* and *G. hyalina* may have been confused by some authors, as they are similar, but separate species (101) (Carbonell-Moore & Mertens, 2019). Both produce copious mucus from their apical pore, resulting in noticeable mucilage in the field even at cell concentrations as low as several thousand cells per litre.

Riccardi et al. (102) (2010) studied the role of *G. fragilis* in producing mucilage events in the N. Adriatic, as well as sterols as potential lipid biomarkers associated with this mucus. They also extracted DNA from *G. fragilis*, and using PCR to characterize it, successfully developed a species-specific DNA probe. In culture, moreover, *G. fragilis* was associated with the 4α-methylsterols. That association between *G. fragilis* and specific sterols was found not to be clear in N. Adriatic mucilage-rich field samples was ascribed to rapid decay or transformation of the dinoflagellate cells and of the sterols. However, the authors suggested that in future, rapid genomic detection coupled with identification of phytoplankton cells in the field could be used to investigate their association with lipid biomarkers, such as sterols.

The dinoflagellate, Karlodinium arminger produces karlotoxins 1, 2, 8 and 9, that have all been implicated in fish kills (5) (Brown et al., 2019). This toxin lysed trout gill cells with a LC_{50} of 125 nM, and it showed a somewhat higher LC_{50} of 400 nM for the copepod Acartia tonsa, a potential predator. Huge numbers of algal toxins, particularly those harmful to humans, have been revealed in the last 20-30 years (reviewed by (30) (5) Schwartz et al., 2016; Brown et al., 2019). While further details are outside the present paper's scope, evaluating the genes associated with these toxins is should be given priority.

Species of the dinoflagellate genus, Dinophysis, produce various toxins, including pectenotoxin 2 (PTX2) and dinophysistoxin 1b (DTX1b) (63) (Nielsen et al., 2013). According to Schwartz (30) (2016), however, calculated field concentrations would have been too low to allow to support the idea these toxins act as allelopathic agents.

Some mechanochemical aspects of disulphide bonds (cross-links)

Zhang and Zhang(103) (2003), using a mechanochemical technique, single-molecule force spectroscopy with an atomic force microscope (AFM), explored the relation between rate-of-strain and opposing stress in pulling and breaking bonds in both polysaccharides and proteins. For example, they found breaking forces in the typically algal polysaccharides, λ-, β-, and ι-carrageenan all to be around 500 to 700 pN.

In contrast, disulphide links in protein were found by Wiita et al.(104) (2006) to have a lower breaking strength of around 100 to 200 pN, and they can be weakened by dithiothreitol (DTT) [show fig of the DTT and the cysteine molecules]. Disulphide links are important as they strengthen both proteins (105) (106) (Alting, 2003; Quigg et al., 2021) and polysaccharides (106) (Quigg et al., 2021) in biological systems by forming cross-links between polymer chains.

12. Mechanisms of killing microbes

Direct killing may be the strongest signal. Some bacteria produce toxins that are lethally toxic to microalgae. Hu et al. (107) (2019) found that algicidal bacterium, CZBC1, is lethal to the cyanobacteria, Oscillatoria chlorina, O. tenuis and O. planctonica, to the extent that the authors have patented culturing these bacteria to control cyanobacteria in aquaculture facilities. Hu et al. (107) (2019) also reviewed the effects of other algicidal bacteria on microalgae, including cyanobacteria. Bacteria of the genera, Cytophaga and Saprospura, contact and lyse dinoflagellates and diatoms. A strain of Pseudomonas putida kills the diatom, Stephanopyxis, by direct alginolysis, but most algicidal bacteria act indirectly by secreting algicidal compounds. Bacillus strain LZH-5 from Lake Taihu, China, acts strongly on Microcystis aeruginosa.

Concerning the size of the signalling (toxic) molecules, the marine bacterium, *Bacillus cereus* Strain CZBC1, produces an alginolytic compound retained by a 10 kDa filter (107) (Hu et al., 2019). On the other hand, Lee et al. (108) (2000) found that *Pseudoalteromonas* Strain A28 produces a serine protease activity responsible for algal lysis, but they also had DNase activity; the supernatant from Strain A28, which passed through a 10-kDa filter could kill the diatom, Skeletonema costatum. In addition, Hu et al. (107) (2019) showed that that Strain CZBC1 lysed O. chlorina and O. tenuis by direct alginolysis, while its extracellular products lysed O. planctonica. Various authors cited by Hu et al.(107) (2019) showed that algolytic effects of bacteria are concentration-dependent.

13. Quorum sensing

Quorum sensing (QS) is a density-dependent communicating mechanism that allows organisms to regulate a wide range of important processes and can be inhibited by quorum quenching (QQ), for example in marine organic aggregates (MOAs) (109) (Su et al., 2021) and probably also at larger scales. Falciatore et al. (70) (2000) may have weakened Svedrup et al.'s (110) (1942) old paradigm that plankton are passive and incapable of resisting physical forces at any scale. Reviewing post-Sverdrup findings that "[some] plankton control buoyancy, local fluid viscosity and life cycles", Falciatore et al. (70) (2006) showed experimentally that diatoms detect and respond to physicochemical changes in their environment using sophisticated perception systems based on changes in cytoplasm concentrations of Ca^{2+} as a second messenger (111) (Endo, 2006).

Microbes communicate with each other using diffusable molecules such s N-acetylhomosereine lactones (AHL). Communication of the information in a signal requires sensing of the signal and it is not clear whether the different types of sensing use secondary messengers sensu Endo (111) (2006). Nevertheless, these different signals are likely physiological and behavioural cell-density-dependent gene regulators (112) (Ianora et al., 2006), involving quorum sensing and controlling microbial processes.

Whether in bacteria, algae or metazoans, tighter spatial association will increase intensity of interactions, as well as reducing the distances and, mostly, the times of signal transmission (113) (Jenkinson and Wyatt, 1992), whether by diffusion or by radiation, of information agents such as pheromones, light, sound or other electrical or mechanical signals. Association may be effected by attractive behaviour or by rheological means, such as increasing the viscosity or the yield stress of the ambient medium. When yield stress is larger than the shear stresses tending to deform the ambient medium, the spatial distribution of particles, such as organisms, in the medium is gelled. Even when the yield stress is less than the ambient mechanical stresses, the increases viscosity will slow the medium's deformation and hence dispersion of the particles and molecules.

Modification of the mechanical (rheological) properties, such as viscosity (31) (54) (114) (88) (Jenkinson & Sun, 2010; Guadayol et al., 2020; Seuront et al., 2007; Kang at al., 2020), of the transmitting medium will also tend to reduce the intensity of signal transmission. Such modification is largely carried out by secreted EPS, particularly that bearing saccharide groups. Such rheological modification by EPS will therefore also modify the signals that signalling molecules, including toxins, transmit. Such EPS may thus be considered to include "auxiliary signalling molecules", which participate in niche engineering(115) (116) (117) (109) (110) (Hastings, 2007; Reddington et al., 2020), formerly called "physical environmental management"(118) (Jenkinson and Wyatt).

MOAs may be considered as 3D equivalents of marine biofilms (MBs) (119) (120) (8) (Camacho-Chab et al., 2016; Sretenovic et al., 2017; Wurl et al., 2017). In MOA- and BF-associated prokaryotes, including the Gram-negative alphabacterium, Paracoccus carotinifaciens, and the gammaproteobacterium, Pantoea ananatis, resistance to viral infection and to protozoan predation is achieved by secretion of various homosereine lactones and ammonium, respectively(121) (122) (109) (Jatt et al., 2014; Decho & Guttieriez, 2017; Su et al., 2021). In the bacterium, Vibrio cholerae, living in biofilms, resistance to protozoan grazing is effected by secretion of the metabolite at concentrations of up to 3.5 mM, which was found to reduce concentrations of the protistan grazer, Rhynchomonas nasuta, by >80% (123) (Sun et al., 2015).

By contrast, other bacteria, including the fish pathogen, Vibrio anguillarum, defend against viral (phage) infection by increasing expression of the ompK gene, which correlates with the degree of cell aggregation, being low in free-living variants (124) (Tan et al., 2015).The gene, ompK, produces N-acylhomoserine lactone (AHL) a molecule with QS signalling and many metabolic functions, and there may thus be a link among ompK, AHL and aggregation. So far, however, no causal mechanism among ompK, AHL and aggregation has been demonstrated. . Indeed, investigation of which genes are involved in producing enzymes involved in producing sugars and assembling them into polysaccharides such as EPS, as well as in EPS destruction, either in pro- or eukaryotic aquatic, single-celled organisms, appears to have started only recently (109) (Su et al., 2021).

AHLs are probably the most intensively studied class of mediators in cell-density-dependent gene regulation (112) (125) (Ianora et al., 2006; Pappas et al., 2004), and have been found in bacterial biofilms and marine snow, in which it is believed that bacteria, interacting with ambient pressures and constraints, control its form and phenotypic traits (126) (127) (Gram et al., 2002; Parsek & Fuqua, 2004). In biofouling, surface sensing via AHLs of bacterial biofilms is the initial step in the settling of the macroalga, Ulva (128) (129) (Tait et al., 2005; Wheeler et al., 2006).

Outside of biofilms and MOAs, microalgae, too, may alter behaviour in multi-celled organisms. Increases in water viscosity due to secretion of polymers by the haptophyte, Phaeocystis globosa, were observed to make swimming patterns in the copepod, Temora longicornis, more compact (87) (Seuront & Vincent, 2008), while the same species reduced measured feeding rates and filtering rates in Temora stylifera (130) (Li et al., 2021).

In bacterially-dominated biofilms, reviewed by Karn et al. (49) (2020) for their role in promotion or inhibition of corrosion, carbohydrates are generally the most abundant constituents, accounting for 40-95% by mass, while proteins typically contribute 1-60%, lipids 1-40%and nucleic acids 1-10%. The biofilm matrix acts as a recycling centre, by preventing the molecular products of live cells from dispersing and becoming lost to the consortium (131) (122) (Flemming and Wingender, 2010). These products include DNA, which could represent a reservoir of genes for horizontal gene transfer over small distances. Proteins, along with humic substances, might play a role as electron donors or acceptors by forming bacterial pili and nanowires. Modulation of rheological properties in biofilms, such as binding and stabilization, which affect retention of enzymes, may take place mainly by interactions with polysaccharides and proteins in the biofilm in reaction to mechanical forces, including those caused by deformation in the surrounding milieu (132) (131) (Hohne et al., 2009; Flemming and Wingender, 2010).

In a study related to photo-aggregation related to reactive oxygen species (ROS), Sun et al.(133) (2019) found that MOA size was positively related to protein/carbohydrate (P/C) ratio. The authors measured MOA size after ultrafiltration through 0.2-µm polycarbonate filters, which are hydrophilic, and allowing the polymer particles to re-form spontaneously in the filtrate, indicating that the inter-protein bonds were stronger than inter-polysaccharide bonds. In this respect, microrheological measurement carried out near phytoplankton cells (54) (Guadayol et al., 2020) found that viscosity increased by up to a factor of 2 to 5 at distances of 2 to 5 µm from the cell, typically declining to a factor of 1.2 at 10 £m from the cell. Furthermore, Stehnach et al. (69) (2021) report viscophobic turning in the flagellate, *Chlamydomonas reinhardtii*. Such behaviour might be critical to avoid being slowed down or trapped in mucus-reinforced zones of high viscosity, such as mucous traps (67) (96) (Blossom et al., 2012).

Like marine organic aggregates (MOAs), sewage sludge organic aggregates (SOAs) consist mainly of bacteria and diverse debris held together with loosely-bound EPS, in a slimy matrix of closely-bound or unbound EPS. The more concentrated nature of SOAs sewage sludge compared with the ocean, together the need to dewater it for economical transport and disposal, drives lively research activity on the rheology and surface science of SOAs (134) (Zhang et al., 2018), as well as on ecological chemistry of SOAs and biofilms (135) (49) (Lear, 2016; Karn et al., 2020). This activity provides results and expertise with a strong potential to inspire and guide research on MOAs.

14. Scales (granulometry) of toxicity

The term, toxicity, is usually used in the sense of causing harm by toxic molecules to living organisms. This implies one length scale of the chemical action (nm) and another at that of a cell (1-100 µm) or even of multicellular organisms. Toxic effects of molecules produced genomes may act at an environmental scale of km to 1000s of km and be more difficult to identify. In both spontaneously aggregated OM (136) (137) (Verdugo, 2012, 2021), or in biologically produced mucus, fluid flow and often molecular diffusion are reduced, while physical density may be increased or decreased (138) (139) (Drost-Hansen, 2006; Mari et al., 2008).

Much research is currently under way on the allelopathic effects of polyunsaturated aldehydes (PUAs), which act as signalling compounds (5) (Brown et al., 2019), which some diatoms release amongst the copious DOM, particularly towards the end of their blooms. Bartual et al. (140) (2017), working with laboratory blooms of the diatom, Thalassiosira rotula, studied the effect of adding PUA (2.5 µM mixture of three PUAs, 2E, 4E-heptadienal; 2E,4E-octadienal; 2E,4E-decadienal) on the aggregation of diatom-secreted TEP into OAs. They found that when the presence of PUA resulted in larger OAs and they suggested that PUA acts as glue, consolidating the OAs. Since larger OAs sinks faster as marine snow, the diatom-produced PUA might be contributing to increased vertical organic flux. The physico-chemical mechanisms of how these PUAs stick within TEP, as well as the genes responsible for PUA production require investigation.

15. Hydrophobicity, organic aggregate size and rheology

The polymeric secretions of algae and bacteria include polysaccharides, proteins, lipids and nucleic acids. Proteins are amphiphilic: they bear both hydrophilic (polar, wettable) and hydrophobic (non-polar) domains and they are considered to contribute most of the hydrophobicity of EPS. In contrast, polysaccharides are mostly hydrophilic through their polar oxygen groups. An increase in the degree of internal hydrogen bonding, however, can increase their relative hydrophobicity (52) (Santschi et al., 2020). Klun et al. (141) (2022) investigated colloidal OM (COM) secreted in culture by a chlorophyte nanoflagellate, *Tetraselmis* sp., a diatom, *Chaetoceros socialis* and a dinoflagellate, *Prorocentrum minimum*, all isolated from the Gulf of Trieste. Table 2 summarizes their results. The OM had been 0.45 µm e-filtered. It was then ultrafiltered through membranes with nominal molecular-weight cut-off of 5 kDa. The polysaccharide fraction was the highest in the retentate of *Tetraselmis* sp. (61%), while lipids and proteins each accounted for 19%. In the permeate, protein represented the highest portion (41%). The *C. socialis* retentate and permeate contained the highest polysaccharide levels (63% and 46%, respectively), followed by proteins (22% and 36%) and lipids (14% and 16%). *P. minimum* retentate and permeate showed very different compositions of secreted OM, with polysaccharide proportions of only 32 % and 25%, respectively, compared with high proportions of proteins (46% and 57%, respectively) and with intermediate proportions of lipids (22% and 17%, respectively). For all three taxa, the proportion of polysaccharides was thus higher in the retentate than in the permeate, while the proportion of proteins was higher in the permeate, while for lipids the corresponding situation varied. The overall proportion of lipids found in both the retentates and the permeates was surprisingly high, from 14% to 36%.

Table 2. Distribution of the integrated main groups of proton resonances (lipids, proteins and carboxyl-rich alicyclic molecules (CRAM), polysaccharides and formate) in 1H MNR spectra (6/ppm), concentrations of $C_{org.}$ (µmol L^{-1}) in retentates and permeates and % COC from exudates of cultured phytoplankters. Protons that resonated in certain chemical shift range of integrated main groups are in bold (second row). Summarized from ref (141) (Klun et al., 2022).

	Lipids	**Proteins and CRAM**	**Polysaccharides**	**Formate**	$C_{org.}$	**% COC ***
	HCH2-CH2-	**HC-HCOR**	**HC-OH HC-O-C**	**HCOO**		
6 **/ppm	0-1.8	1.8-3.0	3.0-4.6	8.0-9.0	µmol L^{-1}	%
			Tetraselmis sp.			

0.2 µm filtrate					915.1	
Retentate	19.4	18.8	61.4	0.4	364	39.8
Permeate	35.7	40.9	20.8	2.6	507	
Chaetoceros socialis						
0.2 µm filtrate					2285	
Retentate	14.4	21.9	62.9	1.1	526	23.0
Permeate	16.4	36.4	45.5	1.7	1765	
Prorocentrum minimum						
0.2 µm filtrate					439.3	
Retentate	21.8	45.6	31.9	0.8	154	35.1
Permeate	17.4	56.7	24.6	1.2	418	

Note(s): * Colloidal organic carbon percentage: %COC = C_{org} (retentate) x 100%/C_{org}. (0.2 µm filtrate).
** Chemical shift range in ^{1}H NMR spectra for each group of compounds.

16. Molecules, produced by other organisms and associated bacteria, that are toxic and allelopathic to phytoplankton

Vidal-Melgosa et al.(142) (2021) reported a polysaccharide of still unknown structure, called fucose-containing sulphated polysaccharide (FCSP) that appears to be directly secreted by diatoms. Detected by monoclonal antibody technique, it was found abundantly distributed on cell surfaces and spines of the diatom, Chaetoceros socialis, in spring blooms in the Helgoland Bight. It appears to have a complicated structure, and unlike other polysaccharides present, it lasted »10 days in laboratory culture. This suggests that, over a certain concentration, it might be very important in aggregating to particulate organic matter (POM), and thus mediating vertical flux (143) (Denis et al., 2022). This FCSP is strongly negatively charged, and thus form part of the complex of acid polysaccharides secreted by phytoplankton as diverse as dinoflagellates(66) (Honsell et al., 2013) and cyanobacteria(144) (Liu et al., 2015).

Some seaweeds and seagrasses also exert allelopathic action on harmful algae. Laabir et al. (145) (2013) showed that the methanolic and aqueous extracts of the seagrasses, Zostera marina and Z. noltii, inhibited the harmful dinoflagellate, Alexandrium catenella. These extracts contained flavinoids and phenolic acids, which were themselves toxic to A. catenella, The authors suggested that phenolic acids were the likely candidates for allelopathic action, and that increases in A. catenella blooms in lagoons and other French waters may have been partly caused by declines in seagrass beds.

Subsequently, Onishi et al. (146) (2014) showed that only whole-plant extracts of seagrasses, and not exudates, were algicidal. Two strains of Flavobacteriaceae isolated from biofilms on the seagrass leaves show algicidal activity on Alexandrium tamarense. This suggests that the above mentioned findings of Laabir et al.(145) (2013) might have been due to bacteria epiphytic on seagrass, leaves rather than to the seagrasses themselves, particularly as Flavobacteriaceae have been shown be algicidal towards several fish-killing rhaphidophytes, dinoflagellates and diatoms. Similarly in the freshwater Lake Biwa, Japan, the bacterium, Agrobacterium vitis, which colonises surfaces of leaves of the water plant, Egeria densa, is strongly allelopathic to the harmful cyanobacterium, Microcystis aeruginosa, and an increase over several years of E. densa has coincided with a reduction in blooms of M. aeruginosa (147) (Imai et al., 2013).

Bacteria in the mucus phycosphere of the diatom, Skeletonema costatum, and of the dinoflagellate, Scrippsiella trochoidea, were found by Yang et al.(148) (2013) to be able to lyse their host cells, leading to mass deaths of the hosts. The mechanisms for this lysis were not elucidated.

Research on metabolomics in consortia (see section 6), particularly in biofilms, is intense in the fields of biocorrosion (49) (Karn et al., 2020), medicine (149) Qian et al., (2020) and sewage sludge (150) (Kotay & Das, 2010). It appears, however, still too rare in aquatic plankton ecosystem (116) (117) (Reddington et al., 2020). In such biofilm consortia, progress is being made in semi-automated data mining of intra- and extra- cellular DNA to identify gene sets involved in microbial metabolism and production of different molecules. The software is inspired by homologous data mining of texts on the internet. Thakur et al. (151) (2023) have made a promising start on bacterial consortia in biofilms associated with biocorrosion. The technique may be capable of development to mine pro- and eu-karyotic gene sets from ecosystems such as the world ocean, stored in GenBase. Singh(152) (2021) pointed out that in human bodies, as in the ocean, glycoproteins play crucial roles in biological processes like cell signalling, host-pathogen interaction and disease. Glycoproteomics aims to determine the positions and identities of the complete repertoire of glycans and glycosylated proteins in a given cell or tissue. The roles of glycoproteomics in ocean consortia may be analogous, and the links with genes, as least for key processes, should be established. While the main drivers of Thakur et al.'s (151) study may have been the need to understand and control biocorrosion of steel by sulphur-reducing bacteria, and those of the studies cited in Singh's mini-review are improvement in human health, the purposes of mining ocean-derived data on gene sets might be to understand and control bio-geo-physico-chemical fluxes of matter and energy in the oceans, as well as cell-cell signalling and other interactions and their roles in ecological control (6) Yamasaki et al. 2009).

17. Organic polymers and Gaia

Some molecules polymerize, and the resultant biopolymers strengthen organic aggregates, biofilms and volumes of water with increased viscosity (135) (153) (4) (Lear, 2016; Alldredge et al., 1993; Jenkinson et al., 2015). Biopolymers tend to concentrate at surfaces, particularly in the surface microlayer (SML). Here they will thus tend to change properties including surface tension and 2D viscoelasticity (154) (Williams et al., 1986), as well as 3D viscosity(155) (156) (Carlson, 1987; Zhang, et al., 2003), thus modulating ocean-atmosphere fluxes of various types of matter and energy (157) (Jenkinson et al., 2018). Since organisms are genetically controlled and they participate in the production, metamorphoses and breakdown of these biomolecules, their genomes thus influence oceanic and atmospheric physico-chemical conditions. Where they are harmful, this may be considered toxicity at the scale of the Planetary ecosystem, consistent with evolution of Gaia (158) (159) (Lovelock, 198(158)8; Lenton, 1998) by natural selection of its genes (11) (Dawkins, 2016). An example of such Planetary scale toxicity, at least from an anthropic point of view, is the current increase in atmospheric and oceanic CO_2.

18. Polymer modulation of fluxes: discovering the genomes involved.

Fluxes of matter and energy between the ocean and the atmosphere are functions of physical, chemical and biological parameters. In particular, viruses, bacteria *sensu lato* and eukaryotic protists are expelled towards the atmosphere by bursting bubbles, and may then be carried by updrafts and winds from a few metres(160) (Thornton, 1999) to thousands of km (161) (Hamilton & Lenton 1998). The surface charge and hydrophobicity of cells and non-living matter strongly influences tendency to be expelled(9) (Jenkinson et al., 2021). For species in which such expulsion leads to dispersion and greater Darwinian fitness, it is may represent a pre-adaptation leading to further evolution of hydrophobic/hydrophilic control of ocean-atmosphere flux. Irrespective of the length, time or hyperspace scales at which such natural selection is driven, it will have effects also over other biological and chemical species (collateral effects) in driving ocean-atmosphere fluxes, which are important for climate control (157) (9) (12) (Jenkinson et al., 2018; 2021; IPCC, 2021).

Notably in the SML and biofoam, both important to modulating ocean-atmosphere fluxes of matter and energy, the EPS present is shows different characteristics. The different species and their expressed genes that produce the EPS thus determine the different ways in which EPS modulates these fluxes.

19. Vertical organic flux of OM.

The use of metabolomics and proteomics has already illuminated the mechanisms of biological response to many chemical cues and may be helpful in determining their molecular targets. Overall, the ocean represents a vast source of novel interactions and well as new molecules (30) (Schwartz, 2016). As Schwartz (30) (2016) pointed out, both models and laboratory experiments are needed to evaluate the roles of toxic, allelopathic and signalling interactions in the pelagic. To these interactions might be added those involving modulation of fluxes, diffusion and fluid deformation.

Vidal-Melgosa et al.(142) (2021) showed the importance of fucose-containing sulphated polysaccharide (FCSP), which is secreted by diatoms, particularly *Chaetoceros socialis*, which produces mucilaginous colonies and which dominated the North Sea blooms they worked on. FCSP was far more resistant than the non-sulphated polysaccharide, laminarin, to degradation by *Bacteroidea* and *Gammaproteobacteria*. These organisms encode enzymes for laminarin degradation, and they are key degraders of laminarin in the field (162) (Teeling et al., 2012). Because FCSP is degraded far more slowly than laminarin, Vidal-Melgosa et al. (142) (2021) suggested that *C. socialis* and other diatoms that secrete large amounts of FCSP, are likely among the key species that modulate vertical carbon flux in aggregates, thus contributing to the sequester of CO_2 from the atmosphere.

20. Ocean foam

As well as sequestration of CO_2, ocean foams, such as whitecaps, help to keep the Earth cool (9) (Jenkinson et al., 2021). The fraction of incident solar radiant energy that is reflected is known as albedo. Foam-free ocean surface has a typical albedo of only ~0.05, but most foam is white and its albedo is ~0.5. Therefore, when foam is more stabilized by algal DOM percentage foam cover increases and the oceans reflect more solar energy back into space, reducing solar heating of the Earth (163) (164) (Stabeno and Monahan, 1986; Evans et al., 2010). The decay of these foams proceeds by the coalescence of its constituent bubbles as the inter-bubble water drains, allowing the surfaces of adjoining bubbles to touch and burst (165) (Cantat et al., 2013). Draining is retarded and foam lifetime becomes longer if the liquid is a surfactant that binds to bubble surfaces or if it is more viscous. Relative to their duration in waters of low phytoplankton biomass (PB) or low primary production (PP), ocean foam duration is increased in waters of high PP or high PB (166) (Callaghan et al., 2012), particularly in the presence of certain specific taxa. Blooms that produce a lot of foam are dominated by dinoflagellates on North Atlantic and Asian coasts (167) (Pierce et al., 2003), including *Margalefidinium polykrikoides* (168) (Vargas-Montero et al., 2006), *Karenia* spp. blooms dominated by *K. selliformis* in Russian Pacific waters (84) (Orlova et al., 2022) as well as the haptophyte, *Phaeocystis globosa,* in the North Sea (169) (Kesaulya et al., 2008). Blooms of the fish-killing dinoflagellate, *Alexandrium monilatum,* on the Pacific coast of Costa Rica have been associated with cream- or beige-coloured foam, with the water producing violent itching. The species also produces goniodomines (170) (171) (Calvo et al., 2005; Lassus et al., 2016). The primary chemistry of the EPS and associated genomes of these organisms, which also frequently increase viscosity and stabilize foam, requires further investigation.

21. Conclusions

Ocean ecosystems that need data mining of pro- and eu-karyotic genomes may include: biofilms on marine plastic debris, macroalgae and seagress, sea-ice structures, marine organic aggregates, the sea-surface microlayer and ultimately the whole ocean. Boundaries of consortia, at all granularities, need to be investigated, particularly the ocean-atmosphere boundary. Because the physical properties of polymers, both proteins and polysaccharides control water shearing and molecular diffusion, such studies should be combined with rheological studies at appropriate scales.

Fluxes of many types of matter and energy in the oceans are modulated, not only by proteins and lipids, but more especially by different dissolved and particulate polysaccharides. An important key to understanding, and perhaps ultimately controlling, these oceanic fluxes thus lies in exploring associations between these polymers and the genes present and expressed in the planktonic microbial community. Polysaccharides, as well as glycoproteins, glycolipids and some proteins are assembled by enzymes, which are themselves proteins. Different polysaccharides are therefore unlikely to be "mirrored" directly by corresponding genomes. This difficulty has slowed progress in ocean glycomics. Recently, however, enzymes responsible for selective cleavage of specific links in different marine microbial polymers have been linked to their roles in bacteria and diatoms in facilitating or preventing aggregation and de-aggregation of OM and adhering microbes(142) (Vidal-Melgosa et al., 2021). This exciting avenue needs to be accelerated and combined with quantitative multi-scale sampling and analysis of biomolecules as well as matching sampling of genes (already in *GenBase*), organisms, with the addition of a new database of measured rheological properties in the same environment. Intelligent data-mining of these database may take advantage of GNPS (55) (Aron et al., 2020) and techniques already developed for bacterial biofilms involved in corrosion (151) (Thakur et al 2023) (see sections 6 and 18). Expansion of such studies to ocean exploration is likely to vastly improve understanding of ecological and metabolic interactions, as well as fluxes, in the ocean. As a bonus they are almost certain to reveal commercially exploitable natural products.

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