DOES BLOOM PHYTOPLANKTON MANAGE THE PHYSICAL OCEANOGRAPHIC ENVIRONMENT?

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1. ABSTRACT

We briefly review three classes of physical process that are modified by phytoplankton. They are: 1) light absorption and reflection; 2) stratification; 3) ambient, local deformation. It is concluded that biomodification is likely to be generally more marked in blooms than elsewhere. Evolutionary pressure to develop environmental management of physical processes as part of a life strategy is likely to be stronger on bloom species than on those which habitually remain rare. Such pressure is also likely to be stronger on organisms which habitually occur in sheltered water than on those adapted to turbulent conditions.

2. INTRODUCTION

Chemical constituents in the sea modulate phytoplankton dynamics, and it is well known that phytoplankton dynamics control the sea's chemistry (Redfield, 1934). Physical processes control the dynamics both of phytoplankton production (Rothschild & Osborn, 1988; Cushing, 1989). Phytoplanktonic interaction with the light field by absorption, reflection and scattering (and hence interaction also with their deeper-living relations) has long been appreciated and modelled as a two-way process (Platt, 1978), yet the way phytoplankton influences other aspects of the physical environment has received less attention (Jenkinson, 1986; Wyatt et al., 1993).

Where different physical regimes occur over a short distance, some phytoplankton is able to select one regime over another by migration (Crawford & Purdie, 1992; Jenkinson & Wyatt, 1992). Phytoplankton, however, can also modify aspects of its ambient physical regime. This paper discusses whether some of this modification may have come about by Darwinian evolution of environmental management strategies.

3. FACTORS SUSCEPTIBLE TO MODIFICATION

3.1. The light field. The more competition there is for light in a forest, the more overall advantage tall trees have over short ones (Frontier & Pichod-Viale, 1991, p. 29). Like the leaf canopy, phytoplankton, when suffi-
ciently abundant, reduces illumination lower down, and so can shade out competitors. Migration of shaded-out phytoplankton to the surface is a frequent precursor of surface red tides (Wyatt & Horwood, 1973). In sheltered waters, floating plants, such as *Ulva* (Sfriso & Pavoni, 1993), duckweed or water lilies (Frontier & Pichod-Viale, 1991), may substitute for phytoplankton as the most successful competitor for light.

3.2. **The temperature field and thermal stratification.** Lewis et al. (1983) predicted that layered populations of plankton would, by their absorption of sunshine, change the thermal stratification field. Subsequently Sathyendranath et al. (1991) showed that the surface temperature of the Arabian Sea could be increased by up to 4°C by phytoplanktonic sunshine absorbance, a phenomenon already noted more locally in patches of decaying, slimy *Noctiluca* (Grindley & Taylor, 1964).

3.3. **The (local) deformation and dispersion field.**

3.3.1. Floculation, adhesion and cohesion. Smayda (1970) pointed out a large discrepancy between laboratory measurements of phytoplankton sinking rates, carried out mainly on single cells and colonies, and evidence from deep-water sampling of much faster sinking. The principal origin of this discrepancy was later found to be flocculation of phytoplankton and other material into organic aggregates, held together by a complex mix of surface forces, polymeric adhesives and the glycocalyx of actively growing bacteria, the whole often reinforced by fibres (Massalski & Leppard, 1979; Biddanda, 1986; Allredge & Silver, 1988). Since sinking speed is related to the size of the aggregate, it is the amount, the density and the adhesive properties of mucus which modulate this flux and the associated draw-down of fixed CO₂. Aggregates are also turbulence-free zones low in dispersion, which can thus support processes such as anaerobic N₂-fixation otherwise impossible in oxygenated water (Paerl et al., 1987).

3.3.2. Cell-to-cell adhesion and communication. Polymeric, functional adhesives, often observed as a glycocalyx, but sometimes as more tenuous "strings", hold colonies of phytoplankton cells together. Even non-colonial phytoplankton may be surrounded by a glycocalyx (Yokote et al., 1985). The role of these polymers has been much explored in relation to their chemical, adsorbent and ion-exchange properties (Decho, 1990). The mechanical and stereomorphic recognition properties of cell adhesion in higher organisms act in the glycocalyx, are controlled genetically, and themselves determine the organism’s form (Edelman, 1993).

Schmid (1993) has shown that planktonic algal gametes use both pheromones and matching of cell-surface polymers for cell-cell recognition. At the length scales of polymers, recognition grades into control of adhesion. The research reviewed by Edelman suggests avenues for further study of cell-cell recognition and adhesion in planktonic phytoplankton cells in relation to abundance can be closely related to growth, produce previously overlooked transparencies (Kierboe & Hansen, 1993).

3.3.3. Mucus as a thickener. Mucus was used here of an agent which reduces adhesion. Where the thickness is largely a function of the local scales of length, time and forces. The rate of sedimentation to water and salt, which is carried by phytoplankton-produced polymers is inversely related to shear rate. Elastic properties of the same material. Both well with phytoplankton abundance distribution in situ is hierarchically ordered and increased viscosity should reduce the smallest turbulent eddies and increase inson, 1993). We have suggested a "mechanical" (as well as adhesion) mechanism to keep mechanical mechanisms both in theory (Jenkinson, 1993a) and in modification (1992; Wyatt et al., 1993).

3.3.4. Modulation of cell-to-cell communication. The long-chain colloids which communicate with other cells as "ropes" are polymeric exudates from Adradiana and other microorganisms. Only cross-linked colloids produced by exudates from Adradiana are likely to pass through the chemical environment. The chemical environment may thus be able to change cell-cell interactions as well as to regulate these means, the plankton may multiply in numbers and predator attack time, the cells (shear rate/rate of a given present microzones and patch formations (Jenkinson & Wyatt, 1992).

It is generally accepted (Whitman, 1985) that the bloom formation may depend on environmental factors, and that the increase in the reduction of grazing. With sufficient the active exopolymers, the rate
recognition and adhesion in plankton. Recent work on differential adhesion by phytoplankton cells in relation to ambient shear rate has also shown that stickiness can be closely related to growth phase in diatoms, which furthermore produce previously overlooked transparent exopolymeric particles (TEPs) in the medium (Kiorboe & Hansen, 1993).

3.3.3. Mucus as a thickening agent. The term, "thickening" is used here of an agent which reduces deformation rate, without stopping it altogether like adhesion does. Where the difference lies, depends of course on the scales of length, time and forces. The viscosity of seawater comprises a component due to water and salt, which is unaffected by shear rate, plus one due to phytoplankton-produced polymers and fibres. This polymeric viscosity is inversely related to shear rate. Elasticity in seawater is apparently produced essentially by the same material. Both elasticity and polymeric viscosity correlate well with phytoplankton abundance, and their variance is Gaussian (that their distribution in situ is hierarchically lumpy) (Jenkinson, 1993b). This elasticity and increased viscosity should reduce dissipation-scale shear rate, enlarge the smallest turbulent eddies and increase turbulence intermittence (Wyatt & Jenkinson, 1993). We have suggested a few paradigms for evolution of such thickening (as well as adhesion) mechanisms by plankton, as well as possible roles of mechanical mechanisms both in the toxic action of some fish-killing species (Jenkinson, 1993a) and in modifying community structure (Jenkinson & Wyatt, 1992, Wyatt et al., 1993).

3.3.4. Modulation of deformation, dispersion, trophic dynamics. The long-chain colloids which comprise mucus can take a variety of configurations. Important for their physical properties are the degree both of bunching together as "ropes" (as well as their diameter and "mesh" size) and of cross-linking. Only cross-linked colloids produce gels. Reduction of copepod grazing by polymeric exudates from Adriatic diatoms seems to be partly mechanical and partly due to unknown causes, probably chemical (Malej & Harris, 1993). By slightly changing the chemical environment around their exopolymers, phytoplankton may thus be able to change the mechanical properties of these polymers markedly, as well as to regulate their adsorption and release of ions. By these means, the plankton may manage not only local shear rates, encounter rates and predator attack time, thereby increasing or decreasing Deborah numbers (shear rate/rate of a given process) associated with grazing, but also nutrient microzones and patch formation, thus influencing trophic and nutrient dynamics (Jenkinson & Wyatt, 1992).

It is generally accepted (Wyatt & Horwood, 1973) that the intensity of bloom formation may depend on reduction of grazing pressure. Malej and Harris's results suggest that exopolymeric thickening of the water plays a part in this reduction of grazing. With such a mechanism, moreover, the more abundant the active exopolymers, the more they would be expected to reduce cope-
pod grazing. Such control may thus be generally more important in blooms than elsewhere.

3.3.5. To what extent does structural (thickening) mucus co-vary with toxins? By incorporating them in, and perhaps binding them to, polymeric gels, phytoplankton regulates diffusion of extracellular products such as toxins. Incorporation of toxin may have evolved also to protect extracellular mucus against predation. For either reason, or both, mechanical thickening and toxin occurrence may frequently co-vary in the field. For instance, association of the bactericide, acrylic acid, with *Phaeocystis* mucus (Sieburth, 1964; Grossel & Delesmont, 1986) may explain its accumulation during blooms, facilitating its subsequent spectacular transformation into foam.

4. MANAGEMENT, OR JUST BIOMODIFICATION?

4.1. Abundance. The more abundant organisms become, the more environmental impact potential they must generally have. It is in bloom organisms that biomodification of physical processes, including the light field, stratification and polymeric structuring, is likely to occur the most. An organism which becomes abundant for the first time in a particular environment will modify the environment as a side effect of its abundance. Darwinian selection pressure will then tend to act by favouring the genotypes pre-adapted to the modification and those which modify the environment to their own best advantage. Furthermore, organisms with most highly evolved powers of acting in concert to modify their environment may have the greatest potential to develop this biomodification into a strategy of environmental management. Additionally, biomodification is likely to be more marked in blooms than elsewhere, allowing research here to be relatively easy, precise and cheap.

4.2. Limitation by physical forces. All structuring mechanisms, including biological, whether terrestrial or aquatic, are limited by ambient deformation rates and forces: in the water (too much current or turbulence); in the air (too much wind); on land (too much ploughing, erosion, etc.). Exceptional blooms develop most frequently during calm conditions, and increases in wind or current speed tend to precede their demise. A physical environmental management strategy may thus be of potential advantage to plankton, more particularly to those organisms which habitually form dense blooms. Organisms which usually remain rare, however, and those specialised for life at high shear rates, are unlikely to have evolved strategies of physical environmental management to the same extent.

5. REFERENCES


Population studies of *Dinophysis acuminata* embayment

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Abstract

Population abundance of *Dinophysis norvegica* Clap. et Lach. was studied. The long-term objective of establishing a relationship between stratification and *Dinophysis* population abundance is to determine whether future warming will result in an increase or decrease in *D. norvegica* blooms. The population remains unknown in the population of *D. acuminata* in the Mid-Atlantic Bight.

Introduction

Diarrheic shellfish disorder resulting from the ingestion of polyether-type toxins being produced by bivalves. The association of *Dinophysis* species with shellfish has been confirmed (Quilliam et al., 1991). The purpose of this study is to determine the relationship of *Dinophysis* spp. in the Greenwic

Material and Methods

A one-liter surface water sample was collected in an area with no tidal influence. The sample was concentrated by filtration through a 50 μm filter. This processing method was used to concentrate the sample for subsequent analysis. Cells were counted live in a hemacytometer and stored at -20°C until analysis. The cells were stained with DAPI and mounted in *Dinophysis* spp. fluoresce blue.