



*J. Plankton Res.* (2015) 37(6): 1100–1109. First published online August 27, 2015 doi:10.1093/plankt/fbv071

## HORIZONS

# Thalassorheology, organic matter and plankton: towards a more viscous approach in plankton ecology

IAN R. JENKINSON<sup>1,2\*</sup>, XIAO XIA SUN<sup>3</sup> AND LAURENT SEURONT<sup>4</sup>

<sup>1</sup>CHINESE ACADEMY OF SCIENCES INSTITUTE OF OCEANOLOGY, STATE KEY LABORATORY OF MARINE ECOLOGY AND ENVIRONMENTAL SCIENCES, 7, NANHAI ROAD, QINGDAO 266071, PR CHINA, <sup>2</sup>AGENCE DE CONSEIL ET DE RECHERCHE Océanographiques, LAVERGNE, 19320 LA ROCHE CANILLAC, FRANCE, <sup>3</sup>JIAOZHOU BAY MARINE ECOSYSTEM RESEARCH STATION, CHINESE ACADEMY OF SCIENCES INSTITUTE OF OCEANOLOGY, 7, NANHAI ROAD, QINGDAO 266071, PR CHINA AND <sup>4</sup>CNRS, UNIV LILLE. UNIV LITTORAL COTE D'OPALE, UMR 8187, LOG L'OBORATOIRE D'Océanologie et de Géosciences, F-59000 LILLE, FRANCE

\*CORRESPONDING AUTHOR: ianjenkinson@qdio.ac.cn

Received December 17, 2014; accepted August 4, 2015

Corresponding editor: John Dolan

Rheology is the study of how materials deform, particularly those materials not conforming to ideal solid or ideal liquid models. This is the case for much ocean water, due largely to the presence of organic exopolymeric substances, including mucilage, derived mostly from phytoplankton and bacterioplankton. This material makes the water more viscous and gives it elasticity. Thalassorheology concerns the rheology of seawater and other natural waters. Ocean scientists and rheologists generally know little of each other's work. The aim of this paper is to show that collaboration would be beneficial to modelling the oceans, and to guide the formation of interdisciplinary teams, and a working has been formed for this purpose.

**KEYWORDS:** rheology; polymers; exopolymeric substances; harmful algal blooms; phytoplankton; zooplankton; bacterioplankton; climate change; viscosity; biology-physics interaction

## INTRODUCTION

Nearly 30 years have elapsed since Jenkinson (Jenkinson, 1986) measured viscosity increased up to 400 times in phytoplankton cultures, while Carlson (Carlson, 1987)

and Zhang *et al.* (Zhang *et al.*, 2003) measured increased bulk-phase viscosity in water from, respectively, sea-surface slicks and the sea-surface micro-layer. Jenkinson (Jenkinson, 1986) also cited published reports of striking

bulk(-phase) rheological properties in phytoplankton blooms described as viscous, slimy, ropy or springy, like egg white, and in which phytoplankton mucus clogged and even broke fishing nets, as well as trapping gas bubbles and mineral particles. Jenkinson (Jenkinson, 1993b) and Jenkinson and Biddanda (Jenkinson and Biddanda, 1995) measured viscosity and elasticity in seawater, and found that viscosity was positively related to chlorophyll *a* levels. Viscosity was measured in *P. globosa* blooms by Seuront *et al.* (Seuront *et al.*, 2006, 2007), Seuront and Vincent (Seuront and Vincent, 2008) and Kesaulya *et al.* (Kesaulya *et al.*, 2008). These authors showed how viscosity and foam formation, as well as zooplankton swimming, is modified by *Phaeocystis*-derived exopolymeric substances (EPS), as a function of the development phase of *Phaeocystis* blooms.

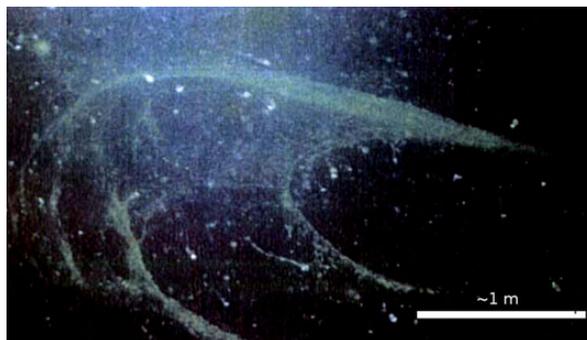
Figure 1 shows accumulation of *Phaeocystis* sp.-produced foam. EPS can also form aggregates of gel (thus of much increased viscosity), up 1 m in size. Figure 2 shows a giant organic aggregate of EPS, which can form during “mucus events,” for example in the Northern Adriatic (Stachowitsch, 1984). These examples are exceptional events representing only the “tip of the iceberg” in EPS thickening of natural waters. Despite the many published observations of large, exceptional increases in viscosity, few quantitative data on biologically modulated natural-water viscosity are yet available, to allow modelling of their effects.

This paper briefly intends to bridge the gap between organic matter (OM) dynamics and thalassorheology, which is the rheology, particularly the viscosity, of ocean water and other natural waters. We aim to draw attention to this promising and novel area of research and to stimulate further field and experimental work to improve models of different ocean processes at scales from micrometre to millimetre (see next section).

We expressly consider only molecular viscosity, which is defined either as dynamic viscosity  $\eta$  or as kinematic viscosity  $\nu = \eta/\rho$ , where  $\rho$  is fluid density. Turbulent viscosity, which exists only at scales above the length scale of the smallest turbulent structures, at which the Reynolds number = 1 (Kolmogorov, 1962), is outside our scope. The paper will, however, consider the effects of swarming and synchronized swimming on viscosity. We also stress that communities of marine scientists and rheologists are too little aware of each other, and this hampers progress that would result from a trans-disciplinary thalassorheological approach. The aim of this Horizons paper is not to review the field, which was initiated by Jenkinson and Sun (Jenkinson and Sun, 2010), but rather to draw the attention of the ocean and freshwater plankton research community to how thalassorheology in its different aspects, constrains and is manipulated by the plankton, with major effects caused by cascading to scales from



**Fig. 1.** Foam on the beach at Yamba, north of Sydney, Australia, produced from EPS, believed to be primarily secreted by *Phaeocystis* sp. Remastered from [http://cfb.unh.edu/phycokey/Choices/Prymnesiophyceae/PHAEOCYSTIS/Phaeocystis\\_Image\\_page.html#pic08](http://cfb.unh.edu/phycokey/Choices/Prymnesiophyceae/PHAEOCYSTIS/Phaeocystis_Image_page.html#pic08) (consulted 30 July 2015). (c) Icon Images.



**Fig. 2.** Marine organic mega-aggregate during a mucus event in the northern Adriatic. Its form reflects deformation by a large turbulent eddy. Remastered from Stachowitsch *et al.* (Stachowitsch *et al.*, 1984).

the subcellular to the global. Symmetrically, other work is needed to draw thalassorheology to the attention of the rheological community.

## THALASSORHEOLOGY

Molecular (i.e. non-turbulent) viscosity is produced by friction between its molecules of water and salt (scale  $\sim 0.1$  nm) and of molecules of EPS (scale  $> \sim 100$  nm) (Conlisk, 2013). To learn more about rheology, readers are referred to textbooks such as Barnes *et al.* (Barnes *et al.*, 1989) or online sources such as Wikipedia (Wikipedia, 2015). Viscosity controls most hydrodynamic processes at the ocean micro-scale, within which most currently studied planktonic processes occur. The present paper thus considers only properties measured and processes occurring at length scales from  $1 \mu\text{m}$  to  $\sim 1$  cm. These include viral, bacterial and parasitic infection, nutrient uptake, aggregate formation, light harvesting,

competition, predation and much social behaviour. At scales smaller than  $\sim 1 \mu\text{m}$ , viscosity grades into microviscosity and surface science, and is treated elsewhere (Jenkinson, 2014; Mohammed, 2015; Jenkinson *et al.*, in press).

Secondary effects can cascade across length scales, for example down to molecule-scale chemistry and up to global-scale biogeochemistry. Examples of cascading to larger scales are given by Ho and Nossair (Ho and Nossair, 1981) for small turbulence structures morphing into larger structures, by Calleja *et al.* (Calleja *et al.*, 2009) for OM in the sea-surface layer driving global-scale dynamics of  $\text{CO}_2$ , by Prairie *et al.* (Prairie *et al.*, 2012) for up- and down-scale cascading of biophysical interactions in plankton, by Mitchell *et al.* (Mitchell *et al.*, 2008) for cascading from the primary scales of plankton organisms up to those of fisheries and productivity and finally by Falkowski *et al.* (Falkowski *et al.*, 2008) for scale transfer from microbes to Earth-scale biogeochemical cycles.

Seawater viscosity is generally, often just implicitly, considered to be controlled by temperature and salinity (i.e. by water and salt molecules) alone. The role of EPS in modulating seawater viscosity is poorly known despite claims that polymers and mucus may be used by phytoplankton to manage, or engineer, flow fields (Margalef, 1978; Jenkinson, 1986; Wyatt and Ribera d'Alcalà, 2006) and many other aspects of their environment (Reynolds, 2007; Harel *et al.*, 2012).

Under the assumption of spatially and temporally homogeneous viscosity produced by EPS, Jenkinson (Jenkinson, 1986, 1993b) modelled how increased viscosity in the sea would damp isotropic turbulence by increasing the length and time scales of Kolmogorov eddies. The widely observed biological modifications of seawater viscosity (Jenkinson and Sun, 2010) are compatible with a habitat modification that creates more favourable, turbulence-free, conditions critical for the development of plankton such as dinoflagellates (Margalef, 1978; Margalef *et al.*, 1980; Wyatt, 2014) and colony-forming *Phaeocystis*.

A body of literature on measurements and the effects of thalassorheology is growing (Jenkinson, 1986, 1993b, 2014; Seuront *et al.*, 2006, 2007, 2010; Kesaulya *et al.*, 2008; Rhodes, 2008; Seuront and Vincent, 2008; Jenkinson and Sun, 2011). Jenkinson and Sun (Jenkinson and Sun, 2010) reviewed thalassorheology, while Jenkinson (Jenkinson, 2014) and Mohammed (Mohammed, 2015) provide reviews of small-scale and surface effects in relation to plankton.

Despite considerable recent efforts to couple biological and physical measurements (Doubell *et al.*, 2009), there remains a lack of measurements of ocean viscosity at spatial and temporal resolution compatible with that of turbulence and with that of turbulence measurements.

## ORGANIC MATTER IN NATURAL WATERS

OM in natural waters may be classified into dissolved OM (DOM, in the range  $0.1\text{--}0.5 \mu\text{m}$ ), and larger particulate OM (POM) (Chin *et al.*, 1998) that scale up to 5-m-sized aggregates observed in the Northern Adriatic (Fig. 2) (Stachowitsch, 1984; Žutić and Svetličić, 2006). Most DOM and POM in the oceans originate from primary production (Hansell *et al.*, 2009), and a large proportion from EPS (Thornton, 2014). Intermediate between DOM and POM in molecular mass and mechanical (rheological) properties, the class of colloidal OM is sometimes distinguished.

In the oceans, the total amount of DOM is more than 200 times that of the biomass (Hansell *et al.*, 2009), with a mean concentration of  $\sim 0.5 \text{ g C m}^{-3}$ . Most of this DOM is recalcitrant, with a half-life of millennia (Jiao *et al.*, 2010), and is distributed fairly homogeneously. Surface-water DOM concentrations range upwards from  $0.48 \text{ g C m}^{-3}$ , with typical values around  $0.90 \text{ g C m}^{-3}$  in the tropics and subtropics, but only  $0.48, 0.60 \text{ g C m}^{-3}$  in sub-polar seas and the Southern Ocean. Concentrations of POM are considered by Druffel *et al.* (Druffel *et al.*, 1992) to be 10- to 30-fold less than those of DOM.

In laboratory systems of natural seawater rendered abiotic, some of the DOM spontaneously aggregates into POM; while some POM also dissolves into DOM (Chin *et al.*, 1998). In the natural environment, biological processes also both produce and consume DOM, as well as POM of different size classes. Thornton (Thornton, 2014) further suggested that compounds of unknown function dominate DOM release by phytoplankton, but some biological functions are known. Sharp (Sharp, 1977) famously asked, “Excretion of organic matter by marine phytoplankton: do healthy cells do it?” In the light of abundant later evidence that they do, Bjørnsen (Bjørnsen, 1988) asked “Why?” Wyatt and Ribera d'Alcalà (Wyatt and Ribera d'Alcalà, 2006) answered that phytoplankton cells do it, partly, for “ecosystem engineering” (Jones *et al.*, 1994), also referred to as “environmental management” (Jenkinson and Wyatt, 1995) or “niche-construction” (Odling-Smee *et al.*, 2003). Wyatt and Ribera d'Alcalà (Wyatt and Ribera d'Alcalà, 2006) proposed many examples of ecological engineering, and then asked a third question, “Do healthy cells have external tissues?” Examples of ecosystem engineering include colony production and maintenance, one role of which may be “keeping the family from drifting apart” (Jenkinson and Wyatt, 1992), and facilitation of both quorum sensing (Ragni and Ribera d'Alcalà, 2004) and quorum action (Quesada *et al.*, 2006) by groups, swarms or colonies of cells.

Evidence of “lumpy” or heterogeneous rheology, perhaps contributed at least partly by organic flocs comes from at least four sources:

- (i) Jenkinson (Jenkinson, 1993b) reported variability in EPS viscosity within 1-L seawater samples, and suggested that “centimetre-scale (or smaller) flocculation may have occurred in the samples during storage and transport”;
- (ii) micro-scale heterogeneity in phytoplankton concentration within a Niskin bottle (Wolk *et al.*, 2004);
- (iii) spontaneous formation of POM from DOM in seawater by abiological processes (Chin *et al.*, 1998);
- (iv) the aggregation found in phytoplankton fluorescence at sub-centimetre scales (Doubell *et al.*, 2009).

The presence of flocs, or “lumps,” is likely to make both mean and variance of EPS viscosity a function of length scale (Jenkinson and Sun, 2011). Further candidate parameters defining this function are size, shape and material properties of the flocs. While the shear rates of rheological measurements had been designed roughly to match those of turbulent eddies at typical ocean shear rates, the length scale of measurements, corresponding to gap between the inner and outer rotating cylinders in a Couette-type rheometer (Barnes *et al.*, 1989; Jenkinson, 1993b), was usually 0.5 mm, zero to two orders of magnitude smaller. Since the 1990s, the science of Rheology is increasingly addressing problems of heterogeneous materials (Coussot, 2005), and thus provides inspiration for modelling and measuring lumpy seawater viscosity.

## ORGANIC MATTER AND THALASSORHEOLOGY

Miyake and Koizumi (Miyake and Koizumi, 1948) provided measurements of seawater viscosity as a function of temperature and chlorinity, using high shear rate capillary flow. They reported, “The most important source of error might be due to a delicate change in the condition of the inner wall of the capillary.” Jenkinson (Jenkinson, 1993b) already suggested this “error” may have been caused by OM. Carlson (Carlson, 1987) observed water from sea-surface slicks to be syrupy, and using a proxy, fluorescence depolarization, measured increased bulk-phase viscosity in water from them.

Although thalassorheology has been measured and reviewed over the last three decades, it has, however, still been relatively seldom considered in co-ordinated plankton research projects. Examples of its manifestation include bubbles that were prevented from rising in a red tide of *Karenia mikimotoi* (Jenkinson and Connors, 1980). In phytoplankton cultures (Jenkinson, 1986), viscosity up

to 400 times that of the culture medium was measured at a shear rate of  $0.0021 \text{ s}^{-1}$ . The elastic modulus of both seawater and phytoplankton cultures is typically  $\sim 10\%$  that of the excess viscous modulus, and total viscosity is that of the aquatic phase (water and dissolved salt) plus that of the OM. The molecular (i.e. non-turbulent) viscosity of the water phase is Newtonian (it depends only on temperature and salinity, and remains constant irrespective of shear rate or length scales down to those of the water-molecule shells,  $\sim 0.2, 0.3 \text{ nm}$ ) (Conlisk, 2013). That of the EPS phase, however, is generally shear-thinning (i.e. non-Newtonian): the faster it shears, the less viscous (i.e. “thinner”) it becomes. So generally, as shear rate is increased, total viscosity thins asymptotically towards the viscosity of the aqueous phase, while the slower the water shears, the more viscous the whole water becomes. Further, seawater viscosity generally shows a positive relationship with chlorophyll *a* concentration (e.g. Jenkinson and Biddanda, 1995; Seuront *et al.*, 2006, 2007), confirming its principal origin as phytoplankton-associated EPS, although marine macroalgae (Boney, 1981) and bacteria (Pedrotti *et al.*, 2010) also secrete polysaccharides, which supports findings of correlation between increased viscosity and bacterial abundance in Antarctic waters (Seuront *et al.*, 2010).

## PHAEOCYSTIS AND VISCOSITY

Jenkinson and Biddanda (Jenkinson and Biddanda, 1995) found a positive relationship between viscoelastic properties of the water and *Phaeocystis* abundance under bloom conditions. This was further refined with evidence that *Phaeocystis globosa* blooms increase seawater viscosity up to 4-fold in the eastern English Channel (Seuront *et al.*, 2006, 2007; Kesaulya *et al.*, 2008; Seuront and Vincent, 2008). More specifically, no correlations were observed by these authors between viscosity and chlorophyll *a* under non-bloom conditions, i.e. typically for concentrations below  $5 \mu\text{g L}^{-1}$  (Seuront *et al.*, 2006, 2007; Seuront and Vincent, 2008). In contrast, viscosity was often strongly positively correlated with chlorophyll *a* concentration during the onset of *P. globosa* blooms, but foam formation led to negative correlation, indicating that at the foam-forming stage of the bloom, there occurred spatial separation between the viscous polymeric materials and the flagellated *Phaeocystis* cells (Seuront *et al.*, 2006, 2007; Seuront and Vincent, 2008). Seuront *et al.* (Seuront *et al.*, 2007) furthermore found that viscosity and chlorophyll *a* concentration sampled in a 3D grid of samplers 5 cm apart by a pneumatically operated water sampler (Seuront and Menu, 2006) often varied strongly over this 5-cm length scale. In these studies,

viscosity was measured in a *ViscoLab400* viscometer consisting of a piston oscillating longitudinally inside a cylinder, the measuring gap between the piston and cylinder being 230  $\mu\text{m}$  (Seuront *et al.*, 2007) or in a Contraves Low-shear 30 or Low-shear 40 rheometer using a bob-and-cup measuring system with a 500- $\mu\text{m}$  measuring gap.

## THALASSORHEOLOGY IN THIN LAYERS AND DENSITY DISCONTINUITIES, AND OUTSIDE THEM

Plankton, OM, chlorophyll *a* and aggregates often concentrate in subsurface thin layers (TLs). TLs are conventionally defined as being no more than 3 m thick (Raine, 2014). They can be up to many kilometres in lateral extent, and frequently coincide with, or occur just above or below structures of high-density gradient (Alldredge *et al.*, 2002; Jenkinson and Sun, 2010; Farrell *et al.*, 2014). The OM is sometimes generated by phytoplankton in the TL, or it may have sunk or risen from outside the TL to accumulate in it (Villareal *et al.*, 1996; Alldredge *et al.*, 2002; Hung *et al.*, 2003; McManus *et al.*, 2003; Azetsu-Scott and Passow, 2004; Mari, 2008; Wang and Goodman, 2009; Baltar *et al.*, 2010). To investigate whether the OM in these TLs reinforces the associated density discontinuities, Jenkinson and Sun (Jenkinson and Sun, 2011) modelled stabilization of density discontinuities by hierarchically lumpy viscosity, incorporating a length-scale exponent of rheological properties,  $d$ ; when  $d = 0$ , the medium is homogeneous, and the medium is increasingly lumpy with increasing  $d$ . To investigate  $d$  empirically, Jenkinson and Sun (Jenkinson and Sun, 2014) then measured the viscosity of cultures of harmful-bloom phytoplankton and a bacterium at a range of length scales in low Reynolds number flowing through capillaries of different radii. Drag increase, ascribed to increased EPS viscosity, was clearly detected, but drag reduction also occurred unexpectedly in some trials, and interfered with the results, preventing determination of  $d$ . Hydrophobic surface effects might cause this drag reduction (Jenkinson, 2014; Jenkinson and Sun, 2014), which imply that phytoplankton and bacteria in pycnocline-associated TLs might be sometimes either increasing or decreasing viscosity around their bodies, thus engineering the environment, and possibility also changing the physical stability of pycnoclines (Jenkinson and Sun, 2011). Such engineering is likely to be partly under genetic control, and thus subject to (neo-)Darwinian evolution.

In the bulk of the ocean, outside of TLs and density discontinuities, to what extent does the background DOM change the background viscoelasticity, and is this

enough to have ecological or biogeochemical consequences? Wells and Goldberg (Wells and Goldberg, 1991, 1992, 1993, 1994) showed the presence of colloidal matter in the oceans, and that it forms spontaneously from DOM, giving submicron-sized aggregates, while sinking organic particles also sequester DOM (Hansell *et al.*, 2009). Furthermore, bacteria (Puddu *et al.*, 2003), appendicularians (Flood *et al.*, 1992) and other organisms take-up DOM. While much of this DOM is respired, some is packaged by grazing, promoting a cascade in length scales from dissolved up to 1 to  $\sim 10^3$   $\mu\text{m}$ . Sometimes this OM will be secreted again as EPS.

The rheological properties of this “background” DOM and colloidal matter are little known. Although Jenkinson (Jenkinson, 1993b) measured them and modelled their effects on turbulence, but, as mentioned above, his modelling assumed viscosity to be independent of length scale. More sophisticated rheometry is required over a range of length scales and shear rates (Jenkinson and Sun, 2014) by interdisciplinary teams (Jenkinson and Sun, 2010) to assess whether and how this DOM significantly impacts ecological and biogeochemical processes, and whether it needs to be incorporated into models of ocean change.

## CLOGGING AND FLOW REDUCTION

Plankton nets (mesh size in the 20–1000  $\mu\text{m}$  range) become clogged under tow, particularly during blooms of phytoplankton or gelatinous zooplankton (Smith *et al.*, 1968). Similarly, filters such as those used for retaining plankton and POM, such as in desalination plants (Villacorte *et al.*, in press; Balzano *et al.*, 2014), become clogged particularly when a large biomass of phytoplankton is present. Some harmful algae cultures at typical bloom concentrations were also found to be so viscous they reduced or stopped flow in fish gills (flow way width  $\sim 30$   $\mu\text{m}$ ) enough to kill the fish (Jenkinson and Arzul, 1998, 2002; Jenkinson *et al.*, 2007b). Similarly, EPS in benthic sediment sometimes reduce flow in the gills of juvenile fish that live in it (Couturier *et al.*, 2007, 2008; Jenkinson *et al.*, 2007a). Blooms of the mucus-secreting dinoflagellate *Karenia mikimotoi* (formerly known as *Gyrodinium aureolum*) have been modelled (Jenkinson, 1989) and observed (Robin *et al.*, 2013) to kill fishes when their EPS asphyxiates the fishes either because it makes the water so viscous that the fish use up more oxygen in pumping the water over their gills than they can extract from this water, or when it clogs fish gills (which may often amount to the same thing). In some cases, particulate cell debris may contribute to the clogging (Kim *et al.*, 2001). Differential sticking or slipping of the EPS at the

surfaces of nets, membranes or gills is likely to have important effects on clogging and nanometre- to micrometre-scale viscosity (Conlisk, 2013; Jenkinson, 2014).

## SWIMMING, SWARMING AND VISCOSITY CHANGES

Viscosity is primarily modulated by temperature (Miyake and Koizumi, 1948). So early empirical investigations assessed to what extent the effects of temperature change on invertebrate swimming was partitioned between viscosity change and physiological change. This partitioning was investigated for swimming speed and ciliary water movement in *Dendroaster excentricus* larvae (Podolsky and Emlet, 1993) and the swimming and sinking velocity in larvae of the serpulid polychaete *Galeolaria caespitosa* (Bolton and Havenhand, 1997). In both cases, the decrease in seawater viscosity with increasing temperature was found to be responsible for part of the positive relationship observed between swimming speed and temperature.

Seuront and Vincent (Seuront and Vincent, 2008) showed that swimming trajectories of *Temora longicornis* were more convoluted in high-viscosity *P. globosa* bloom water than in clear water, suggesting that these copepods avoid zones of high EPS viscosity. Specifically, increased viscosity reduced swimming velocity and increased swimming-path complexity. The authors suggested these two effects may have been related to an area-restricted foraging strategy triggered by the patchiness of phytoplankton biomass and EPS, rather than an adaptive response to the increase in viscosity. Work is still needed on the effects of patchy increased viscosity on swimming, not just in microplankton, but also by nano- and pico-plankton.

Swarming, that is co-ordinated movement in aggregates of organisms, is widespread in motile ocean zooplankton (Wilhelmus and Dabiri, 2014), protists (Jiang *et al.*, 2002; Kaartvedt *et al.*, 2005; Persson *et al.*, 2013) and bacteria (McCarter, 1999; Partridge and Harshey, 2013). In swarming by single-celled organisms, both increased and decreased viscosity has been modelled (Gyrya *et al.*, 2011; Thutupalli *et al.*, 2011). Specifically, cells with flagella that push the cell forward (i.e. pushers), such as many bacteria, tend to reduce the viscosity of the medium. In turn, cells with flagella that pull the cell forward (pullers), such as many eukaryotic flagellates, tend to increase the viscosity. Sokolov and Aranson (Sokolov and Aranson, 2009) measured up to 7-fold reduction of viscosity in suspensions of living bacteria *Bacillus subtilis* compared with the viscosity of medium without bacteria or medium with dead bacteria, while Gachelin *et al.* (Gachelin *et al.*, 2013) measured corresponding but less marked viscosity reductions in *Escherichia coli* at shear rates  $\leq 1$  up to  $2 \text{ s}^{-1}$  and at volume

fractions  $\leq 0.25\%$  up to 1.7%. Rather sensationally, working also with suspensions of living *E. coli*, López *et al.* (López *et al.*, 2015) measured that at volume fraction of 0.4% and shear rate of only  $0.04 \text{ s}^{-1}$ , viscosity of the whole suspension (organisms plus suspending liquid) could be reduced so much that total viscosity became negative. They used a *Contraves* Low-shear 30 rheometer, the same as or similar to that used for measuring the viscoelasticity of cultures and seawater by Jenkinson (Jenkinson, 1986, 1993a,b) and by Jenkinson and Biddanda (Jenkinson and Biddanda, 1995), so that the two sets of measurements can be easily compared. Eukaryote flagellates, in contrast are mostly pullers; Rafai *et al.* (Rafai *et al.*, 2010) measured that suspensions of volume fraction 2–15% of one of them, *Chlamydomonas reinhardtii* increased viscosity by a factor of up to two relative to a corresponding suspension of dead cells, at a shear rate of  $5 \text{ s}^{-1}$ . While increased volume fraction of cells facilitates viscosity change by swimmers, significant effects have been measured at volume fraction  $< 1\%$ .

From the viewpoint of individual microorganisms, rather than swarms, Qin *et al.* (Qin *et al.*, 2015) review considerable literature on swimming in elastic and viscoelastic fluids. They then report their own observations of swimming by *Chlamydomonas*, made at relatively low viscosities and shear rates of 1–10 mPa s, and  $6 \text{ s}^{-1}$ , respectively, concluding that they found that “the net swimming speed of the alga is hindered for fluids that are sufficiently elastic,” and more generally, that “the emerging viewpoint is that fluid microstructure and swimming kinematics together impact motility in a non-linear manner.” More observations, however, are needed at the lower shear rates characteristic of ocean processes (Jenkinson and Sun, 2010) and at the smaller volume fractions characteristic of plankton swarms *in situ*, including in marine snow, in algal blooms and close to surfaces.

## EFFECTS OF ENVIRONMENTAL CHANGE

The oceans are warming and acidifying (Hallegraeff, 2010). At least in many coastal areas, plankton biomass (Anderson *et al.*, 2012) and mucus (Danovaro *et al.*, 2009) are increasing. Ocean warming reduces aquatic-phase viscosity, but increases in plankton biomass and mucus will increase EPS viscosity. Modelling suggests that high levels of turbulence increase primary and secondary production (Allen *et al.*, 2004). Turbulence intensities characteristic of storm conditions were empirically observed by Beauvais *et al.* (Beauvais *et al.*, 2003) and by Garrison and Tang (Garrison and Tang, 2014) to increase the amount of EPS secreted by phytoplankton. Furthermore, intense turbulence has been

observed to reduce EPS sinking (Pedrotti *et al.*, 2010). Increased acidity may be promoting more buoyancy of marine organic aggregates (Mari, 2008), suggesting that this increasing EPS viscosity might accumulate at and near the sea surface. Surface OM content reduces air-sea CO<sub>2</sub> flux (Calleja *et al.*, 2009), apparently due to its mechanical properties (Goldman *et al.*, 1988). These effects and the consequences of changing the depth-distribution of viscosity and OM, including at the sea-surface micro-layer, need to be better studied and incorporated into models of the effects of climate and pH change.

## FUTURE DIRECTIONS

In the last 20 years, there has been consensual demand for more study of viscosity and rheology in the oceans, particularly in regard to harmful algal blooms, mucilage secretion and plankton thin layers (ICES/IOC, 1995; GEOHAB, 2008, 2013; Berdalet *et al.*, 2014). Rheology and ocean science are both extremely interdisciplinary. A major problem is that ocean scientists and rheologists generally are not experts in each other's subject. A working group (WG), "Rheology, nano- and micro-Fluidics and bioFouling in the Oceans" (RheFFO) of experts in these different fields now exists, partly to dynamize new approaches to the way rheology of EPS modulates ecological and biogeochemical processes in the oceans as well as gill- and filter-clogging, toxic action fluidics, surface science and biofouling. It is foreseen that the WG will act to guide RheFFO research and capacity building, to help find the required infrastructure and to do interdisciplinary research on RheFFO. A web site is available at <http://acropagespro-orange.fr/RheFFO/index.htm>.

## ACKNOWLEDGEMENTS

We are grateful to three anonymous reviewers for their extremely helpful comments.

## FUNDING

Project supported by the Natural Basic Research Program of China (No. 2011CB403601, No. 2014CB441504), the National Natural Science Foundation of China (No. 41230963). Supported also under Australian Research Council's Discovery Projects (project numbers DP0664681 and DP0988554) to L.S., and by Australian Professorial Fellowship (project number DP0988554) to L.S. Supported by an Action concertée "Jeunes chercheurs" #3058 from the French Ministry of Research to L.S., the CPER "Phaeocystis" (France) to L.S., and French PNEC "Chantier

Manche Orientale-Sud Mer du Nord" to L.S. and to I.R.J. This is publication #2 of the RheFFO Working Group.

## REFERENCES

- Allredge, A. L., Cowles, T. J., MacIntyre, S., Ruines, J. E. B., Donaghay, P. L., Greenlaw, C. F., Holliday, D. V., Deksheniaks, M. M. *et al.* (2002) Occurrence and mechanisms of formation of a dramatic thin layer of marine snow in a shallow Pacific fjord. *Mar. Ecol. Prog. Ser.*, **233**, 1–12.
- Allen, J. I., Siddorn, J. R., Blackford, J. C. and Gilbert, F. J. (2004) Turbulence as a control on the microbial loop in a temperate seasonally stratified marine systems model. *J. Sea Res.*, **52**, 1–20.
- Anderson, D. M., Cembella, A. D. and Hallegraeff, G. M. (2012) Progress in understanding harmful algal blooms: paradigm shifts and new technologies for research, monitoring, and management. *Ann. Rev. Mar. Sci.*, **4**, 143–176.
- Azetsu-Scott, K. and Passow, U. (2004) Ascending marine particles: significance of transparent exopolymer particles (TEP) in the upper ocean. *Limnol. Oceanogr.*, **49**, 741–748.
- Baltar, F., Arístegui, J., Sintes, E., Gasol, J. M., Reinthaler, T. and Herndl, G. J. (2010) Significance of non-sinking particulate organic carbon and dark CO<sub>2</sub> fixation to heterotrophic carbon demand in the mesopelagic northeast Atlantic. *Geophys. Res. Lett.*, **37**, L09602.
- Balzano, S., Lan, C. L., Ellis, A. V., Compas, H., Newton, K., Jamieson, K. N. T., Brown, M. and Leterme, S. C. (2014) Evaluation of transparent exopolymer particles and microbial communities found post-UV light, multimedia and cartridge filtration pre-treatment in a SWRO plant. *Desal. Water Treat.*, doi:10.1080/19443994.2014.950997.
- Barnes, H., Hutton, J. and Walters, K. (1989) *An Introduction to Rheology*. Elsevier, Amsterdam, pp. 199.
- Beauvais, S., Pedrotti, M. L., Villa, R. E. and Lemée, R. (2003) Transparent exopolymer particle (TEP) dynamics in relation to trophic and hydrological conditions in the NW Mediterranean Sea. *Mar. Ecol. Prog. Ser.*, **262**, 97–109.
- Berdalet, E., McManus, M. A., Ross, O. N., Burchard, H., Chavez, F., Jaffe, J. S., Jenkinson, I. R., Kudela, R. *et al.* (2014) Understanding harmful algae in stratified systems: review of progress and identification of gaps in knowledge. *Deep Sea Res. II*, **101**, 4–20.
- Bjørnson, P. K. (1988) Phytoplankton exudation of organic matter: why do healthy cells do it? *Limnol. Oceanogr.*, **33**, 151–154.
- Bolton, T. and Havenhand, J. (1997) Physiological versus viscosity-induced effects of water temperature on the swimming and sinking velocity of larvae of the serpulid polychaete *Galeolaria caespitosa*. *Mar. Ecol. Prog. Ser.*, **159**, 209–218.
- Boney, A. D. (1981) Mucilage: the ubiquitous algal attribute. *Br. Phycol. J.*, **16**, 115–132.
- Calleja, M. L., Duarte, C. M., Prairie, J. C., Agustí, S. and Herndl, G. J. (2009) Evidence for surface organic matter modulation of air-sea CO<sub>2</sub> gas exchange. *Biogeosciences*, **6**, 1105–1114.
- Carlson, D. J. (1987) Viscosity of sea-surface slicks. *Nature*, **329**, 823–825.
- Chin, W.-C., Orellana, M. V. and Verdugo, P. (1998) Spontaneous assembly of marine dissolved organic matter into polymer gels. *Nature*, **391**, 568–572.
- Conlisk, A. T. (2013) *Essentials of Micro- and Nano-Fluidics*. Cambridge University Press, Cambridge.

- Coussot, P. (2005) *Rheometry of Pastes, Suspensions, and Granular Materials—Applications in Industry and Environment*. Wiley, Hoboken, NJ, 291 p.
- Couturier, C. S., Nonnotte, L., Nonnotte, G. and Claireaux, G. (2008) Interaction between exopolysaccharide and oxygenation levels on habitat selection in the sole *Solea solea* (L.). *J. Fish. Biol.*, **73**, 186–195.
- Couturier, C. S., Rouault, A., McKenzie, D., Galois, R., Robert, S., Joassard, L. and Claireaux, G. (2007) Effects of water viscosity upon ventilation and metabolism of a flatfish, the common sole *Solea solea* (L.). *Mar. Biol.*, **152**, 803–814.
- Danovaro, R., Fonda Umami, S. and Pusceddu, A. (2009) Climate change and the potential spreading of marine mucilage and microbial pathogens in the Mediterranean Sea. *PLoS One*, **4**, e7006.
- Doubell, M. J., Yamazaki, H., Li, H. and Kokubu, Y. (2009) An advanced laser-based fluorescence microstructure profiler (TurboMAP-L) for measuring bio-physical coupling in aquatic systems. *J. Plankton Res.*, **31**, 1441–1452.
- Druffel, E. R. M., Williams, P. M., Bauer, J. E. and Ertel, J. R. (1992) Cycling of dissolved and particulate matter in the open ocean. *J. Geophys. Res.*, **97**(C10), 15639–15659.
- Falkowski, P. G., Fenchel, T. and Delong, E. F. (2008) The microbial engines that drive earth's biogeochemical cycles. *Science*, **320**, 1034–1039.
- Farrell, H., Gentien, P., Fernandez, L., Lazure, P., Lunven, M., Youenou, A., Reguera, B. and Raine, R. (2014) Vertical and horizontal controls of a haptophyte thin layer in the Bay of Biscay, France. *Deep Sea Res. II*, **101**, 80–94.
- Flood, P. R., Deibel, D. and Morris, C. (1992) Filtration of colloidal melanin from seawater by plankton tunicates. *Nature*, **355**, 630–632.
- Gachelin, J., Miño, G., Berthet, H., Lindner, A., Rousselet, A. and Clément, É. (2013) Non-Newtonian viscosity of *Escherichia coli* suspensions. *Phys. Rev. Lett.*, **110**, 268103.
- Garrison, H. S. and Tang, K. W. (2014) Effects of episodic turbulence on diatom mortality and physiology, with a protocol for the use of Evans Blue stain for live–dead determinations. *Hydrobiologia*, **738**, 155–170.
- GEOHAB Global Ecology and Oceanography of Harmful Algal Blooms. (2008) GEOHAB core research project: HABs in stratified systems. In Gentien, P., Reguera, B., Yamazaki, H., Fernandez, I., Berdalet, E. and Raine, R. (eds), *IOC and SCOR*. Paris, France, and Newark, DE, pp. 59.
- GEOHAB Global Ecology and Oceanography of Harmful Algal Blooms. (2013) GEOHAB core research project: HABs in stratified environments. In McManus, M. A., Berdalet, E., Ryan, J., Yamazaki, H., Jaffé, J. S., Ross, O. N., Burchard, H., Jenkinson, I. and Chavez, F. P. (eds), *IOC and SCOR*. Paris and Newark, DE, pp. 62.
- Goldman, J. C., Dennett, M. R. and Frew, N. M. (1988) Surfactant effects on air-sea gas exchange under turbulent conditions. *Deep Sea Res.*, **35**, 1953–1970.
- Gyrya, V., Lipnikov, K., Aranson, I. S. and Berlyand, L. (2011) Effective shear viscosity and dynamics of suspensions of micro-swimmers from small to moderate concentrations. *Math. Biol.*, **62**, 707–740.
- Hallegraeff, G. M. (2010) Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge. *J. Phycol.*, **46**, 229–235.
- Hansell, D. A., Carlson, C. A., Repeta, D. J. and Schlitzer, R. (2009) Dissolved organic matter in the ocean: a controversy stimulates new insights. *Oceanography*, **22**, 202–211.
- Harel, M., Weiss, G., Daniel, E., Wilenz, A., Hadas, O., Sukenik, A., Sedmak, B. and Dittmann, E. (2012) Casting a net: fibres produced by *Microcystis* sp. in field and laboratory populations. *Environ. Microbiol. Rep.*, **4**, 342–349.
- Ho, C.-M. and Nosseir, N. (1981) Dynamics of an impinging jet. I. The feedback phenomenon. *J. Fluid Mech.*, **105**, 119–142.
- Hung, C., Laodong, G., Santschi, P., Alvarado-Quiroz, N. and Haye, J. (2003) Distributions of carbohydrate species in the Gulf of Mexico. *Mar. Chem.*, **81**, 127–135.
- International Council for the Exploration of the Sea (ICES) and Intergovernmental Oceanographic Commission (IOC) (1995). Report of the ICES/IOC Working Group on Harmful Algal Bloom Dynamics (WGHABD). ICES C.M. 1995/L: 4, Ref. C.
- Jenkinson, I. R. (1986) Oceanographic implications of non-newtonian properties found in phytoplankton cultures. *Nature*, **323**, 435–437.
- Jenkinson, I. R. (1989) Increases in viscosity may kill fish in some blooms. In Okaichi, T., Anderson, D. M. and Nemoto, T. (eds), *Red Tides*. Elsevier, New York, pp. 435–438.
- Jenkinson, I. R. (1993a) Viscosity and elasticity of *Gyrodinium* cf. *aureolum* and *Noctiluca scintillans* exudates in relation to mortality of fish and damping of turbulence. In Smayda, T. and Shimizu, Y. (eds), *Toxic Phytoplankton Blooms in the Sea*. Elsevier, Amsterdam, pp. 757–762.
- Jenkinson, I. R. (1993b) Bulk-phase viscoelastic properties of seawater. *Oceanol. Acta*, **16**, 317–334.
- Jenkinson, I. R. (2014) Nano- and microfluidics, rheology, exopolymeric substances and fluid dynamics in calanoid copepods. In Seuront, L. (ed.), *Diversity, Habitat and Behavior*. Nova Science Publishers, New York, pp. 181–214.
- Jenkinson, I. R. and Arzul, G. (1998) Effect of the flagellates, *Gymnodinium mikimotoi*, *Heterosigma akashiwo*, and *Pavlova lutheri*, on flow through fish gills. In Reguera, B., Blanco, J., Fernandez, M. and Wyatt, T. (eds), *Harmful Algae*, Xunta de Galicia, Pontevedra and IOC of UNESCO, Paris, pp. 425–428.
- Jenkinson, I. R. and Arzul, G. (2002) Mitigation by cysteine compounds of the reotoxicity, cytotoxicity and fish mortality caused by the dinoflagellates, *Gymnodinium mikimotoi* and *G. cf. maguelonnense*. In Hallegraeff, G., Blackburn, S., Bolch, C. *et al.* (eds), *Harmful Algal Blooms 2000*. IOC of UNESCO, Paris, pp. 461–464.
- Jenkinson, I. R., Berdalet, E., Chin, W.-C., Herminghaus, S., Leterme, S., Mitchell, J. G., Orchard, M., Qiu, R. *et al.* (in press) Micro- and nano-fluidics around HAB cells. In MacKenzie, L. *et al.* (eds), Proceedings of the 16th International Conference on Harmful Algae. ISSA and IOC of UNESCO, Copenhagen and Paris.
- Jenkinson, I. R. and Biddanda, B. A. (1995) Bulk-phase viscoelastic properties of seawater: relationship with plankton components. *J. Plankton Res.*, **17**, 2251–2274.
- Jenkinson, I. R., Claireaux, G. and Gentien, P. (2007a) Biorheological properties of intertidal organic fluff on mud flats and its modification of gill ventilation in buried sole *Solea solea*. *Mar. Biol.*, **150**, 471–485.
- Jenkinson, I. R. and Connors, P. P. (1980) The occurrence of the red-tide organism, *Gyrodinium aureolum* Hulbert (Dinophyceae) around the south and west of Ireland in August and September, 1979. *J. Sherkin Isl.*, **1**, 127–146.
- Jenkinson, I. R., Shikata, T. and Honjo, T. (2007b) Modified ichthyoviscometer shows high viscosity in *Chattonella* culture. *Harmful Algae News*, **35**, 1–5.

- Jenkinson, I. R. and Sun, J. (2010) Rheological properties of natural waters with regard to plankton thin layers. A short review. *J. Mar. Syst.*, **83**, 287–297.
- Jenkinson, I. R. and Sun, J. (2011) A model of pycnocline thickness modified by the rheological properties of phytoplankton exopolymeric substances. *J. Plankton Res.*, **33**, 373–383.
- Jenkinson, I. R. and Sun, J. (2014) Drag increase and drag reduction found in phytoplankton and bacterial cultures in laminar flow: are cell surfaces and EPS producing rheological thickening and a Lotus-leaf Effect? *Deep Sea Res. II*, **101**, 216–230.
- Jenkinson, I. R. and Wyatt, T. (1992) Selection and control of Deborah numbers in plankton ecology. *J. Plankton Res.*, **14**, 1697–1721.
- Jenkinson, I. R. and Wyatt, T. (1995) Does bloom phytoplankton manage the physical oceanographic environment? In Lassus, P., Arzul, G., Erard, E. *et al.* (eds), *Harmful Marine Algal Blooms*. Lavoisier Intercept, Paris, pp. 603–607.
- Jiang, H., Osborn, T. R. and Meneveau, C. (2002) Hydrodynamic interaction between two copepods: a numerical study. *J. Plankton Res.*, **24**, 235–253.
- Jiao, N., Herndl, G. J., Hansell, D. A., Benner, R., Kattner, G., Wilhelm, S. W., Kirchman, D. L., Weinbauer, M. G. *et al.* (2010) Microbial production of recalcitrant dissolved organic matter: long-term carbon storage in the global ocean. *Nat. Rev. Microbiol.*, **8**, 393–399.
- Jones, C. G., Lawton, J. H. and Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.
- Kaartvedt, S., Røstad, A., Fiksen, Ø., Melle, W., Torgesen, T., Breien, M. T. and Klevjer, T. A. (2005) Piscivorous fish patrol krill swarms. *Mar. Ecol. Prog. Ser.*, **299**, 1–5.
- Kesaulya, I., Leterme, S. C., Mitchell, J. G. and Seuront, L. (2008) The impact of turbulence and phytoplankton dynamics on foam formation, seawater viscosity and chlorophyll concentration in the eastern English Channel. *Oceanologia*, **50**, 167–182.
- Kim, D. (K.), Okamoto, T., Oda, T., Tachibana, K., Lee, K., Ishimatsu, A., Matsuyama, Y., Honjo, T. and Muramatsu, T. (2001) Possible involvement of the glycocalyx in the ichthyotoxicity of *Chattonella marina* (Rhaphidophyceae): immunological approach using antiserum against cell surfaces of the flagellate. *Mar. Biol.*, **139**, 625–632.
- Kolmogorov, A. N. (1962) A refinement of previous hypotheses concerning the local structure of turbulence in a viscous incompressible fluid at high Reynolds number. *J. Fluid Mech.*, **13**, 82–85.
- López, H. M., Gachelin, J., Douarache, C., Auradou, H. and Clément, E. (2015) Turning bacteria suspensions into superfluids. *Phys. Rev. Lett.*, **115**, 028301.
- Margalef, R. (1978) Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta*, **1**, 493–509.
- Margalef, R., Estrada, M. and Blasco, D. (1980) Functional morphology of organisms involved in red tides, as adapted to decaying turbulence. In Taylor, D. L. and Seliger, H. H. (eds), *Toxic Dinoflagellate Blooms*. Elsevier, North Holland, pp. 89–94.
- Mari, X. (2008) Does ocean acidification induce an upward flux of marine aggregates? *Biogeosciences*, **5**, 1023–1031.
- McCarter, L. (1999) The multiple identities of *Vibrio parahaemolyticus*. *J. Mol. Biotechnol.*, **1**, 51–57.
- McManus, M. A., Alldredge, A. L., Barnard, A. H., Boss, E., Case, J. F., Cowles, T. J., Donahay, P. L., Eisner, L. B. *et al.* (2003) Characteristics, distribution and persistence of thin layers over a 48 hour period. *Mar. Ecol. Prog. Ser.*, **261**, 1–19.
- Mitchell, J. G., Yamazaki, H., Seuront, L., Wolk, F. and Li, H. (2008) Phytoplankton patch patterns: seascape anatomy in a turbulent ocean. *J. Mar. Syst.*, **69**, 247–253.
- Miyake, Y. and Koizumi, M. (1948) The measurement of the viscosity coefficients of seawater. *J. Mar. Res.*, **7**, 63–66.
- Mohammed, J. S. (2015) Micro- and nanotechnologies in plankton research. *Prog. Oceanogr.*, **134**, 451–473.
- Odling-Smee, F. J., Laland, K. N. and Feldman, M. W. (2003) *Niche Construction: The Neglected Process in Evolution*. Princeton Univ. Press, Princeton, New Jersey.
- Partridge, J. D. and Harshey, R. M. (2013) Swarming: flexible roaming plans. *J. Bacteriol.*, **195**, 909–918.
- Pedrotti, M. L., Peters, F., Beauvais, S., Vidal, M., Egge, J., Jacobsen, A. and Marrasé, C. (2010) Effects of nutrients and turbulence on the production of transparent exopolymer particles: a mesocosm study. *Mar. Ecol. Prog. Ser.*, **419**, 57–69.
- Persson, A., Smith, B. C., Wikfors, G. H. and Alix, J. H. (2013) Differences in swimming pattern between life cycle stages of the toxic dinoflagellate *Alexandrium fundyense*. *Harmful Algae*, **21–22**, 36–43.
- Podolsky, R. and Emlet, R. (1993) Separating the effects of temperature and viscosity on swimming and water movement by sand dollar larvae (*Dendraster excentricus*). *J. Exp. Biol.*, **176**, 207–221.
- Prairie, J. C., Sutherland, K. R. and Kaltenberg, A. M. (2012) Biophysical interactions in the plankton: a cross-scale review. *Limnol. Oceanogr. Fluids Environ.*, **2**, 121–145.
- Puddu, A., Zoppini, A., Fazi, S., Rosati, M., Amalfitano, S. and Magaletti, E. (2003) Bacterial uptake of DOM released from P-limited phytoplankton. *FEMS Microbiol. Ecol.*, **46**, 257–268.
- Qin, B., Gopinath, A., Yang, J., Gollub, J. P. and Arratia, P. E. (2015) Flagellar kinematics and swimming of algal cells in viscoelastic fluids. *Sci. Rep.*, **5**, 9190.
- Quesada, I., Chin, W.-C. and Verdugo, P. (2006) Mechanisms of signal transduction in photo-stimulated secretion in *Phaeocystis globosa*. *FEBS Lett.*, **580**, 2201–2206.
- Rafai, S., Jibuti, L. and Peyla, P. (2010) Effective viscosity of microswimmer suspensions. *Phys. Rev. Lett.*, **104**, 098102.
- Ragni, M. and Ribera d'Alcalà, M. (2004) Light as an information carrier underwater. *J. Plankton Res.*, **26**, 433–443.
- Raine, R. (2014) A review of the biophysical interactions relevant to the promotion of HABs in stratified systems: the case study of Ireland. *Deep Sea Res. II*, **101**, 21–31.
- Reynolds, C. S. (2007) Variability in the provision and function of mucilage in phytoplankton: facultative responses to the environment. *Hydrobiologia*, **578**, 37–45.
- Rhodes, C. J. (2008) Excess acoustic absorption attributable to the biological modification of seawater viscosity. *I.C.E.S. J. Mar. Sci.*, **65**, 1747–1750.
- Robin, R. S., Kanuri, V. V., Muduli, P. R., Mishra, R. K., Jaikumar, M., Karthikeyan, P., Kumar, C. S. and Kumar, C. S. (2013) Dinoflagellate bloom of *Karenia mikimotoi* along the Southeast Arabian Sea, bordering western India. *J. Ecosyst.*, 2013, Art. ID 463720, 11 p.
- Seuront, L., Lacheze, C., Doubell, M. J., Seymour, J. R., Van Dongen-Vogels, V., Newton, K., Alderkamp, A. C. and Mitchell, J. G. (2007) The influence of *Phaeocystis globosa* on microscale spatial patterns of chlorophyll *a* and bulk-phase seawater viscosity. *Biogeochemistry*, **83**, 173–188.
- Seuront, L., Leterme, S. C., Seymour, J. R., Mitchell, J. G., Ashcroft, D., Noble, W., Thomson, P. G. and Davidson, A. T. (2010) Role of

- microbial and phytoplanktonic communities in the control of seawater viscosity off East Antarctica (30–80° E). *Deep Sea Res. II*, **57**, 877–886.
- Seuront, L. and Menu, D. (2006) A pneumatically-operated, submersible, three-dimensional water sampler for microscale studies. *Limnol. Oceanogr. Methods*, **4**, 260–267.
- Seuront, L. and Vincent, D. (2008) Increased seawater viscosity, *Phaeocystis globosa* spring bloom and *Temora longicornis* feeding and swimming behaviours. *Mar. Ecol. Prog. Ser.*, **363**, 131–145.
- Seuront, L., Vincent, D. and Mitchell, J. G. (2006) Biologically induced modification of seawater viscosity in the Eastern English Channel during a *Phaeocystis globosa* bloom. *J. Mar. Sys.*, **61**, 118–133.
- Sharp, J. H. (1977) Excretion of organic matter by marine phytoplankton: do healthy cells do it? *Limnol. Oceanogr.*, **22**, 381–399.
- Smith, P. E., Counts, R. C. and Clutter, R. I. (1968) Changes in filtering efficiency of plankton nets due to clogging under tow. *J. Cons. Perm. Int. Explor. Mer.*, **32**, 232–248.
- Sokolov, A. and Aranson, I. (2009) Reduction of viscosity in suspension of swimming bacteria. *Phys. Rev. Lett.*, **103**, 148101.
- Stachowitsch, M. (1984) Mass mortality in the Gulf of Trieste: the course of community destruction. *P.S. Z. N. I. Mar. Ecol.*, **5**, 243–264.
- Thornton, D. C. (2014) Dissolved organic matter (DOM) release by phytoplankton in the contemporary and future ocean. *Eur. J. Phycol.*, **49**, 20–46.
- Thutupalli, S., Seemann, R. and Herminghaus, S. (2011) Swarming behavior of simple model squirmers. *New J. Phys.*, **13**, 073021.
- Villacorte, L., Tabatabai, S. A. A., Dhakal, N., Amy, G., Schippers, J. and Kennedy, M. in press Algal blooms: an emerging threat to seawater reverse osmosis desalination. *Desalin Water Treat.* doi:10.1080/19443994.2014.940649.
- Villareal, T., Woods, S., Moore, J. and Culver-Rymsza, K. (1996) Vertical migration of *Rhizosolenia* mats and their significance to NO<sub>3</sub><sup>-</sup> fluxes in the central North Pacific gyre. *J. Plankton Res.*, **18**, 1103–1121.
- Wang, Z. and Goodman, L. (2009) Evolution of the spatial structure of a thin phytoplankton layer into a turbulent field. *Mar. Ecol. Prog. Ser.*, **374**, 57–74.
- Wells, M. and Goldberg, E. (1991) Occurrence of small colloids in the sea. *Nature*, **353**, 342–344.
- Wells, M. and Goldberg, E. (1992) Marine submicron particles. *Mar. Chem.*, **40**, 5–18.
- Wells, M. and Goldberg, E. (1993) Colloid aggregation in seawater. *Mar. Chem.*, **41**, 353–358.
- Wells, M. and Goldberg, E. (1994) The distribution of colloids in the North Atlantic and Southern Oceans. *Limnol. Oceanogr.*, **39**, 286–302.
- Wikipedia (2015) Rheology. <http://en.wikipedia.org/wiki/Rheology>.
- Wilhelmus, M. M. and Dabiri, J. O. (2014) Observations of large-scale fluid transport by laser-guided plankton aggregations. *Phys. Fluids*, **26**. Art. No. 101302. (Consulted 15 August 2015.)
- Wolk, E., Seuront, S., Yamazaki, H. and Leterme, S. (2004) Comparison of biological scale resolution from CTD and microstructure measurements. In Seuront, L. and Strutton, P. G. (eds), *Handbook of Scaling Methods in Aquatic Ecology: Measurement, Analysis and Simulation*. CRC Press, Boca Raton, FL, USA, pp. 3–15.
- Wyatt, T. (2014) Margalef's mandala and phytoplankton bloom strategies. *Deep Sea Res. II*, **101**, 32–49.
- Wyatt, T. and Ribera d'Alcalà, M. (2006) Dissolved organic matter and planktonic engineering. *C. I. E. S. M. Workshop Monogr.*, **28**, 13–23.
- Zhang, Z. B., Cai, W. J., Liu, L. S., Liu, C. Y. and Chen, F. Z. (2003) Viscosity of sea surface microlayer in Jiaozhou Bay and adjacent sea area. *Chin. J. Oceanol. Limnol.*, **21**, 351–357.
- Žutić, V. and Svetličić, V. (2006) Production and fate of dissolved organic matter in the Mediterranean: formation and function of giant gels in the northern Adriatic. *C. I. E. S. M. Workshop Monogr.*, **28**, 45–48.