The semiotics of slime: visual representation of phytobenthos as an aid to understanding ecological status

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Abstract

'Ecological status' is a core concept of the Water Framework Directive (WFD). Many papers have been published throughout Europe describing methods for assessing ecological status by comparing observed assemblages with those expected under unimpacted conditions. However, the quantitative rigour necessary to develop these methods has been achieved by reducing complex community structure to simple metrics. One of the costs associated with this is the loss of higher level understanding of community structure which otherwise may have informed data interpretation. It also pushes the debate about ecological status further into the realm of abstract scientific ideas and away from engagement with stakeholders, another core concept of the WFD. These matters are particularly acute for microscopic organisms such as the algae, which play a key role in freshwater ecosystem functioning but are little known beyond a narrow group of specialists. Examples of phytobenthos communities from streams and rivers in the UK are used to show how visual representation can inform both peer-to-peer debate within the scientific community and communication with non-technical stakeholders.

Keywords: algal ecology, diatoms, freshwater monitoring, Water Framework Directive.

Introduction

The Water Framework Directive (WFD: European Parliament & Council, 2000) redefined the parameters for monitoring the aquatic environment, giving ecology a central role by creating the need to assess 'ecological status' in all types of water bodies. Ecological status is a property of an aquatic ecosystem, defined as 'an expression of the quality of the structure and functioning of aquatic ecosystems… ' (Article 2, European Parliament & Council, 2000). It's assessment, therefore, needs to encompass

'health checks' across all trophic levels in order to ensure the overall wellbeing of a water body. As a result, many new methods have been developed, embracing all trophic levels for all ecosystems, marine and freshwater, from arctic regions to the Mediterranean (Birk et al., 2012).

This review addresses one of these new 'biological quality elements': phytobenthos[1], generally taken to

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[1] Strictly speaking, 'phytobenthos' is one component of the 'macrophytes and phytobenthos' biological quality element, but most Member States have chosen to develop separate methods for each component.

encompass the benthic algae found in fresh waters. These form thin 'biofilms' on submerged surfaces which, in healthy ecosystems, provide an important source of energy for higher trophic levels (Allan, 1995). 'Semiotics' is the study of signs; assessment of biofilms, in effect, uses the structure and distinctive species composition of biofilms as signs of their health, and then transmits these signs to end-users and stakeholders in a form that can be easily understood.

Various methods have been developed for assessing phytobenthos (Schaumburg et al., 2004; Kelly et al., 2008a; Feio et al., 2009; Delgardo et al., 2010) and these methods have been intercalibrated across Europe (Kelly et al., 2009a). The purpose is not to question the science behind these methods but rather to examine ways of assessing phytobenthos in light of stakeholder engagement, another core concept enshrined in the WFD (Article 14, European Parliament and Council, 2000):

Member States shall encourage the active involvement of all interested parties in the implementation of this Directive, in particular in the production, review and updating of the river basin management plans. Member States shall ensure that, for each river basin district, they publish and make available for comments to the public, including users …… background documents and information used for the development of the draft river basin management plan.

In developing suites of methods that are objective and quantitative have we lost the capacity to communicate with non-technical stakeholders and end-users? Simply providing background documents and information is of little use if the underlying concepts are not understandable by the general public, many of whom will face substantial increases in their water service bills as a result of the WFD (DEFRA, 2011). Willby (2011) introduced the idea of the 'guiding image' to WFD assessments, arguing that this informed debates both within the community of ecologists and between ecologists, policy makers and the public. He makes a case for reclaiming a holistic 'vision' of a healthy ecosystem from the reams of data that we have produced.

The development of diatom-based methods for phytobenthos assessment

Early studies on the effect of pollution on river ecosystems examined all groups of algae (e.g. Butcher, 1946, 1947). At about the same time, the first high resolution mountants for diatoms were developed, providing greater taxonomic resolution yet, at the same time, necessitating a preparation procedure that destroyed all soft-bodied algae. Zelinka & Marvan (1961) introduced the first 'transfer function', allowing ecological assemblages to be related quantitatively to environmental gradients. Whilst their methods encompassed all algae, subsequent developments tended to focus just on diatoms (Descy, 1979). Meanwhile, palaeolimnologists were also developing quantitative methods for relating diatoms to environmental change (Renberg & Hellberg, 1982; Flower & Battarbee, 1983). Compared to other groups of algae, where species can be difficult to resolve with light microscopy, or which relied upon reproductive organs rarely found under natural conditions, identification of diatoms, based on the cleaned silica valve, was relatively straightforward.

During the 1990s a software program, Omnidia, became available, facilitating the calculation of several water quality indices (Lecointe et al., 1993). At about the same time, the Urban Wastewater Treatment Directive (European Community, 1991) created a demand for assessment of eutrophication in rivers that diatom-based methods were able to fulfil (Kelly & Whitton, 1995; Rott et al., 1999). By the time the WFD was adopted by the European Union (EU), diatom-based techniques were available throughout Europe and adaptation of these to fulfil the needs of the WFD seemed like the next logical step.

Diatoms alone were adequate in pre-WFD assessments, where they were subsidary or, at best, complementary to water chemistry, and in paleoecology, where soft-bodied algae are no longer available (Flower & Battarbee, 1983; Bennion et al., 1996). However, the WFD ecological status is, in essence, an evaluation of the fitness of the entire biological community compared to an ideal, unimpacted state.

Methods based on a partial analysis of the entire phytobenthos often give strong correlations with pressure gradients (e.g. Hering et al., 2006) and can, in principle, be benchmarked by calculation of an 'expected' value. Diatom-only methods also reflect patterns in the entire phytobenthos (Kelly, 2006; Kelly et al., 2008b), but is this intensive focus on one group of algae, to the exclusion of others, sufficient to give the insights into ecosystem functioning that will be essential once biologists move beyond placing water bodies into the appropriate ecological status class and start to advise catchment managers on realistic steps for ecosystem restoration? And, keeping the principle of transparency to the fore, has the reductionist approach (by which complex community characteristics are distilled into 'Ecological Quality Ratios' (EQRs)) made the task of communicating the need for healthy phytobenthos communities to policy makers and stakeholders more difficult?

Developing a vision of the microscopic world

Willby (2011) uses Barton Broad as a case study where modern ecological methods are supplemented by historical records to reconstruct centennial-scale changes in aquatic vegetation (Madgwick et al., 2011). He comments:

We emerged with a detailed list of species and how these had changed over time. However, there were numerous possible configurations of these species which meant that we still lacked a basic vision of what this lake really looked like 150 years ago. It was only through integrating this information with old paintings, photographs, diagrams and eyewitness accounts that we could achieve a satisfactory vision of Barton Broad in the late 1800s and could slot the known species into this framework. We concluded that re-establishing this overall habitat structure is the key to restoration – when the structure is right the right species will ultimately follow (dispersal limitation permitting) but not until then.

In other words, the 'guiding image' does more than just provide a bridge between ecologists and stakeholders; it also focuses discussions amongst ecologists themselves. Ecologists who study the macroscopic world have a

reference point: they can look at their data and visualise the communities, even if they did not perform the original survey. Should this same rationale be extended to the microscopic world? Would a 'guiding image' of a good status phytobenthos community add value to the lists of data that we all produce to either stimulate discussion amongst ecologists or facilitate communication with stakeholders?

The 'null hypothesis' to this proposal is that reduction of community characteristics to summary statistics provides all the information needed to interpret the status of that community, and the risks and hazards posed by and to human populations. An example here would be bacteriology: pathogenic bacteria each have their own ecological stories to tell (e.g. Colwell & Spira William, 1992) but, for practical purposes, these can be treated as randomly-organised suspensions, and limited information on presence and abundance of key taxa is sufficient to determine the health risks posed (European Community, 1976).

This is not a polemic against reductionism: it is about the extent to which the trend towards reductionist, quantitative approaches benefits from synergy with a holistic, often qualitative view of the same system (see Fryer, 1986). This guiding image may exist only as an abstract construct: mention Arctic charr (*Salvelinus alpinus*) and a fish biologist will have a mental picture of a fish dwelling in the depths of cool temperate and boreal lakes, even if they only know this as an inference from data. However, hold this image in your head and pressures such as eutrophication and climate change (Winfield et al., 2008) suddenly have a tangible and explainable 'victim', that relates directly to ecosystem services which are understandable to a lay person. By contrast, mention *Achnanthidium minutissimum*, extremely common in the littoral of lakes where *S. alpinus* thrives, and most diatomists probably think first of a microscopic piece of silica on a slide.

So would a 'guiding image' of phytobenthos help those involved in ecological status assessment and water body management? Diatomists focus their attention on cleaned valves because they can achieve greater precision with these. *Achnanthidium minutissimum* is actually an aggregate, whose members have subtly different preferences for physicochemical variables (Potapova & Hamilton, 2007).

However, in the process of unlocking this variation, we take one step further into an alternative, abstract reality far removed from the stream or lake bed. Ecological status requires more than just an indication of a chemical state and stepping back from an intensive focus on cleaned valves to consider live algae may yield less taxonomic precision, but more ecological insight (Gillett et al., 2009). We can start to think about how diatoms knit together with other algae and with other trophic levels to provide ecosystem services. And we have a starting point from which stakeholders can begin to understand phytobenthos as an important component of the 'engine room' of a healthy stream.

Examples

The synergy between quantitative data and qualitative observations will be illustrated by reference to four examples, based on lakes and rivers in the UK. The approach is similar to that used to derive dioramas of prehistoric life (Rudwick, 1993), insofar as the limited 'hard' evidence is combined with analogies with other ecosystems and informed speculation to produce imagined, but hopefully not imaginary, worlds. Such images are widespread in popular culture and have made palaeontological research findings accessible to a wide audience. The evidence, in each case, is based on field visits, microscopic examination of fresh samples in order to identify and quantify the relative abundance of diatoms and non-diatoms, and finally identification and enumeration of 'cleaned' diatoms after digestion with hydrogen peroxide. These then formed the basis for sketches, culminating in the illustrations presented here. The objective is to show how visual interpretation of data can enrich and inform the more usual approaches to inferring ecological status from diatom assemblages alone.

River Wear, Wolsingham, June 2009

This site (UK National Grid Reference [NGR]: NZ 073 368) was chosen as an example of a river at 'good status' and the sample discussed here is part of a sequence collected at monthly intervals during 2009. Thirty diatom taxa were recorded in the sample collected in June 2009 (Table 1): one third of the total number of species recorded in the river during the course of the year. Early in the year, the biofilm was thick and samples were dominated by stalked diatoms (e.g. *Gomphonema olivaceum* aggregate) and motile diatoms (*Navicula lanceolata, Nitzschia dissipata*); by March, the river bed was covered with bright green growths of *Ulothrix zonata* then, from April onwards, the biofilm became noticeably thinner, and *Achnanthidium minutissimum* became the most abundant alga in the samples (Fig. 1). At the same time, chironomid larvae became evident on the upper surface of the stones and, later in the summer, these were joined by caddis larvae. During this same period, blue-green algae (Cyanobacteria: *Homoeothrix varians, Phormidium retzii*) also increased in abundance. Shortly after the July sample, heavy rainfall caused a spate in the river and the sample from August had a much thicker biofilm than a month earlier, with fewer Chironomidae in evidence, and large numbers of a motile diatom, *Nitzschia archibaldii.*

Table 1. Diatoms found at relative abundances (RA) ≥1 % on 12 June 2009 on cobbles in the River Wear, Wolsingham, north-east England.

Taxon	RA (%)
Achnanthidium minutissimum ag.	46.1
Achnanthidium pyrenaicum	3.5
Cocconeis placentula var. *euglypta*	1.2
Cocconeis placentula var. *pseudolineata*	1.2
Encyonema minutum	7.9
Encyonema silesiacum	16.1
Gomphonema olivaceum ag.	2.3
Nitzschia archibaldii	4.1
Nitzschia dissipata	2.0
Nitzschia paleacea	1.2
Reimeria sinuata	2.6
Surirella brebissonii	3.5
Unidentified small naviculoid	1.5
Total number of taxa recorded (including taxa present at <1%)	**32**

Fig. 1. Diorama showing the biofilm on cobbles from the River Wear at Wolsingham in June 2009. The community, dominated by the diatom *Achnanthidium minutissimum*, was being grazed by chironomid larvae; clumps of the cyanobacterium *Homoeothrix varians* (foreground left) and filaments of *Phormidium* were also abundant. *Achnanthidium minutissimum* cells in this sample are typically 10-12 μm long.

In a survey of the diatoms found at 'reference sites' (i.e. streams with no or very little human disturbance), *Achnanthidium minutissimum* aggregate was the most frequently recorded and, often, the most abundant diatom in samples from all over Europe (Kelly et al., 2012). Yet, despite this ubiquity, the authors had problems unravelling the relationship between *A. minutissimum* ag. and ecological status. Although species within the *A. minutissimum* ag. have distinct preferences for physico-chemical conditions, Kahlert et al. (2012) showed that such fine taxonomic discrimination is difficult to achieve in routine assessments, particularly when several analysts are involved. How do these interlocking factors influence our interpretation of ecological status?

A complementary view of *A. minutissimum* ag. is that these are, typically 'R strategists' (*sensu* Grime, 1979; see Biggs et al., 1998): early colonisers of denuded habitats which will dominate when there are continual physical stresses (e.g. from high water velocity, physical abrasion or grazing). Members of this group often have small cells with high resistance to removal, high immigration and growth rates, and low half-saturation coefficients for nutrient uptake. The dominance of *A. minutissimum* ag. in the River Wear during extended periods of base flow, coupled with the observations of grazing invertebrates present on

cobbles, the shift in composition after the spate, and the rise in Cyanobacteria (generally less favoured by grazers: Moore, 1975; Hart, 1985) suggest that here, at least, it is grazers, rather than physical disturbance, which are shaping the phytobenthos assemblage.

The analogy that emerges is a heavily-grazed pasture, in which *A. minutissimum* ag. takes the role of the fast-growing, grazer-tolerant grasses, within which other low-growing species grow, and amongst which patches of relatively grazer-intolerant Cyanobacteria (equivalent to *Cirsium* spp. in terrestrial grasslands) flourish. Fig. 1 presents such an underwater landscape as a 'guiding image' specifically for the fast-flowing rivers such as the Wear that drain the Pennines in northern England in summer but which may also be relevant to many other European streams. The metaphor of a pasture takes ecological status beyond a property that is defined in terms of a correlation with a pressure gradient and towards a view that emphasises interactions with other trophic levels. Kelly et al. (2009b) suggested that the changes in diatoms observed as pressures increase can be explained, in part, by a shift in the composition of the whole assemblage towards one dominated by competitive algae such as *Cladophora glomerata* and *Vaucheria* spp.; that such shifts have been linked to grazing intensity (Dudley & D'Antonio, 1991; Law, 2011) adds weight to this view of the guiding image proposed here for good status streams, at least for the warmer parts of the year (when most monitoring takes place).

Achnanthidium minutissimum ag. is the most abundant diatom in just over half the samples analysed in Kelly et al. (2012) and, in 12 monthly samples from the Wear at Wolsingham, it dominated only on six occasions (author, unpublished), so the generalised guiding image described above needs qualification. There are some stream types where *A. minutissimum* ag. may not be the most likely 'pioneer' species, and some instances where the small size of *A. minutissimum* relative to other algae will give a misleading impression of the most abundant species in a sample. Another possibility is that those samples where *A. minutissimum* ag. is less abundant represent situations where grazing and other disturbances

occur at a lower intensity, allowing non-R-strategists to thrive (see Biggs et al., 1998, for more details), and later stages in the microsuccession (see illustrations in Kelly, 2011).   The winter samples from the River Wear, for example, were dominated by stalk-forming *Gomphonema olivaceum* ag., which formed a matrix within which motile diatoms such as *Nitzschia dissipata* thrived. Such assemblages are more likely to proliferate when grazing intensity is low (Steinman et al., 1987; Law, 2011) so do not contradict the model proposed here.

River Wylye, Kingston Deverill, May 2011

The second example is a very different example of a 'good status' stream, a stretch of a southern English chalk stream, the River Wylye, approximately 4.5 km from its source (NGR: ST 844 372).   The distinctive character of streams draining the Cretaceous chalk of southern England has been recognised for a long time (Butcher, 1946; Macan & Worthington, 1951).   In essence, rain water percolates into aquifers within the permeable chalk from where it

emerges via springs to form rivers with relatively stable flow regimes, compared to rivers such as the Wear, whose flow responds rapidly to run-off following rainfall.

This site has a substratum that is approximately 70 % pebbles and gravel, 10 % sand and 20 % cobbles.   The cobbles, the preferred substratum for most monitoring studies (Kelly et al., 1998) each had a thick biofilm throughout the study period, often very dark brown or almost black in colour.   In contrast to the previous site, the diatom assemblage here was dominated by motile taxa (*Diatoma tenuis* and *Nitzschia* spp.: Table 2); however, the diatoms formed only a minor part of the total algal biomass, which was dominated by the cyanobacterium *Phormidium* (probably *P. flavosum*).   The mats may form as a result of the stable hydrological regime along with a relatively sparse invertebrate fauna (the product of a lack of inocula and habitat variability in the headwaters: Berrie & Wright, 1984; Giller & Malmqvist, 1998).   An interpretation of the biofilm at this site is given in Fig. 2, showing a mat of intertwined filaments of *Phormidium* (forming approximately 95 % of the total biovolume) through which motile diatoms glide in search of light and nutrients. The only non-motile diatom found in any numbers in this sample was *Staurosirella pinnata*, a diatom which is often found on smaller, less stable substrata in hardwater rivers in southern England (Round & Bukhtiyarova,
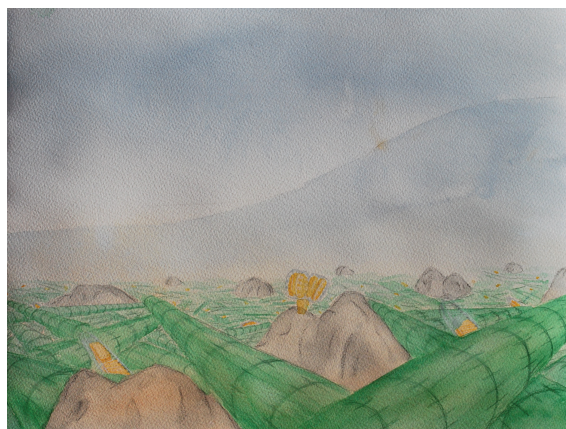
Table 2. Diatoms found at relative abundances (RA) ≥1 % on 10 May 2011 on cobbles in the River Wylye at Kingston Deverill, Wiltshire, southern England.

Taxon	RA (%)
Achnanthidium minutissimum ag.	3.8
Amphora pediculus	3.5
Denticula tenuis	7.0
Encyonema silesiacum	1.6
Eolimna minima	1.3
Fragilaria gracilis	2.6
Fragilaria vaucheriae	4.8
Fragilariforma bicapitata	1.3
Melosira varians	1.3
Navicula tripunctata	1.3
Nitzschia dissipata	9.0
Nitzschia fonticola	37.1
Nitzschia pura	14.1
Staurosirella pinnata	4.2
Total number of taxa recorded (including taxa present at <1%)	**29**

Fig. 2. Diorama showing the biofilm on cobbles from the River Wylye at Kingston Deverill in May 2011. The biofilm is dominated by a thick mat of *Phormidium* filaments, within which motile diatoms (*Nitzschia fonticola*, on this occasion) move. *Staurosirella pinnata* is also present, attached to sand grains. The *N. fonticola* cells are typically 20-30 μm long.

1996). Its precise habitat in this particular sample is not clear: the suggestion in Fig. 2 is that it is attached to sand grains trapped within the *Phormidium* matrix.

In summary, a low level of physical disturbance has allowed the community to develop beyond one dominated by R-strategists, as seen in the River Wear (although the most likely pioneers in hard water streams such as this include *Amphora pediculus* as well as *Achnanthidium minutissimum* ag.) to a community that has moved from density-independent to density-dependent growth. Intense competition for light coupled with relatively low nutrients has favoured mats of *Phormidium* which, in turn, requires a shift in the growth strategy of diatoms, if they are to survive.

River Nent, Nentsberry, July 2011

How are these views of good status streams modified by increased human pressure? Kelly et al. (2009b) suggested one scenario for organically-polluted rivers and the next example considers a different pressure: heavy metal pollution. The River Nent drains an area of the northern Pennines that was a major centre for lead mining in the 19th and early 20th centuries, with lead, zinc and cadmium entering the river from several adits and spoil heaps upstream of the sampling point (NGR: NY 767 449). Zinc is regarded as the main toxic metal in the Nent (Say & Whitton, 1981) and concentrations at Nentsberry are approximately 1.5 mg L^{-1}, well within the range where toxic effects on the biota should be evident (Whitton, 1980).

As for the previous examples, the starting point is the diatom assemblage (Table 3) which shows one of the key characteristics of heavy metal-polluted streams – an attenuated species list dominated, in this case, by *Achnanthidium minutissimum* ag. Although it has not been shown conclusively for this species, the likelihood is that these strains are, in common with other algae from metal-polluted rivers in this region, metal tolerant (Harding & Whitton, 1976; Say et al., 1977; Ivorra et al., 2001).

Hirst et al. (2002), de Yonge et al. (2008), Morin et al. (2008) and others have shown that it is possible to establish relationships between diatom assemblage composition and metal concentrations. But do such

relationships offer any insights into ecological status? The first impression of the River Nent is of the thick green biofilm covering all substrata: this is approximately 80 % (by biovolume) *Stigeoclonium tenue* with the remainder split mostly between *Phormidium* and *Achnanthidium minutissimum* ag. In other words, the 64% *A. minutissimum* that the diatomist observes comprises, in reality, less than five per cent of the total biovolume.

Stigeoclonium is classed as a 'C-S selected' taxon by Biggs et al. (1998), characteristic of stable, moderately nutrient-rich habitats. In the Nent it smothers the upper surfaces of not just bedrock and large boulders but also cobbles and larger pebbles, suggesting that its abundance reflects more than just physical stability. Again, the high biomass of phytobenthos may represent a breakdown in the relationship between algae and grazers: in this case, the short generation time of *Stigeoclonium tenue* may have allowed it to develop metal tolerance much faster than the invertebrate grazers. The high biomasses which are able to develop as a result smother rock surfaces and fill interstices, reducing habitat quality for grazers, even if they were able to develop metal tolerance (Armitage, 1979; Armitage et al., 2007). In this respect, *Stigeoclonium* may represent a bona fide example of an 'undesirable disturbance' to the balance of organisms, a term used in the normative definitions of ecological status (Annex V,

Table 3. Diatoms found at relative abundances (RA) ≥1 % on 2 July 2011 on cobbles in the River Nent at Nentsberry, Cumbria, northern England.

Taxon	RA (%)
Achnanthidium minutissimum ag.	64.0
Eolimna minima	11.1
Meridion circulare	8.2
Fragilaria capucina var. *gracilis*	4.1
Nitzschia fonticola	4.1
Surirella terricola	2.1
Amphora oligotraphanta	1.2
Fragilaria vaucheriae	1.2
Nitzschia sp.	1.2
Total number of taxa recorded (including taxa present at <1%)	**15**

European Parliament & Council, 2000) and normally used in reference to eutrophication (Tett et al., 2006). The Nent does receive some nutrient enrichment from a small sewage works at Nenthead (3 km upstream) which will contribute to the growth of *Stigeoclonium*, but the toxic effects of the metals on the invertebrates then exacerbates the situation.

Fig. 3 summarises this situation, showing the intertwined basal filaments of the *Stigeoclonium* which, along with *Phormidium*, forms a mat from which the erect filaments arise (many of which terminate in colourless hairs, see Gibson & Whitton, 1987). Where, then, does the R-selected *Achnanthidium minutissimum*, along with the other diatoms, fit into this picture? Are they an 'understory' within the predominant *Stigeoclonium* matrix, or are they surviving in open areas ('clearings') within this? While some controlled speculation may enrich our vision of ecological status, it is equally important not to push too hard to find neat explanations for every nuance in an assemblage of largely opportunistic organisms six orders of magnitude smaller than ourselves.

Round Loch of Glenhead, August 2011

The final example is a lake in a granitic catchment in south-west Scotland (NGR: NX 450 804), which was the focus of a number of studies in the 1980s concerned with its acidified state. Palaeolimnological studies showed that the loch was naturally acidic (pH ~5.5), but had become more acidic from approximately 1850 onwards (pH <5.0), due to sulphur deposition, originating from industrial areas over 100 km away (Flower & Battarbee, 1983; Jones et al., 1989). Over this time the diatom assemblage shifted from one dominated by *Brachsyira vitrea* along with *Achnanthidium minutissimum*, *Tabellaria flocculosa* and *Stauroforma exiguiformis* to one dominated by *Eunotia incisa* and *T. quadriseptata*. As a result of legislation on sulphur emissions, introduced partly as a result of studies on Round Loch of Glenhead and other softwater lakes in the UK and Scandinavia, the pH of the loch has gradually increased since this point (currently ~5.2). This has been accompanied by a change in the diatom assemblage. Interestingly, the assemblage recorded now is different

Fig. 3. Diorama showing the biofilm on cobbles from the River Nent at Nentsberry, July 2011. Erect filaments (tapering to hyaline hairs) of *Stigeoclonium* emerge from a basal mat entangled with filaments of *Phormidium*. A few cells of *Achnanthidium minutissimum* (typically 10-12 μm long) are present at the front left foreground.
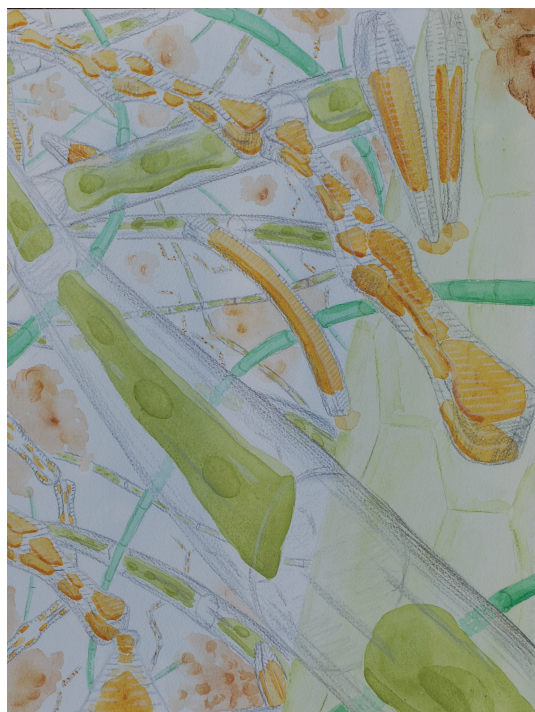

Fig. 4. Diorama showing the biofilm associated with stems of *Isoetes lacustris* in Round Loch of Glenhead, August 2011. Filaments of the green alga *Mougeotia* and chains of the diatom *Tabellaria quadriseptata*, along with narrow cynaobacterial filaments (possibly a species of *Pseudanabaena*) and trapped humic particles, create a matrix within which the diatoms *Frustulia* and *Navicula leptostriata* are found. *Eunotia* spp. and *Peronia fibula* are epiphytic on the *Isoetes*.

to that associated with pre-impact conditions, with *Navicula leptostriata* now accounting for about 50 % of the total diatoms.

There has, in other words, been a recent shift from largely sessile, or only sporadically motile diatoms, towards a motile taxon. Abundant motile diatoms often suggest a 'significant absence': a non-diatom alga, for example, which dominates the architecture of the biofilm such that diatoms which are efficient competitors for light are favoured. There has been a significant reduction in the quantity of sulphates in bulk deposition in the vicinity of Round Loch of Glenhead, but no significant reduction in nitrates. This, combined with recent evidence that many upland lakes are nitrogen- rather than phosphorus-limited (Maberly et al., 2003) led to suggestions

Table 4. Diatoms found at relative abundances (RA) ≥1 % on 3 August 2011 on stems of either *Isoetes lacustris* and *Lobelia dortmana* in Round Loch of Glenhead, south-west Scotland.

Taxon	RA (%)	
	Isoetes lacustris	*Lobelia dortmana*
Adlafia bryophila		1.3
Brachysira vitrea		3.9
Chamaepinnularia mediocris		2.0
Chamaepinnularia soehrensis		1.3
Eunotia exigua	1.6	
Eunotia incisa	16.5	10.8
Eunotia naegelii	5.2	4.0
Eunotia rhomboidea	0.6	2.3
Frustulia rhomboides		1.6
Frustulia saxonica	1.9	7.2
Navicula leptostriata	33.6	46.4
Peronia fibula	19.1	4.0
Tabellaria flocculosa	5.8	4.0
Tabellaria quadriseptata	13.9	6.2
Total number of taxa recorded (including taxa present at <1%)	**12**	**24**

that the reason for the recovery trajectory following a different path to that expected from palaeolimnogical observations, is that the loch, originally very nutrient poor, is now enriched with nitrogen (Flower et al., 2010).

Fig. 4 summarises these observations in a visual form. Stems of emergent plants (*Lobelia dortmana* and *Isoetes lacustris*) and surfaces of submerged stones are smothered with an amorphous, slimy dark brown biofilm which, under the microscope, resolves into a mixture of algae, including *Tabellaria* spp., *Mougeotia*, a thin cyanobacterium (possibly *Pseudanabaena* spp.), along with particles of humic material. These form a matrix within which *Navicula leptostriata* and *Frustulia saxonica* were living, whilst *Eunotia* spp. and *Peronia fibula* lived epiphytically on the plant stems. There is anecdotal evidence that these brown growths were much less developed in the early 1980s when regular visits to the loch started (R. Flower, personal communication).

Flower et al. (2010) provide a comprehensive summary of the changes in Round Loch of Glenhead and other softwater lakes in the UK whose recovery from acidification

has been evaluated, and they appraise the evidence of increased nutrient enrichment. Fig. 4 attempts to link the quantitative data from Round Loch of Glenhead (Table 4) with qualitative observations to suggest mechanisms by which the increased nutrient concentrations, particularly of nitrogen, may drive changes in the diatom assemblage. Palaeolimnology has made significant progress based on a core assumption that each species has an optimum and a tolerance for the variable under investigation (Birks et al., 1990). As these variables are usually chemicals, the implication is that the diatoms have ecophysiological adaptations to particular states; however, the diatom species found in a sample will also be influenced by other organisms and overall community architecture.

Discussion

Contemporary palaeontology?

The previous section opened by drawing analogies between visualising the world of phytobenthos and the familiar reconstructions of dinosaurs which now permeate popular culture. It closed with an example where a palaentological approach to diatoms yielded valuable insights that prompted tighter environmental legislation and, in time, improvements in ecological quality (Battarbee et al., 1999). Palaeontologists draw inferences from the limited number of remains that resist organic decay; they adopt various approaches – including analogies with contemporary environments – in order to place those remains in context. The question that I am posing is whether applying the same approach to contemporary systems – i.e. deliberately removing the organic matter before starting analysis and interpretation – yields sufficient insights into ecological status to underpin environmental regulation on a large scale. In the case of Round Loch of Glenhead, the 'paleontological' approach is justified as annual samples collected using sediment traps provide data that can be compared directly with the record from lake sediment cores (Flower et al., 2010); even here, however, the story of recovery is not straightforward and may benefit from supplementing analysis of cleaned diatoms with investigations of contemporary phytobenthos assemblages.

In other words, although there are strong justifications for using diatoms – their importance in ecosystems, their ability to indicate environmental conditions and their ease of use (Stevenson & Pan, 1999) – there are also problems associated with the current approaches based on cleaned valves. Despite strong correlations with water chemistry variables (Hering et al., 2006) and with other components of the phytobenthos (Kelly, 2006; Kelly et al., 2008b), they may sometimes not tell the whole story. This may not be a problem for national-scale classifications (where standardisation of methods is important) but pragmatic decision-making

at the catchment and sub-catchment scale will benefit from an approach that encompasses all phytobenthos, and considers interactions with other trophic levels.

The overwhelming evidence, however, is that diatom-only approaches, despite being 'contemporary palaeontology', do give valuable evidence for ecological status assessment and, at a purely practical level, the focus on diatoms means that, for many EU Member States, phytobenthos status is now defined, legally, in terms of diatom-based metrics (European Council, 2008). However, the 'contemporary palaeontology' approach has two principal limitations: the deliberate removal of part (occasionally a large part) of the phytobenthos biomass during preparation will mean that some mismatches between measured and 'true' status may occur; and it is hard to communicate the results beyond a narrow group of specialists.

The semiotics of slime

Fine-scale taxonomy based on the cleaned valve produces data that are amenable to sophisticated multivariate analyses, producing valuable insights into ecological quality (Birks et al., 1990; Lancaster et al., 1996; Feio et al., 2009) albeit in a somewhat abstract form. However, as the implications of the WFD become clear, these insights will feed into efforts to improve those water bodies that currently fail to achieve good ecological status (GES), the costs of which will be passed to consumers. There is, therefore, a need for phytobenthos specialists to communicate not just amongst themselves, but also with decision-makers (who may not be ecologists) and with the wider public. The debate can be summarised as follows: if the phytobenthos of a river fails to achieve at least good status, the authorities are required to implement measures to raise the status of that river. This may necessitate reducing concentrations of phosphorus and/or nitrogen, which will require investment by utility operators and other polluters in the catchment. They, in turn, will pass their increased operating costs to consumers. The regulators therefore need to know that there is a cause-effect relationship (not just a correlation) between the phytobenthos and the

pressure variable in order to be sure that there is a high probability of genuine ecological benefits accruing from any investment. Meanwhile, the utility operators will need to be able to explain to their customers why cost increases are necessary. Neither phosphorus nor nitrogen is toxic in the concentrations normally encountered in the environment; and a reasonable interpretation of the WFD would mean that the difference between moderate and good status is not superficially apparent to anyone without biological training. Phytobenthos, in short, has a serious image problem.

The reductionist approach has produced quantitative expressions of ecological status that are far removed from what stakeholders see when they look into a river or a lake. Because managing nutrient pollution is expensive, it is possible that both regulators and regulated industries will find loopholes in the WFD to avoid the need to take action on rivers that fail to attain good status solely on the basis of phytobenthos. The challenge here is for diatomists to move out of a comfortable zone where they communicate mostly with a narrow group of fellow specialists and start to explain the benefits of a healthy phytobenthos community to the people who will pay for improvements.

Phytobenthos enters the consciousness of non-biologists where excessive growths cause aesthetic problems or interferes with other legitimate water uses. Examples include growths of *Cladophora glomerata* in the littoral zone of Windermere (Parker & Maberly, 2000), mass growths of *Didymosphenia geminata* interfering with sports fishermen in New Zealand (Whitton et al., 2009) and toxic algal mats leading to livestock deaths (Mez et al., 1997). With the exception of *D. geminata* (where the reason behind the mass growths is still a matter of debate), there is a clear link with human pressures, constituting an 'undesirable disturbance' as recognised in the WFD and, therefore, a rationale for a programme of measures. However, a shift from a 'healthy' to an impacted phytobenthos assemblage may not have such visible outcomes; shifts in taxonomic composition take place within an apparently amorphous, slippery brown biofilm.

How, then, do we communicate the positive benefits of a healthy biofilm to stakeholders? Again, the analogy

with dinosaurs bears consideration, as imaginative but informed interpretations of scant evidence has brought dinosaurs to life for the lay public. The dioramas shown here present the slippery brown biofilms as unexpected repositories of biodiversity. The organisms themselves may be strange and unfamiliar, but many of the activities that take place within these can be related to more familiar ecosystems. Expressing ecological status in quantitative terms has many benefits but, at some point, the 'Ecological Quality Ratios' (EQR) needs to be translated back into a form that relates more directly to ecological process and to the experience of stakeholders. Reconstructing data into a vision of the functioning biofilm emphasises the role of phytobenthos as the base of an aquatic food chain that, ultimately, sustains ecological services to which stakeholders can relate. The focus of the debate moves from phosphorus concentrations or EQRs (which mean nothing to most stakeholders) to protecting tangible benefits (e.g. salmonid fisheries, in the case of the Wear and Wylye).

Conclusion

The focus on the cleaned valve is simultaneously a benefit and a problem for those involved in applied diatom ecology. It allows fine-level taxonomy which, in some cases, permits subtle changes in the chemical environment to be discerned (Potapova & Hamilton, 2007; Poulíčková et al., 2008) and tracked over time (Flower et al., 2010). Yet, in the process, the outputs from this become harder to integrate into mainstream ecology, particularly in situations where non-diatom algae are also important. Approaches to ecological status assessment have been evaluated largely in terms of the strength of associations with pressure variables (Hering et al., 2006); assessing methods in terms of their ability to show their fitness in relation to other trophic levels, or in terms of their potential to cause 'undesirable disturbances', is a more difficult task yet one that is closer to the spirit of the WFD. Just as a protein scientist gains little from simply knowing what amino acids are present and in what proportions, so phytobenthos specialists need more than a list of taxa and

their relative abundances if they are to advise catchment managers on options for ecosystem restoration.

Indeed, we should remember that the spirit of the WFD extends beyond assessing ecological status. The focus is on restoring water bodies to good ecological status (Article 4), financed by water users (Article 9) so long as it is not disproportionately expensive (Article 4 clause 5) and doing this in a manner that is open and transparent (Article 14). This is the context within which ecologists must present biofilms as the 'engine room' of a healthy river, crammed with microscopic life and not just as slippery brown gunk. Such an approach may make the public more aware of the benefits of healthy river ecosystems and, as a result, more understanding of increased water charges. On the other hand, these 'guiding images' are not definitive statements of the architecture of submerged biofilms but a mixture of evidence, analogy and speculation. This was the approach adopted by Leonardo da Vinci for his anatomical drawings yet even his meticulous observation could not completely eradicate traditional (and erroneous) wisdom (Kemp, 2004; Clayton & Philo, 2012). Rather, these dioramas are offered in the hope of stimulating debate on how biofilms are structured, and the roles different species play in this. They supplement, rather than replace, the new generation of methods for ecological status assessment.

By giving a sense of how biofilms are structured and function and why they are important to both professionals and stakeholders, they in turn fuel a debate on what we mean by healthy freshwater ecosystems and provide a tool for communication. In moving ecology to the centre of the decision-making process, the WFD has placed a large responsibility on us: we will be spending large sums of someone else's money and now need to show that we are doing this wisely.

Acknowledgements

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