The "forgotten" ecology behind ecological status evaluation: re-assessing the roles of aquatic plants and benthic algae in ecosystem functioning

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Abstract

Aquatic plants and benthic algae have long been used as indicators for nutrient enrichment in lakes and streams. Evaluations of the performance of indices calculated from species assemblages of aquatic plants and algae are generally based on correlations with water nutrient concentrations. We argue that this is a misinterpretation, because water chemistry is both cause and effect: higher nutrient concentrations may cause enhanced plant and algal growth and change their assemblages, but plants and benthic algae also remove nutrients from the water. Additionally, biotic interactions blur water chemistry – aquatic plant relationships. We suggest that indices can be improved by relating biotic responses to quantifiable causal stressors, such as nutrient loading, instead of using water chemistry for performance evaluation of the indices. In addition, a tiered approach, i.e. the use of simpler indices for getting an overview and of sophisticated methods in doubtful cases, could avoid unnecessary costs and efforts while giving important monitoring and management information.

Keywords: ecological indicators, water quality, eutrophication, water plants, macrophytes, benthic algae, diatoms

1. Introduction

Clean waters ensure the provision of safe drinking water, protect human health, support economic and recreational activities and provide healthy habitats for flora and fauna. Regular monitoring of the condition of water is, therefore, a prerequisite to its safe and sustainable use. Proponents of ecological assessment of rivers and lakes argue that this complements chemical monitoring because the biota provide a longer-term insight into prevailing conditions than chemical measurements, and because living elements may respond to all stressors within an ecosystem (Karr 1999). Aquatic ecologists have long been aware that macrophytes and benthic algae are affected by, but also shape their chemical, physical and hydrological environment (Butcher, 1933). Aquatic plants are considered useful as indicators for what has been termed "ecological status" in Europe (EC 2000) and "ecosystem health" or "biotic integrity" elsewhere (Karr 1991, 1999). In Europe, the Water Framework Directive (WFD; EC 2000) has boosted the interest of scientists and water managers in aquatic plants and algae, because phytoplankton and phytobenthos are mandatory elements in status assessment of rivers and lakes, along with benthic invertebrates and fish. The WFD was welcomed by many for putting aquatic ecology, rather than chemistry alone, at the base of management decisions (Hering et al. 2010). But are we using the biological indicators well? Do present-day biological indicators perform better than their predecessors, some of which were developed more than 100 years ago? Does the way we use water plants and algae as indicators for the WFD constitute a "Progress in Botany"? In this review, we argue that a large part of the potential information aquatic plants could provide is ignored. This is due mainly to the lack of well-defined cause-effect-relationships. In addition, the imprecise use of the term "eutrophication", which has continued over the last century, and the unfortunate use of "hydrochemistry-response" correlations for performance evaluation of biological indicators have introduced considerable confusion.

In order to explain our reasoning, we briefly review the history of ecological assessment in freshwater, and point to the underlying ecological interactions, which appear to have been "forgotten" in the use of benthic floral indicators for the WFD. We then argue that an index that is based on well-defined stressor-response relationships indeed would have the potential to become a tool that is useful for overall status assessment, for identifying and quantifying stressors that likely are responsible for the deterioration of a water body and for planning suitable management measures to improve ecosystem health. In this review we focus on the benthic flora in rivers, though many of our examples are from lakes (when no data exist from rivers), and many of our arguments are also valid for other organism groups (= “biological quality elements” in the terminology of the WFD).

2. A short history of ecological status assessment in rivers

The first methods for ecological assessment were not all based on strictly scientific evidence, but instead were rooted in a sound and often lifelong practical experience. The modern history of biological monitoring in rivers began in Europe, at a time when the human population was sufficiently large to produce both well-educated scientists and spectacularly polluted rivers. The most widely known example is probably the river Thames in London, which – in the nineteenth century, produced such a horrible smell that sheets soaked in vinegar were hung in the Parliament in the hope of offsetting the noxious air wafting in from the river (Cairns and Pratt 1993). Hassall (1850) used evidence of algae and other microscopic life present in reservoirs around London as a means of raising awareness of the potential link between water quality and health, some 30 years before the discovery of the actual causal agents. At these times, organic pollution and associated diseases were the most widespread impact on rivers due to human population increase and industrial activities combined with lack of advanced sewage treatment (Billen et al. 1999). It is therefore not surprising that the first assessment systems targeted organic pollution.

The idea of using biological indicators as a means of assessing river water quality probably originated with the work of Kolkwitz and Marsson (1902). These authors observed that different benthic taxa occurred sequentially downstream of a source of organic pollution, and changed in a predictable way along the course of the river. Based on these observations they developed a list of organisms which would indicate “saprobity” (the degree of organic pollution) in rivers. The presence of these indicator organisms at a river or stream site could then be used as a measure of the degree of contamination by organic matter (primarily sewage) and the resulting decrease in dissolved oxygen. This first list of indicator organisms was based on empirical observations, combined with deductions of possibly causal relationships. Pantle and Buck (1955) were the first to propose a means by which the list of indicator organisms present at a site could be converted to a quantitative measure of the “saprobity” at a river or stream location (the “Saprobienindex”).

The first lists of indicator organisms for the Saprobienindex contained both macro-invertebrates and benthic algae (Kolkwitz and Marsson 1908). However, primary producers were generally believed to relate more directly to inorganic nutrients, rather than to organic pollution (Schmedtje and Kohmann 1987), such that later revisions of the Saprobienindex (Friedrich 1990) used heterotrophic organisms exclusively as indicators. During the second half of the 20th century, due to the increasing standard of wastewater treatment, the degradation of organic matter was moved more and more from the river into the wastewater treatment facilities, whilst inorganic nutrients such as nitrogen and phosphorus continued to be released into the rivers. Thus, a need developed to differentiate heterotrophic processes, which are related to organic pollution ("Saprobie"), from autotrophic processes, which are related to inorganic nutrients ("Trophie"). In parallel to improvements in wastewater treatment and the increased importance of inorganic nutrients relative to organic pollution, trophic rankings of macrophyte species were developed for rivers (e.g. Kohler et al. 1974; Newbold and Palmer 1979). They paved the way for the development of various macrophyte indices (Holmes et al. 1999; Schneider and Melzer 2003; Haury et al. 2006). The main advantage of such indices compared to hydrochemistry was their simplicity (Tremp and Kohler 1995), and because they provide information about the **effects** of nutrient discharges rather than merely quantifying their load (Holmes et al. 1999). This is important because sensitivity and resilience to nutrient-enrichment may vary substantially across ecosystems (Janse et al. 2008). Nevertheless, the validity of macrophyte indices was generally shown by relating them to water nutrient concentrations. This introduced a logical inconsistency: on the one hand, indices were "validated" against hydrochemistry, whilst at the same time proponents argued that these biological indices do not indicate hydrochemistry but, rather, the effects of nutrient loading.

The evolution of algal-based methods followed a slightly different trajectory, with early methods (Descy 1979; Lange-Bertalot 1979; Coste in CEMAGREF 1982) not differentiating between organic and inorganic pollution for monitoring river quality. Much of the work subsequently has focused on one group: the diatoms, to the exclusion of other groups of algae (Kelly 2013; Kelly et al. 2015). In particular, Coste in CEMAGREF (1982) proposed the diatom-based Indice de Polluosensibilité Specifique (IPS) which was adapted and adopted by the Agence de l'Eau Artois-Picardie in northern France for routine environmental assessments in a region where invertebrate analyses proved to be insufficiently sensitive (Prygiel and Coste 1993). A second generation of methods did attempt to differentiate between inorganic and organic pollution (Kelly and Whitton 1995; Rott et al. 1999) in response to new European Union legislation. However, the IPS, which is calibrated against a "general degradation" gradient, continues to be popular throughout Europe (see Kelly 2013).

There is evidence that diatoms do act as good proxies for the entire phytobenthos (Kelly 2006; Kelly et al. 2008; Schneider et al. 2013b), though a lot of photosynthetic diversity is overlooked by adherence to a diatom-only system. Some national assessment systems do include larger algae within their macrophyte survey methods (see Kelly 2013, for details) whilst a few have developed methods based on soft-bodied algae that are used either in conjunction with diatoms (Schaumburg et al. 2004) or alone (Schneider and Lindstrøm 2011). Diatom assessment systems generally have strong correlations with water nutrient concentrations (Hering et al. 2006a), although such correlations are mostly based on spatial associations, and little reliable experimental data exist that could underpin these relationships.

3. Aquatic plants, benthic algae and the Water Framework Directive

The WFD (EC 2000) did not introduce an entirely new concept, but it did put the importance of biological monitoring into a common legal framework relevant for all member states of the European Union. Now deterioration and improvement of ecological quality were defined by the response of the biota, rather than by physical or chemical variables, and the benthic flora became a mandatory element for river status assessment. However, in spite of this fundamental change, many methods eventually adopted for WFD assessment were largely modifications of metrics that had been in use before (Kelly et al. 2009; Bennett et al. 2011; Birk et al. 2012). There are several possible reasons: i) a reluctance amongst policy makers and managers to spend money for developing new assessment methods, ii) a desire among scientists and managers to continue using existing time series, or iii) the conclusion that existing methods actually were well-suited for the WFD.

While each of these reasons is understandable, one consequence is that many “new” WFD-compliant ecological assessment methods using aquatic plants and benthic algae were still based on correlations with measured water chemical parameters. This was not seen as a disadvantage; on the contrary. Hering et al. (2006b) pointed out that correlating the results of a metric to the stressor gradient is a central part of developing an index for ecological assessment of aquatic ecosystems. They recommended data on BOD (biochemical oxygen demand) or oxygen content to describe the impact of organic pollution, or concentrations of phosphorus and nitrogen to describe the trophic status of a sampling site. Indeed, a large number of studies have been published in recent years, testing different WFD metrics based on correlations between the metrics and measured water total phosphorus concentrations (e.g. Penning et al. 2008; del Pozo et al. 2010; Timm and Moels 2012; Lyche-Solheim et al. 2013). Such studies are usually based on the underlying assumption that the metric having the strongest correlation with measured phosphorus concentration is “best”, and consequently this is the one that should be used for future monitoring of eutrophication.

While it can hardly be doubted that well-explained stressor-response relationships should underpin ecological assessment methods, this also leaves us with a conundrum: if it is necessary for an ecological metric (e.g. species composition of benthic flora) to correlate closely with a measured chemical variable (e.g. water phosphorus concentration), then what is gained by putting ecology rather than chemistry at the base of management decisions? A possible answer could be that the correlation between measured variable and ecological response may have various shapes (Fig. 1). In case of threshold, asymptotic or exponential responses, critical values for the measured variable may be set to match ecological response (Fig. 1). Indeed, sudden shifts from macrophyte to phytoplankton dominance have been reported in response to nutrient loading for rivers as well as lakes (Scheffer et al. 1993; Hilt et al. 2011). However, apart from the fact that **linear** correlations would not be appropriate for comparing response sensitivity of different ecological metrics (Penning et al. 2008; Lyche-Solheim et al. 2013), this also would mean that ecological monitoring is no longer necessary once the relationship between the measured variable (e.g. water total phosphorus concentration) and ecological response (e.g. species composition of aquatic flora) has been established. In all cases depicted in Fig. 1, the ecological response could easily be calculated from the measured variable, so there would be no need for water managers to spend money for additional monitoring of the ecological response. In other words: the "fundamental change" introduced by the WFD would cease to exist.

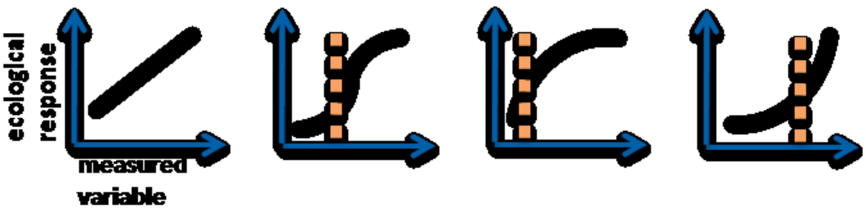

Fig. 1. Potential relationships between a measured variable (e.g. water total phosphorus concentration) and an ecological response (e.g. species composition of aquatic flora); the figures exemplify a linear, threshold, asymptotic and exponential response (from left to right); vertical dashed lines exemplify where critical values of the measured variable may be set, such that they lie before or after steep parts of the ecological response.

The solution to the conundrum is to recognize that water chemistry – ecological response relationships are purely descriptive tools that rank data more or less correctly along a gradient from unimpacted to the most impacted water bodies, rather than being causal dose-response relationships. Although water phosphorus concentration has been widely used as a general proxy for the stressor "eutrophication", neither phosphorus concentration nor eutrophication actually is the stressor.

4. The "forgotten ecology": nutrient uptake by plants – nutrient cycling

Water chemistry is both cause and effect, although testing of WFD indices generally only assumes the former. On the one hand, enhanced nutrient-concentrations may cause enhanced plant and algal growth and lead to changes in assemblage composition. On the other hand, however, plants and benthic algae also remove nutrients from the water, directly by incorporating them into their biomass, and indirectly through their effects on biogeochemical processes. For example, aquatic macrophytes can create biochemical conditions that favor phosphorus (P) deposition (Chambers et al. 1989; Dodds 2003 and references therein; Blindow et al. 2014). CO_2 assimilation during photosynthesis results in increased pH and a lowered solubility of $CaCO_3$ and consequently calcite precipitation on the surface of macrophytes. Most photosynthetic aquatic plants in hard water are capable of precipitating calcite. The charophytes, in particular, can be heavily calcified and more than 50% of the total plant dry weight has been reported to originate from $CaCO_3$. Phosphorus co-precipitates with calcite and can constitute up to 23% of total P in calcified charophytes (Siong and Asaeda 2006 and references therein). In addition, root oxygen release of macrophytes can form iron crusts in anaerobic sediment leading to an enhanced sorptive P fixation (Dollan and Hupfer 2003). Decomposing plants, in turn, may lead to sudden increases in dissolved nutrient concentrations (Barko and Smart 1981; Twilley et al. 1986). Macrophyte beds can also affect nutrient retention by trapping suspended particulate matter from the turbulent overlying water (Vermaat et al. 2000; Schulz et al. 2003).

However, while aquatic plants may remove nutrients from the water, these may nevertheless still be available to them. Indeed, most rooted aquatic plants take up the majority of their nutrients from sediments (Carignan and Kalff 1980; Barko and Smart 1981; Chambers et al. 1989) and sediment nutrient concentrations are by no means always correlated with water nutrient concentrations (Schneider and Melzer 2004). Aquatic plants and benthic algae can reduce water exchange across the sediment-water boundary thus decreasing advective transport of P away from sediments (James et al. 2004). They may also use groundwater-born nutrients (Perillon and Hilt 2016).

As a consequence of these processes, the ecological status indicated by benthic algae and macrophytes in the littoral zone of shallow lakes is not necessarily consistent with open-water concentrations of phosphorus and/or nitrogen, e.g. in Lake Tahoe (Loeb 1986), Lake Taupo (Hawes and Smith 1993), Lake Huron (Barton et al. 2013) and Lake Ohrid (Schneider et al. 2014). In Norway, mass development of macrophytes can occur in streams with extremely low water nutrient concentrations (Schneider et al. 2013a). This phenomenon also applies to water bodies that recently underwent restoration measures aiming at the reduction of nutrient loading. Phytoplankton has been found to respond rapidly to external nutrient loading reduction in lakes, whereas a significant delay was observed for submerged macrophytes colonizing the littoral areas as lake sediments still stored nutrients from earlier periods with higher loading (Hilt et al. 2010, 2013). This delayed response of macrophytes compared to phytoplankton is partly due to their use of nutrients stored in sediments, to which phytoplankton have no access. In addition, a number of biological interactions may prevent a recolonization with species indicating less eutrophic conditions in water bodies that underwent a strong decline in nutrient loading (Hilt et al. 2013; Eigemann et al. 2016). The shading effect of periphyton (a complex matrix of algae and microbes growing on underwater surfaces such as stones or plants) on macrophytes might be one of the most common of these interactions (Phillips et al. 1978; Köhler et al. 2010). In contrast to earlier assumptions, periphyton density is often not controlled by nutrient loading but top-down by a fish-grazer-periphyton cascade (a high number of fish feeding on grazing macroinvertebrates results in high periphyton biomass, whilst a low number of fish results in greater grazing activity by macroinvertebrates, leading to a lower periphyton biomass; Jones and Sayer 2003). In addition, herbivory by birds and fish might play a significant role in preventing macrophyte reestablishment (Bakker et al. 2013), particularly when combined with periphyton shading (Hidding et al. 2016). All these interactions blur a simple correlation between water chemistry and assemblages of aquatic plants and benthic algae.

But then, if water nutrient concentration can be both cause and effect of changes in aquatic plant and algal assemblages and therefore cannot simply be “the stressor”, what “stressor” should we measure instead? In the early days of ecological assessment, managers accepted indicator lists inferred from expert judgment also without reliable data as to what the indicators actually indicate. Now we have to provide evidence that a metric indeed “responds” to a stressor (Birk et al. 2012) and scientists search for easily quantifiable parameters in order to provide this evidence. This resulted in the use of water chemistry (often total phosphorus concentrations) as a proxy for “eutrophication”. However, it has been known for a long time (Ohle 1955) that water nutrient concentrations alone are not sufficient to determine eutrophication. We have explained above why water phosphorus concentrations may not be useful as a proxy for the stressor, and we will now show why “eutrophication” is not a stressor either.

5. Wanted: the stressor!

The principle behind ecological assessment is straightforward: if a stressor affects biota, then the condition of the biota can be used to assess the intensity of the stressor (Fig. 2). Most metrics based on aquatic flora have been developed to assess “eutrophication” (e.g. Kelly and Whitton 1995; Fisher et al. 2010; Kolada et al. 2014).

Unfortunately, ever since their coining (Naumann 1929), the terms “eutrophication”, “oligotrophic” and “eutrophic” have variously and confusingly been used to describe ecosystem processes (e.g. increased plant growth) or ecosystem characteristics (e.g. water nutrient concentrations; Rodhe 1969). The inconsistent use of the term “eutrophication” has repeatedly been pointed out (e.g. Rodhe1969; Hutchinson 1973; Wetzel 2001). Attempting to reach a common understanding, the OECD defined eutrophication as “response in water to over-enrichment by nutrients”, resulting in “symptoms such as algal blooms” or the “heavy growth of certain rooted aquatic plants” (Vollenweider and Kerekes 1982). Similar definitions, i.e. describing an enrichment of water by nutrients that causes an accelerated growth of algae and plants, were used in national and international legislation (e.g. DIN 4049-2 1990; European Court of Justice 2009; European Commission 2009).

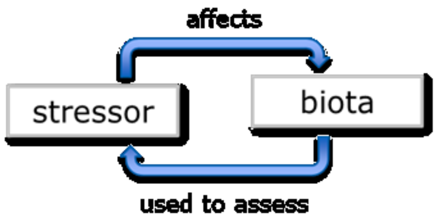

Fig. 2. The principle of ecological assessment: if a stressor affects biota, then the condition of the biota may be used to assess the intensity of the stressor.

This means that eutrophication is a **process**, and its meaning includes several linked “cause and effect” relations from nutrient enrichment through to accelerated plant and algal growth, rather than merely the **cause** of this process (Fig. 3). Eutrophication is caused by nutrients entering the ecosystem via different internal and external sources that are used by aquatic plants and algae. We therefore argue that the stressor which benthic plants and algae react to, and consequently against which benthic floral indices should be regressed, is nutrient loading (from external and internal sources) rather than “eutrophication” (= the process that leads from nutrient enrichment to accelerated plant and algal growth) or “nutrient concentration” (= cause and effect of specific aquatic flora assemblages). In rivers and streams, nutrient loading should be expressed relative to stream discharge, because benthic plants generally are not exposed to the entire water column. Using “loading relative to discharge” instead of concentration would prevent the confusion of cause and effect. It would circumvent the problem that is caused by the uptake of nutrients by benthic algae and plants, leading simultaneously to reduced water nutrient concentrations and enhanced plant and algal growth at a site. It would also take into account the temporal variability in water nutrient concentrations that cause uncertainty in average concentrations. We hypothesize that average nutrient concentrations should reflect nutrient loading in anthropogenically unimpacted headwater streams, as well as in eutrophic rivers receiving a more or less continuous nutrient input. In these systems, nutrient concentrations may well be useful for understanding benthic floral responses. However, in systems with variable or steadily-declining nutrient concentrations, e.g. because measures have been taken to reduce external nutrient loading, any relationship between spot-measured nutrient concentration and benthic floral indices will be blurred due to nutrient uptake by plants and benthic algae, nutrient storage in sediments and temporal variability in nutrient inputs from various sources. Therefore we have to question the perception that the biological metric with the strongest correlation with measured water phosphorus concentration is, automatically, the one which best indicates “the stressor”.

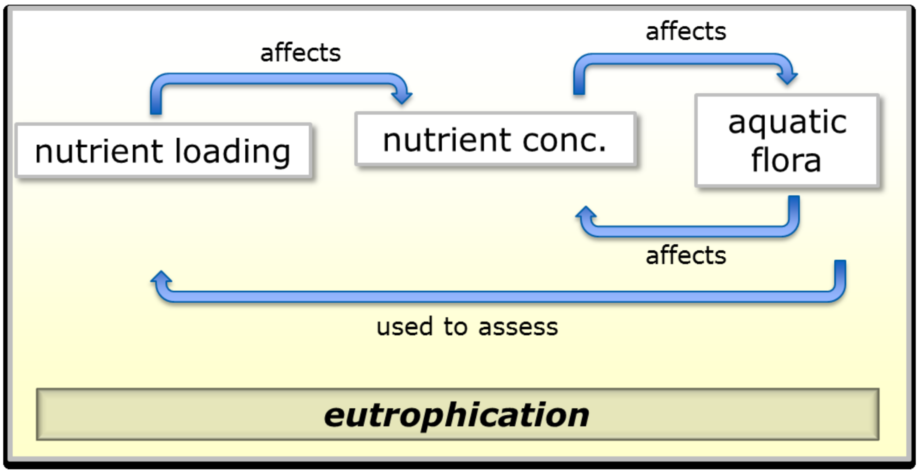

Fig. 3. Eutrophication is a process in which increased nutrient loading leads to increased growth of macrophytes and algae and changes in their species composition. Since the stressor (nutrient loading) is difficult to quantify, water chemistry (mainly total phosphorus) is used as a proxy, and water chemistry – biota relationships were used to develop metrics for aquatic flora.

The WFD added an additional layer of complexity: the biota present at a site have to be compared with the biota at anthropogenically unimpacted reference sites: the greater the difference, the poorer the ecological status. Accepting the possible complications of identifying true reference sites (Pardo et al. 2012; Bouleau and Pont 2015), this approach has the advantage that it is comparable across countries and ecoregions, because a relative difference is quantified instead of absolute indicator values. It comes, however, with a drawback: biota are affected by a multitude of stressors including over-enrichment with nutrients, acidification, habitat degradation, siltation, changes in hydrological regime, increased water temperature, toxic substances, competition or interference from invasive alien species (Von der Ohe et al. 2014). Many rivers are subject to multiple stressors, and these often have interactive effects on the biota, including the benthic flora (Schneider et al. 2013b; Piggott et al. 2015). Just quantifying the difference in species composition and abundance of aquatic flora between impacted sites and the (presumed) reference state for those sites fulfills the demands of the WFD by indicating whether one (or several) stressors are affecting the flora at the sampling site (Fig. 4). It does, however, not necessarily determine which of the stressors actually caused the difference. For a water manager, however, this is highly relevant: s/he needs to understand which measures are required to restore a degraded ecosystem.

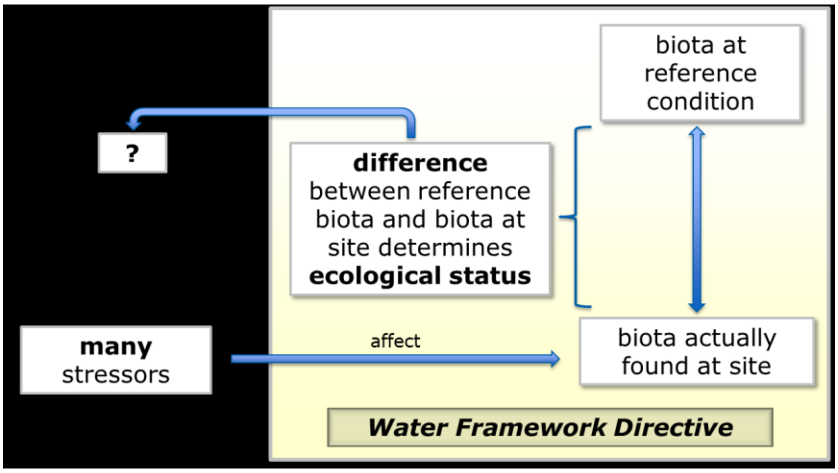

Fig. 4. Assessment according to the Water Framework Directive (WFD) is based on the difference between the biota at the sampling site, and those at unimpacted reference sites. While this approach has many advantages, such as comparability across ecoregions, it also has the drawback that many different stressors may impact the aquatic flora. Water managers can thus not easily infer which stressor caused degradation.

The countries in the European community have adopted different approaches to deal with the challenges posed by the WFD. Some researchers developed new indices and related them to “general degradation” (e.g. Hering et al. 2004; Gabriels et al. 2010). Although such an approach fulfills the demands of the WFD, it is of limited use to water managers since the indices may not diagnose the cause of degradation (Friberg 2014). Others adjusted “pre-WFD-indices” by re-calculating the index values relative to reference conditions (Kelly 2013); these indices also fulfill the demands of the WFD, but since they were designed to correlate closely with water chemistry, their additional value to hydrochemical measurements remains unclear. So how should we progress between Scylla and Charybdis?

6. What information can we get from benthic flora?

We do not question the principles of the WFD, which has brought many achievements, among them the re-organization of water management by hydrological catchments rather than by administrative borders, the harmonization of classification and monitoring tools across Europe, the focus on ecosystem integrity instead of mere pollution control (Hering et al. 2010; Birk et al. 2012) and active engagement with stakeholders (Steyaert and Ollivier 2007). However, we argue that there is room for improvement of the ecological tools. Ecological assessment should be able to:

- quantify degradation,
- diagnose causes of degradation: identify the main stressor(s),
- pick up warning signals of unknown or underestimated stressors,
- identify management priorities by differentiating heavily impacted from less impacted sites,
- document improvements following restoration/rehabilitation, and
- communicate key information to non-specialist stakeholders.

Multi-metric indices have been recommended before as a highly reliable ecological assessment tool (Hering et al. 2006b). A multi-metric index combines individual measurements into a single metric, which can be used to assess a site's overall condition. If each component that constitutes the multi-metric index is related to a specific stressor, information about both type and magnitude of the stressor that causes the overall degradation can easily be extracted by tracing each individual metric. The benthic flora has mainly been used to assess nutrient enrichment (Birk et al. 2012), but is sensitive to a number of additional stressors, among them acidification (Arts et al. 1990; Schneider and Lindstrøm 2009; Juggins et al. 2016), salinization (Smith et al. 2009), hydromorphological alterations (Mjelde at al. 2013), siltation (Wagenhoff et al. 2013), increased dissolved organic carbon concentrations (Brothers et al. 2014), exotic herbivores (Krupska et al. 2012), and contaminants (Ricard et al. 2010). It should therefore be possible to develop a multi-metric index that can do both overall status assessment (by combining the individual metrics, for example by following the "worst case" principle), and diagnose different causes of degradation (by tracing each individual metric; Fig. 5). The value of each individual metric can be calculated relative to its value at reference sites, such that the demands of the WFD are fulfilled. Individual metrics may include "classical" metrics that are based on species composition and abundance of aquatic flora. In some cases, different metrics that infer different stressors may even be calculated separately from the same species list. This is done in Norway, where metrics for nutrient enrichment and acidification are calculated from a list of benthic algal taxa present at a river site (Schneider et al. 2013b). However, it is important that the individual elements that constitute the multi-metric index are **independent** of each other (e.g. because they indicate different and independent stressors). If they just use the same data to calculate a number of metrics that all indicate more or less the same stressor (and whose performance is “evaluated” by their correlation with water total phosphorus concentration), information about causal relationships is difficult to infer. In addition, the risk of failing to achieve “good ecological status” will increase with the number of constituent metrics (when the worst case principle is used for combining the individual metrics)!

This problem arises, however, partly because the constituents of existing multimetrics are organized in parallel (i.e. the index value results from many individual metrics that all have to be calculated). Were they to be organized, at least partially, in series then it would be possible to tailor the “package” of metrics closely to individual circumstances (Kelly 2013; DeNicola and Kelly 2014), thereby avoiding unnecessary expense and effort. We suggest that this may be addressed by using more general, comparatively simple and cheap methods like the TDI, TI or PIT (Trophic Diatom Index, Trophic Index, Periphyton Index of Trophic Status; Kelly and Whitton 1995; Rott et al. 1999; Schneider and Lindstrøm 2011) for ecological “triage” to sort out the “clearly very good” and “clearly degraded” sites (Kelly 2013; Kelly et al. 2015), and only use sophisticated methods

i) at sites which are close to the boundary between good and moderate status,
ii) when small or slow improvements in ecological status (for example after measures have been taken) need to be demonstrated,
iii) in cases where there is doubt about which stressor may have caused degradation, or
iv) when there is reason to suspect a slow degradation where sophisticated methods may give an early warning signal that would be overlooked with the simpler methods.

Such an approach may be compared with the daily work of a family doctor, who uses simple “indicators” such as body temperature, blood pressure, presence of spots or tender areas, or heart rate patterns to obtain an overview. Only the more “complicated” cases are sent to specialists who have access to sophisticated and expensive methods such as magnetic resonance imaging, to diagnose causes, quantify the severity of the problem, or monitor its development.

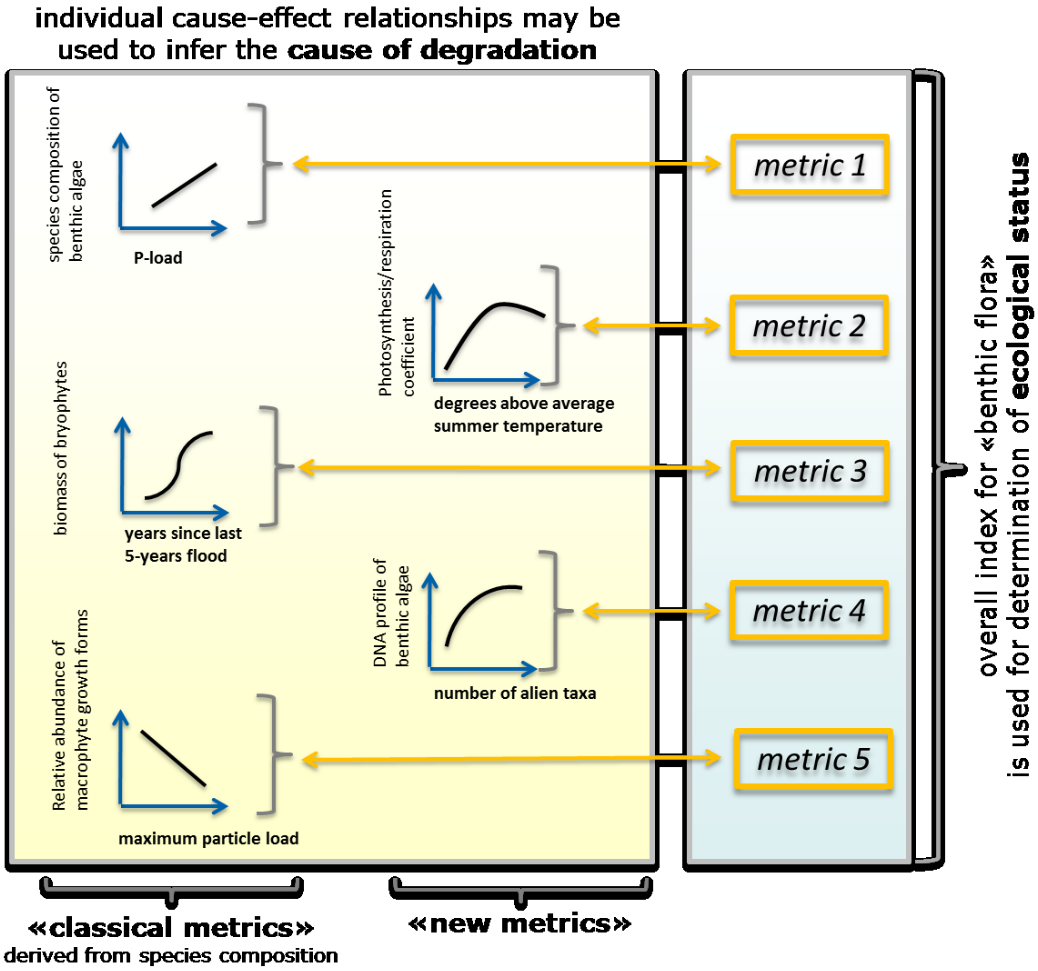

Fig. 5. Hypothetical construction of a multimetric index for status assessment based on aquatic flora. Note that individual relationships are hypothetical. Each metric that constitutes the multimetric index must be based on a cause-effect relationship. Additional metrics may readily be added (e.g. with respect to the effect of different pollutants); Different metrics may be combined, for example by following the "worst case" principle, into a single value that indicates ecological status. By tracing each individual metric, the type and magnitude of the stressor that caused degradation can be diagnosed. Individual metrics may include "classical" metrics that are based on species composition and abundance of aquatic flora, but also "new metrics" that may e.g. be based on physiological measurements. Note that the individual elements that constitute the multimetric index should be independent of each other (i.e. indicate different stressors).

Such a tiered approach also opens the way for new metrics, e.g. based on physiological processes and functional ecology that provide more powerful diagnostic capabilities than is possible from analysis of assemblage composition and abundance. Although to our knowledge no ready-to-use methods exist yet, new tools based on e.g. molecular biological data, ecosystem functioning, or physiological measurements may well add important information to the "classical" methods. New methods may for example be more sensitive to a given stressor, or react to different or previously ignored stressors (e.g. an increase in water temperature). If water managers make clear statements about the stressors which need to be addressed, then ecologists should be able to design a suite of useful tools.

Hill et al. (2000) combined metrics based on periphyton taxonomy, biomass and phosphatase activity into an index of biotic integrity, and the different constituent metrics were related to different chemical, physical habitat and landscape variables. Our approach is similar to Hill et al. (2000), but we suggest organizing the constituent metrics at least partially in series instead of in parallel, and we suggest putting a stronger focus on inferring the causes of ecosystem degradation from the constituent metrics. In that way, unnecessary expense and effort can be avoided, and causes of degradation can be inferred, which provides important information to managers. In interpreting these indices, however, we should take the "classical" ecological interactions between biota and their environment into account: if a scientifically soundly developed ecological metric indicates high nutrient load at a site where water phosphorus concentrations are low, then this is a clear sign for i) internal nutrient supply via the sediment, ii) discontinuous nutrient supply at times when water chemistry was not measured, and/or iii) significant uptake of nutrients into plant and benthic algal biomass. In any case, scientists and water managers should start searching for the source of nutrient supply instead of criticizing a "poor" index that does not adequately mirror water chemistry.

7. Conclusions

The aquatic benthic flora is an integral part of well-functioning aquatic ecosystems. It is important that catchment managers have access to effective means of assessing the "health" of the benthic flora in order to ensure delivery of essential ecosystem services. This must move beyond the approach that has been used so far, where the biota are regarded as simplistic "mirrors" of water chemistry. For developing and interpreting assessment tools, we should

- use water chemistry – biotic response relationships as descriptive tools only, and not confuse them with quantitative stressor – response relationships
- should make sure stressor-response relationships are based on experimental evidence, instead of on diffuse associations between biota and hydrochemistry where the uncertainty in quantifying the intensity of the stressor is blamed on a poor performance of the ecological metric

- consider a tiered approach, i.e. using more general and comparatively “simple” indices (which nevertheless must be firmly based on scientific evidence) for an overview and more sophisticated methods in doubtful or complicated cases; this could avoid unnecessary costs and efforts while giving important ecological and management information.

The next generation of biotic indices must take into account the underlying ecological processes. If we make sure to not “forget” the ecology behind ecological status evaluation, then aquatic plants and benthic algae do have the potential to become progressive assessment tools that meet future challenges in water management and will aid our understanding of ecosystem responses to a variety of stressors.

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References

Arts GHP, Roelofs JGM, De Lyon MJH (1990) Differential tolerances among soft-water macrophyte species to acidification. Can J Bot 68:2127-2134

Bakker ES, Sarneel JM, Gulati RD, Liu ZW, van Donk E (2013) Restoring macrophyte diversity in shallow temperate lakes: biotic versus abiotic constraints. Hydrobiologia 710:23-37

Barko JW, Smart, RM (1981) Sediment-based nutrition of submersed macrophytes. Aquat Bot 10:339-352

Barton DR, Howell ET, Fietsch CL (2013) Ecosystem changes and nuisance benthic algae on the southeast shores of Lake Huron. J Great Lakes Res 39:602-611

Bennett C, Owen R, Birk S, Buffagni A, Erba S, Mengin N, et al. (2011) Bringing European river quality into line: an exercise to intercalibrate macro-invertebrate classification methods. Hydrobiologia 667:31–48

Billen G, Garnier J, Deligne C, Billen C (1999) Estimates of early-industrial inputs of nutrients to river systems: implication for coastal eutrophication. Sci Total Environ 243/244:43–52

Birk S, Bonne W, Borja A, Brucet S, Courrat A, Poikane S, Solimini A, van de Bund WV, Zampoukas N, Hering D (2012) Three hundred ways to assess Europe's surface waters: An almost complete overview of biological methods to implement the Water Framework Directive. Ecol Ind 18:31-41

Blindow I, Hargeby A, Hilt S (2014) Facilitation of clear-water conditions in shallow lakes by macrophytes: differences between charophyte and angiosperm dominance. Hydrobiologia 737:99-110

Bouleau G, Pont D (2015) Did you say reference conditions? Ecological and socio-economic perspectives on the European Water Framework Directive. Env Sci Pol 47:32-41

Brothers S, Köhler J, Meyer N, Attermeyer K, Grossart HP, Mehner T, Scharnweber K, Hilt S (2014) A feedback loop links brownification and anoxia in a temperate, shallow lake. Limnol and Oceanogr 59:1388-1398

Butcher RW (1933) Studies on the Ecology of Rivers: I. On the Distribution of Macrophytic Vegetation in the Rivers of Britain. J Ecol 21:58-91

Cairns J, Pratt JR (1993) A history of biological monitoring using benthic macroinvertebrates. In: Freshwater Biomonitoring and Benthic Macroinvertebrates. Rosenberg DM and Resh VH (eds.), Chapman and Hall, NY

Carignan R, Kalff J (1980) Phosphorus sources for aquatic weeds: water or sediments? Science 207:987-988

CEMAGREF (1982) Etude de méthodes biologiques quantitatives d'appreciation de la qualité des eaux. Rapport Q.E. Lyon-A.F.B. Rhône-Mediterranée-Corse

Chambers PA, Prepas EE, Bothwell ML, Hamilton HR (1989) Roots versus shoots in nutrient uptake by aquatic macrophytes in flowing waters. Can J Fish Aquat Sci 46:435-439

del Pozo R, Fernandez-Alaez C, Fernandez-Alaez M (2010) An assessment of macrophyte community metrics in the determination of the ecological condition and total phosphorus concentration of Mediterranean ponds. Aquat Bot 92:55-62

DeNicola DM, Kelly MG (2014) Role of periphyton in ecological assessment of lakes. Freshwater Science 33:619-638

Descy JP (1979) A new approach to water quality estimation using diatoms. Nova Hedwigia 64:305–323

DIN 4049-2 (1990) Hydrologie; Begriffe der Gewässerbeschaffenheit. Deutsches Institut fuer Normung. Berlin, 25 pp

Dodds WK (2003) The role of periphyton in phosphorus retention in shallow freshwater aquatic systems. J Phycol 39:840–849

Dollan A, Hupfer M (2003) Immobilisation of phosphorus by iron-coated roots of submerged macrophytes. Hydrobiologia 506–509:635–640

Eigemann F, Mischke U, Hupfer M, Schaumburg J, Hilt S (2016) Biological indicators track differential responses of pelagic and littoral areas to nutrient load reductions in German lakes. Ecol Ind 61:905–910

European Commission (2000) Directive 2000/60/EC. Establishing a Framework for Community Action in the Field of Water Policy. European Commission PE-CONS 3639/1/100 Rev 1, Luxembourg

European Commission (2009) Guidance document on eutrophication assessment in the context of European water policies. Technical Report - 2009 – 030, Luxembourg

EUROPEAN COURT OF JUSTICE (2009) Judgment of the Court (Third Chamber) of 10 December 2009 (Case C-390/07). European Commission v United Kingdom of Great Britain and Northern Ireland. Failure of a Member State to fulfill obligations – Environment – Directive 91/271/EEC – Urban waste water treatment – Article 3(1) and (2), Article 5(1) to (3) and (5) and Annexes I and II – Initial failure to identify sensitive areas – Concept of 'eutrophication' – Criteria – Burden of proof – Relevant date when considering the evidence – Implementation of collection obligations – Implementation of more stringent treatment of discharges into sensitive areas. Official Journal of the European Union, C 24/4

Fisher J, Deflandre-Vlandas A, Coste M, Delmas F, Jarvie HP (2010) Assemblage grouping of European benthic diatoms as indicators of trophic status of rivers. Fund Appl Limnol 176:89-100

Friberg N (2014) Impacts and indicators of change in lotic ecosystems. WIREs Water 1:513–531

Friedrich G (1990) Eine Revision des Saprobiensystems. Zeitschrift für Wasser- und Abwasserforschung 23:141-152

Gabriels W, Lock K, De Pauw N, Goethals PLM (2010) Multimetric Macroinvertebrate Index Flanders (MMIF) for biological assessment of rivers and lakes in Flanders (Belgium). Limnologica 40:199–207

Hassall AH (1850) Memoir on the organic analysis or microscopic examination of water supplied to the inhabitants of London and the suburban districts. Lancet 1:230–235

Haury J, Peltre MC, Tremolieres M, Barbe J, Thiebaut G, Bernez I, et al. (2006) A new method to assess water trophy and organic pollution – The Macrophyte biological index for rivers (IBMR): Its application to different types of river and pollution. Hydrobiologia 570:153–158

Hawes I, Smith R (1993) Effect of localised nutrient enrichment on the shallow epilithic periphyton of oligotrophic Lake Taupo, New Zealand. New Zeal J Mar Fresh 27:365-372

Hering D, Meier C, Rawer-Jost C, Feld CK, Biss R, Zenker A, Sundermann A, Lohse S, Bohmer J (2004) Assessing streams in Germany with benthic invertebrates: selection of candidate metrics. Limnologica 34:398-415.

Hering D, Johnson RK, Kramm S, Schmutz S, Szoszkiewicz K, Verdonschot PFM (2006a) Assessment of European streams with diatoms, macrophytes, macroinvertebrates and fish: a comparative metric-based analysis of organism resonse due to stress. Freshwat Biol 51:1757-1785

Hering D, Feld CK, Moog O, Ofenbock T (2006b) Cook book for the development of a Multimetric Index for biological condition of aquatic ecosystems: Experiences from the European AQEM and STAR projects and related initiatives. Hydrobiologia 566:311-324

Hering D, Borja A, Carstensen J, Carvalho L, Elliott M, Feld CK, Heiskanen AS, Johnson RK, Moe J, Pont D, Lyche Solheim A, van de Bund W (2010) The European Water Framework Directive at the age of 10: A critical review of the achievements with recommendations for the future. Sci Total Environ 408:4007–4019

Hidding B, Bakker ES, Hootsmans MJM, Hilt S (2016) Synergy between shading and herbivory triggers plant loss and regime shifts in aquatic systems. Oikos in press: DOI 10.1111/oik.03104

Hill BH, Herlihy AT, Kaufmann PR, Stevenson RJ, McCormick FH, Johnson CB (2000) Use of periphyton assemblage data as an index of biotic integrity. J N Am Benthol Soc 19: 50-67.

Hilt S, Van de Weyer K, Köhler A, Chorus I (2010) Submerged macrophyte responses to reduced phosphorus concentrations in two peri-urban lakes. Restor Ecol 18, S2:452-461

Hilt S, Köhler J, Kozerski HP, Scheffer M, Van Nes E (2011) Abrupt regime shifts in space and time along rivers and connected lakes systems. Oikos 120:766-775

Hilt S, Adrian R, Köhler J, Monaghan MT, Sayer C (2013) Clear, crashing, turbid and back – long-term changes of macrophyte assemblages in a shallow lake. Freshwat Biol 58:2027-2036

Holmes NTH, Newman JR, Chadd S, Rouen KJ, Saint L, Dawson FH (1999) Mean Trophic Rank: A user’s manual. R&D Technical Report E38. Environment Agency, Bristol

Hutchinson GE (1973) Eutrophication – The scientific background of a contemporary practical problem. American Scientist 61:269-279

James WF, Barko JW, Butler MG (2004) Shear stress and sediment resuspension in relation to submersed macrophyte biomass. Hydrobiologia 515:181–191

Janse JH, De Senerpont Domis LN, Scheffer M, Lijklema L, Van Liere L, Klinge M, Mooij W (2008) Critical phosphorus loading of different types of shallow lakes and the consequences for management estimated with the ecosystem model PCLAKE. Limnologica 38:203-219

Jones JI, Sayer CE (2003) Does a fish-invertebrate-periphyton cascade precipitate plant loss in shallow lakes? Ecology 84:2155–2167

Juggins S, Kelly M, Allott T, Kelly-Quinn M, Monteith D (2016) A Water Framework Directive-compatible metric for assessing acidification in UK and Irish rivers using diatoms. Science of the Total Environment (in press)

Karr JR (1991) Biological integrity: a long-neglected aspect of water resource management. Ecol Appl 1:66-84

Karr JR (1999) Defining and measuring river health. Freshwat Biol 41:221-234

Kelly MG (2006) A comparison of diatoms with other phytobenthos as indicators of ecological status in streams in northern England. In: Proceedings of the 18th

International Diatom Symposium 2004 (Witkowski A, editor), 139–151. Biopress, Bristol

Kelly MG (2013) Data rich, information poor? Phytobenthos assessment and the Water Framework Directive. Eur J Phycol 48:437-450

Kelly MG, Whitton BA (1995) The Trophic Diatom Index: a new index for monitoring eutrophication in rivers. J Appl Phycol 7:433–444

Kelly MG, King L, Jones RI, Barker PA, Jamieson BJ (2008). Validation of diatoms as proxies for phytobenthos when assessing ecological status in lakes. Hydrobiologia 610:125–129

Kelly MG, Bennett C, Coste M, Delgado C, Delmas F, Denys L, et al. (2009) A comparison of national approaches to setting ecological status boundaries in phytobenthos assessment for the European Water Framework Directive: results of an intercalibration exercise. Hydrobiologia 621:169–182

Kelly MG, Schneider SC, King L (2015) Customs, habits and traditions: the role of non-scientific factors in the development of ecological assessment methods. WIREs Water 2:159-165

Köhler J, Hachoł J, Hilt S (2010) Regulation of submersed macrophyte biomass in a temperate lowland river: interactions between shading by bank vegetation, epiphyton and water turbidity. Aquat Bot 92:129-136

Kolada A, Willby N, Dudley B, Noges P, Sondergaard M, Hellsten S, Mjelde M, Penning E, van Geest G, Bertrin V, Ecke F, Maemets H, Karus K (2014) The applicability of macrophyte compositional metrics for assessing eutrophication in European lakes. Ecol Ind 45:407-415

Kohler A, Brinkmeier R, Vollrath H (1974) Verbreitung und Indikatorwert der submsersen Makrophyten in den Fliessgewässern der Friedberger Au. Ber. Bayer. Bot. Ges. 45:5-36.

Kolkwitz R, Marsson M (1902) Grundsätze für die biologische Beurteilung des Wassers nach seiner Flora und Fauna. Mitteilungen der königlichen Prüfanstalt für Wasserversorgung und Abwasserbeseitigung 1:33-72

Kolkwitz R, Marsson M (1908) Ökologie der pflanzlichen Saprobien. Mitteilung aus der Königlichen Prüfungsanstalt für Wasserversorgung und Abwässerbeseitigung. Heft 1:508-519

Krupska J, Pełechaty M, Pukacz A, Ossowski P (2012) Effects of grass carp introduction on macrophyte communities in a shallow lake. Oceanol Hydrobiol St 41:35-40

Lange-Bertalot H (1979) Pollution tolerance as a criterion for water quality estimation. Nova Hedwigia 64:285–304

Loeb SL (1986) Algal biofouling of oligotrophic Lake Tahoe: causal factors affecting production. In Evans LV, Hoagland KD (eds), Algal Biofouling, Amsterdam, The Netherlands, Elsevier Science Publishers, 159-173

Lyche-Solheim A, Feld CK, Birk S, Phillips G, Carvalho L, Morabito G, Mischke U, Willby N, Søndergaard M, Hellsten S, Kolada A, Mjelde M, Böhmer J, Miler O, Pusch MT, Argillier C, Jeppesen E, Lauridsen TL, Poikane S (2013) Ecological status assessment of European lakes: a comparison of metrics for phytoplankton, macrophytes, benthic invertebrates and fish. Hydrobiologia 704:57-74

Mjelde M, Hellsten S, Ecke F (2013) A water level drawdown index for aquatic macrophytes in Nordic lakes. Hydrobiologia 704:141-151

Naumann E (1929) Einige neue Gesichtspunkte zur Systematik der Gewässertypen. Arch Hydrobiol 20:191–198

Newbold C., Palmer M (1979) Trophic Adaptations of Aquatic Plants. NCC CST Notes number 18. Nature Conservancy Council, Peterborough

Ohe, von der, PC, Apitz S, Arbaciauskas K, Beketov MA, Borchardt D, de Zwart D, Goedkoop W, Hein M, Hellsten S, Hering D, Kefford BJ, Panov VE, Schafer RB, Segner H, van Gils J, Vegter JJ, Wetzel MA, Brack W (2014) Status and Causal Pathway Assessments Supporting River Basin Management. In: Brils J, Brack W, Müller-Grabherr D, Négrel P, Vermaat JE (Editors) Risk-Informed Management of European River Basins. 395 p. Springer, Heidelberg

Ohle W (1955) Beiträge zur Produktionsbiologie der Gewässer. Arch Hydrobiol, Supplement XXII:456–479

Pantle K, Buck H (1955) Die biologische Überwachung der Gewässer und die Darstellung der Ergebnisse. Gas- und Wasserfach. Wasser/Abwasser 96:609-620

Pardo I, Gomez-Rodriguez C, Wasson JG, Owen R, van de Bund W, Kelly M, Bennett C, Birk S, Buffagni A, Erba S, Mengin N, Murray-Bligh J, Ofenboeck G (2012) The European reference condition concept: A scientific and technical approach to identify minimally-impacted river ecosystems. Sci Total Environ 420:33-42

Penning WE, Dudley B, Mjelde M, Hellsten S, Hanganu J, Kolada A, van den Berg M, Poikane S, Phillips G, Willby N, Ecke F (2008) Using aquatic macrophyte community indices to define the ecological status of European lakes. Aquat Ecol 42:253-264

Perillon C, Hilt S (2016) Groundwater influence differentially affects periphyton and macrophyte production in lakes. Hydrobiologia in press: DOI 10.1007/s10750-015-2485-9

Phillips GL, Eminson DF, Moss,B (1978) A mechanism to account for macrophyte decline in progressively eutrophicated waters. Aquat Bot 4:103-125

Piggott JJ, Salis RK, Lear G, Townsend CR, Matthaei CD (2015) Climate warming and agricultural stressors interact to determine stream periphyton community composition. Global Change Biol 21:206-222

Prygiel J, Coste M (1993) The assessment of water quality in the Artois-Picardie water basin (France) by the use of diatom indices. Hydrobiologia 269/270:343–349

Ricart M, Guasch H, Alberch M, Barcelo D, Bonnineau C, Geiszinger A, Farre M, Ferrer J, Ricciardi F, Romani AM, Morin S, Proia L, Sala L, Sureda D, Sabater S (2010) Triclosan persistence through wastewater treatment plants and its potential toxic effects on river biofilms. Aquat Toxicol 100:346-353

Rodhe W (1969) Crystallization of eutrophication concepts in Northern Europe. – In: Eutrophication: Causes, Consequences, Correctives. Proceedings of a symposium. Washington, D. C., National Academy of Sciences:50–64

Rott E, Pipp E, Pfister P, van Dam H, Ortler K, Binder N, Pall K (1999) Indikationslisten für Aufwuchsalgen in Österreichischen Fliessgewassern. Teil 2: Trophieindikation. Bundesministerium für Land- und Forstwirtschaft, Vienna, Austria

Schaumburg J, Schranz C, Foerster J, Gutowski A, Hofmann G, Meilinger P, Schneider S, Schmedtje U (2004) Ecological classification of macrophytes and phytobenthos for rivers in Germany according to the Water Framework Directive. Limnologica 34:283-301

Scheffer M, Hosper SH, Meijer ML, Moss B, Jeppesen E (1993) Alternative equilibria in shallow lakes. Trends Ecol Evol 8:275–279

Schmetje U, Kohmann F (1987) Bioindikation durch Makrophyten – indizieren Makrophyten Saprobie? Arch Hydrobiol 199:455-469

Schneider S, Melzer A (2003) The trophic index of macrophytes (TIM) – A new tool for indicating the Trophic state of running waters. Int Rev Hydrobiol 88:49–67

Schneider S, Melzer A (2004) Sediment and water nutrient characteristics in patches of submerged macrophytes in running waters. Hydrobiologia 527:195-207

Schneider S, Lindstrøm EA (2009) Bioindication in Norwegian rivers using non-diatomaceous benthic algae: The acidification index periphyton (AIP). Ecol Ind 9:1206-1211

Schneider S, Lindstrøm EA (2011) The periphyton index of trophic status PIT: A new eutrophication metric based on non-diatomaceous benthic algae in Nordic rivers. Hydrobiologia 665:143-155.

Schneider SC, Moe TF, Hessen DO, Kaste O (2013a) Juncus bulbosus nuisance growth in oligotrophic freshwater ecosystems: different triggers for the same phenomenon in rivers and lakes? Aquat Bot 104:15–24

Schneider SC, Kahlert M, Kelly MG (2013b): Interactions between pH and nutrients on benthic algae in streams and consequences for ecological status assessment and species richness patterns. Sci Total Environ 444:73-84

Schneider SC, Cara M, Eriksen TE, Budzakoska Goreska B, Imeri A, Kupe L, Lokoska T, Patceva S, Trajanovska S, Trajanovski S, Talevska M, Veljanoska Sarafilovska E (2014) Eutrophication impacts littoral biota in Lake Ohrid while water phosphorus concentrations are low. Limnologica 44:90-97

Schulz M, Kozerski HP, Pluntke T, Rinke K (2003) The influence of macrophytes on sedimentation and nutrient retention in the lower River Spree (Germany). Water Research 37:569–578

Siong K, Asaeda T (2006) Does calcite encrustation in Chara provide a phosphorus nutrient sink? J Environ Qual 35:490–494

Smith MJ, Ough KM, Scroggie MP, Schreiber ESG, Kohout M (2009) Assessing changes in macrophyte assemblages with salinity in non-riverine wetlands: A Bayesian approach. Aquat Bot 90:137–142

Steyaert P, Ollivier G (2007) The European Water Framework Directive: how ecological assumptions frame technical and social change. Ecology and Society 12(1):25

Timm H, Moels T (2012) Littoral macroinvertebrates in Estonian lowland lakes: the effects of habitat, season, eutrophication and land use on some metrics of biological quality. Fund Appl Limnol 180:145-156

Tremp H, Kohler A (1995) The usefulness of macrophyte monitoring-systems, exemplified on eutrophication and acidification of running waters. Acta Bot Gallica 142:541-550

Twilley RR, Ejdung G, Romare P, Kemp WM (1986) A comparative study of decomposition, oxygen consumption and nutrient release for selected aquatic plants occurring in an estuarine environment. Oikos 47:190-198

Vermaat JE, Santamaria L, Roos PJ (2000) Water flow across and sediment trapping in submerged macrophyte beds of contrasting growth form. Arch Hydrobiol 148:549-562

Vollenweider RA, Kerekes J (1982) Eutrophication of waters. Monitoring, assessment and control. OECD Cooperative programme on monitoring of inland waters (Eutrophication control), Environment Directorate, OECD, Paris. 154 p

Wagenhoff A, Lange K, Townsend CR, Matthaei CD (2013) Patterns of benthic algae and cyanobacteria along twin-stressor gradients of nutrients and fine sediment: a stream mesocosm experiment. Freshw Biol 58:1849-1863

Wetzel RG (2001) Limnology – Lake and River Ecosystems. 3rd edition. Academic Press, San Diego