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Review

Development of an epiphyte indicator of nutrient enrichment: A critical evaluation of observational and experimental studies

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ABSTRACT

An extensive review of the literature describing epiphytes on submerged aquatic vegetation (SAV), especially seagrasses, was conducted in order to evaluate the evidence for response of epiphyte metrics to increased nutrients. Evidence from field observational studies, together with laboratory and field mesocosm experiments, was assembled from the literature and evaluated for a hypothesized positive response to nutrient addition. There was general consistency in the results to confirm that elevated nutrients tended to increase the load of epiphytes on the surface of SAV, in the absence of other limiting factors. In spite of multiple sources of uncontrolled variation, positive relationships of epiphyte load to nutrient concentration or load (either nitrogen or phosphorus) often were observed along strong anthropogenic or natural nutrient gradients in coastal regions. Such response patterns may only be evident for parts of the year. Results from both mesocosm and field experiments also generally support the increase of epiphytes with increased nutrients, although outcomes from field experiments tended to be more variable. Relatively few studies with nutrient addition in mesocosms have been done with tropical or subtropical species, and more such controlled experiments would be helpful. Experimental duration influenced results, with more positive responses of epiphytes to nutrients at shorter durations in mesocosm experiments versus more positive responses at longer durations in field experiments. In the field, response of epiphyte biomass to nutrient additions was independent of climate zone. Mesograzer activity was a critical covariate for epiphyte response under experimental nutrient elevation, but the epiphyte response was highly dependent on factors such as grazer identity and density, as well as nutrient and ambient light levels. The balance of evidence suggests that epiphytes on SAV will be a useful indicator of persistent nutrient enhancement in many situations. Careful selection of appropriate temporal and spatial constraints for data collection, and concurrent evaluation of confounding factors will help increase the signal to noise ratio for this indicator.

1. Introduction

Opportunistic algal growth resulting from elevated nutrients may result in significant negative impacts for biological substrata such as seagrasses, freshwater macrophytes, or macroalgae. A variety of studies have reviewed epiphytes with varying degrees of focus on the response to elevated nutrient levels (Borowitzka and Lethbridge, 1989; Harlin, 1995; Jernakoff et al., 1996; Hillebrand, 2002; Hughes et al., 2004; Borowitzka et al., 2006; Burkholder et al., 2007; Michael et al., 2008; Nelson, 2009; US EPA [Appendix B.5], 2010; Sutula, 2011; Thomsen et al., 2012). One of the first conceptual models of macrophyte decline under increased nutrient input from human activity was derived from lakes by Phillips et al. (1978). This model highlighted the role of increased growth of epiphytes under nutrient addition, which reduced macrophyte growth and survival through shading. The dominant effect of heavy epiphytic cover on macrophyte substrata appears to be decreased growth and a reduced potential for survival caused by reduced light availability (Sand-Jensen, 1977; Borum and Wium-Anderson, 1980; Bulthuis and Woelkerling, 1981; Sand-Jensen and Borum, 1984; Cambridge et al., 1986; Silberstein et al., 1986; Sand-Jensen and Revsbech, 1987), especially at lower ambient light levels (Morgan and Kitting, 1984; Twilley et al., 1985; Wetzel and Neckles, 1986). Depression of photosynthesis by epiphyte loads also may be caused by a reduction in the rate of diffusion of HCO_3^- across the seagrass blade surface (Sand-Jensen, 1977). Increased physical drag from epiphytes may result in increased loss of leaves or plants under high wave or current conditions (Borowitzka and Lethbridge, 1989). Exposure to elevated levels of nitrogen has been shown to decrease the tensile breaking strength of some seagrass species (Kopp, 1999; Nafie et al., 2012), which might further increase loss of leaves under nutrient enhanced epiphyte loads.

Among water body types, epiphyte increases in response to in-

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creased nutrients have been observed in lakes (Moss, 1976; Phillips et al., 1978; Sand-Jensen and Søndergaard, 1981; Sand-Jensen, 1990; Vermaat and Hootsmans, 1994; Strand and Weisner, 1996; Bécares et al., 2008), rivers (Köhler et al., 2010), and estuaries. In estuarine systems, responses have been documented from northern European estuaries (Borum, 1985; Borum and Wium-Andersen, 1980), Baltic brackish waters (Rönnberg et al., 1992), US estuarine waters (Tomasko and Lapointe, 1991; Frankovich and Fourqurean, 1997; Tomasko et al., 1996), Australian estuaries (Bulthuis and Woelkerling, 1983; Silberstein et al., 1986; Neverauskas, 1987a, 1987b; Bryars et al., 2011), Mediterranean estuaries (Balata et al., 2008; Giovannetti et al., 2010), and tropical Atlantic waters (McGlathery, 1995; Stoner et al., 2014), among other locations.

Observations and experiments have demonstrated that elevated levels of water column nutrients can result in increased levels of epiphytic algal material on submerged aquatic vegetation within relatively short time periods. (Bulthuis and Woelkerling, 1983; Borum, 1985; Twilley et al., 1985; Silberstein et al., 1986; Jensen and Gibson, 1986; Neverauskas, 1987a; Dunton, 1990; Tomasko and Lapointe, 1991; Frankovich and Fourqurean, 1997; Neckles et al., 1993; Williams and Ruckelshaus, 1993; Lapointe et al., 1994; Murray et al., 2000). Since macrophyte substrata tend to remain in place long enough to integrate local nutrient loads, the use of epiphyte metrics as indicators of system response to nutrient levels has appeared promising (Gobert et al., 2009; Balata et al., 2010; Giovannetti et al., 2010; Castejón-Silvo and Terrados, 2012; Marbà et al., 2013; McMahon et al., 2013). However, there are also cautionary notes. Wood and Lavery (2000) assessed the role of perception in determining the assessment of coastal condition, and found that while Best Professional Judgement rated epiphyte biomass as an important indicator of seagrass ecosystem condition, the metric failed to distinguish between sites designated "healthy" or "unhealthy". Fourqurean et al. (2010) suggested that epiphyte load is not a reliable nutrient indicator for oligotrophic ecosystems, and US EPA (2010) evaluated epiphyte indicators as not yet useful for setting water quality criteria in the state of Florida.

However, quantitative reviews of epiphytes include a meta-analysis of periphyton responses to increased nutrients and grazing from lakes, streams and a few coastal studies (Hillebrand, 2002), and a similar meta-analysis (Hughes et al., 2004) assessing effects of grazing and nutrients on seagrasses and their epiphytes. Both concluded that nutrients significantly increased and grazers significantly reduced epiphytes/periphyton. The available studies addressing macrophyte epiphytes and nutrients have greatly increased since these meta-analyses were conducted. Therefore, an extensive review of the literature on epiphyte responses to elevated nutrients was conducted based primarily on seagrasses or other rooted aquatic species from coastal systems as the macrophyte host. The review included field observational studies, and both laboratory and field mesocosm experiments that manipulated nutrient levels and observed epiphyte responses. Where feasible, quantitative analyses were used to determine the conditions under which epiphyte responses occurred. The ultimate goal of the review is to provide the weight of evidence to support establishment of threshold levels for use of epiphyte indicators in coastal waters (Nelson, 2017) that may have application in protection of water quality.

2. Methods

2.1. General methods

The literature on seagrass epiphytes, but also including some brackish and freshwater rooted macrophytes, was reviewed to categorize response patterns to excess nutrients. The assessment sought to evaluate whether there was clear, quantitative evidence that excess nutrients lead to negative impacts on host plants. The objective was to determine whether metrics of epiphytic load on seagrasses can be used as quantitative biological indicators for nutrient impacts in estuarine waters. In excess of 400 publications were examined, including peer reviewed literature, theses and dissertations, and "gray" literature technical reports. The focus included observational studies in the field, which included data on seagrass epiphyte responses to nutrient inputs (e.g. waste water, fish farms, bird guano), and experimental studies in both the field and laboratory, which manipulated nutrient levels and recorded epiphyte responses. Searches for relevant studies relied on previous reviews of seagrass epiphytes (e.g. Hughes et al., 2004; Burkholder et al., 2007; Michael et al., 2008; Nelson 2009; Thomsen et al., 2012), and included bibliographic searches for relevant terms using Google Scholar, Web of Science, and search engines for web sites for scientific journals.

If it was necessary to acquire data from scatter plots or bar graphs, data were digitized with Grab It! ™ software (Datatrend Software). Images of graphs from PDF files of publications were copied with the Microsoft Snipping Tool app, saved to JPG format image files, and imported into Grab It! ™, which operates within Microsoft Excel. Repeated measurements of the same data points with the software gave a measurement precision of less than 0.1%. Comparison of the values extracted via software to values for the same data points that were given in the publication gave a measurement accuracy on the order of 3%. Reanalysis of data digitized from the original publications provided a Quality Assurance check for analyses provided in the original papers. In a relatively few cases, authors were ambiguous with regard to units for data presented, and such data sets were excluded.

2.2. Field observation assessment

Evaluation of results from field observational studies generally relied on data collected along nutrient gradients, but results varied so greatly in terms of study sites and conditions, including type and magnitude of nutrient sources, that comparisons were primarily qualitative. However, in a number of cases, data were extracted as described above and regression relationships (linear, nonlinear) were examined between epiphyte responses and nutrient conditions. Regression analyses were conducted with Sigmaplot 13.

2.3. Mesocosm experiments assessment

Results were compiled from a total of 22 laboratory microcosm and mesocosm studies (Supplemental Table 1) that enriched either nitrogen (N), phosphorus (P) or both, and also assessed epiphyte responses for rooted macrophytes (7 species), primarily seagrasses (5 species). A total of 35 separate experiments reported either qualitative (n = 4) or quantitative (n = 31) results, which are summarized in Table 1. Biomass (dry weight (DW), ash free dry weight (AFDW), cell volumes) and chlorophyll-*a* (chl a, ug cm^{-2}) responses were categorized as Increase (I), Decrease (D) or No Response (NR), if measured. Change in community composition of epiphytes was scored as "Yes" if the paper reported any marked shift in taxonomic composition or relative proportions of pigment types, and "No" for no apparent change. Study locations were characterized in terms of climate zone as Temperate, Subtropical, and Tropical. Mesograzer density in experimental mesocosms was qualitatively estimated as High, Medium, or Low, or specified as Unknown (Table 1) where information was not given. A G-test of independence was conducted to determine whether there was a significant association of response of epiphyte biomass to nutrient addition with mesograzer abundance.

2.4. Field experiments assessment

A literature search provided 47 field experiments (Table 2) of nutrient addition where epiphyte response was qualitatively (n = 6) or quantitatively (n = 41) assessed. Experiments consisted of 32 water column addition studies and 15 sediment addition studies. Experimen-