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Eutrophication, harmful algae and biodiversity — Challenging paradigms in a world of complex nutrient changes

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ABSTRACT

Eutrophication is a complex process and often associated with not only a change in overall algal biomass but also with a change in biodiversity. Common metrics of eutrophication (e.g., chlorophyll *a*), total nitrogen (TN) and phosphorus (TP) are not adequate for understanding biodiversity changes, especially those associated with harmful algal bloom (HAB) proliferations. Harmful algae can increase disproportionately with eutrophication, depending on which nutrients change and in what proportion. This paper challenges several classic paradigms in our understanding of eutrophication and associated biodiversity changes. The underlying message is that nutrient proportions and forms can alter biodiversity, even when nutrients are at concentrations in excess of those considered limiting. The global HAB problem is on a trajectory for more blooms, more toxins, more often, in more places. Our approach to management of HABs and eutrophication must consider the broader complexity of nutrient effects at scales ranging from physiological to ecological.

1. Introduction

Without doubt, nutrient loads are changing in many rivers, lakes, estuaries and coastal waters throughout the world due to anthropogenic activities. From population expansion and associated wastewater discharge, to increased use of fertilizer for agriculture, and increasing energy demands (e.g., Smil, 2001; Galloway and Cowling, 2002; Galloway et al., 2002; Howarth, 2008; Glibert et al., 2006, 2010; Glibert et al., 2014a), there have been – and will continue to be – changes to the nutrient chemistry of aquatic systems as land-derived nutrients runoff or otherwise leak into aquatic systems. Adding to this list of causative factors affecting aquatic nutrient chemistry is the construction of water diversion projects, especially large dams that trap sediments and some nutrients, further altering nutrient supply to the waters downstream. Changes in climate are also affecting nutrient availability in complex ways. Consequently, many aquatic systems are awash in nutrients or are experiencing altered nutrient chemistry and eutrophication has emerged as one of grand challenges of the current day (e.g., Galloway and Cowling, 2002; Galloway et al., 2002; de Jonge et al., 2002; Howarth and Marino, 2006; Howarth, 2008). Classic eutrophication symptoms are evident in waters worldwide, with hypoxic and anoxic zones expanding and more and more frequent observations of harmful algal blooms (HABs; Anderson et al., 2002; Glibert et al., 2005; Diaz and Rosenberg, 2008; Heisler et al., 2008; Glibert and Burford, 2017). Yet, much of conceptual understanding of, and management actions related to, nutrient pollution are based on

concepts or paradigms that were developed during a time when nutrient pollution was not as great an environmental problem, or the complexities of biotic interactions and biodiversity responses had not yet been unraveled. This paper, therefore, questions a number of classic paradigms related to nutrient effects on aquatic biota, especially those related to HABs. This paper's framework parallels the conceptual roadmap of Elliott and Whitfield (2011, p. 307), who, in reviewing paradigms of estuarine ecology, recommended that, “There is a constant need to review paradigms in light of new information and understanding, and there is also a need to acknowledge that they may sometimes challenge our view of the topic... [but may] give new directions for future research.”

Classically eutrophication was described as the enrichment of a water body leading to enhanced organic production (e.g., Nixon, 1995). Based on the agricultural model of limiting nutrients, Cloern (2001) described ‘phase 1’ of eutrophication as a direct dose-response relationship: more nutrients fuel more biomass. This notion is at the core of the pressure-state-response approach to characterizing eutrophication and its impacts (e.g., Bricker et al., 1999, 2007; Whitall et al., 2007). Such approaches relate pressures (i.e., increased nutrients) to primary effects such as increased algal biomass and potentially increased algal toxins, and secondary effects such as reduction in light penetration and dissolved oxygen, losses of submersed grasses and associated habitat, and potentially fish kills. While such pressure-state-response approaches may successfully characterize the change in biomass of primary producers (algae, typically as chlorophyll *a* (chl *a*) and

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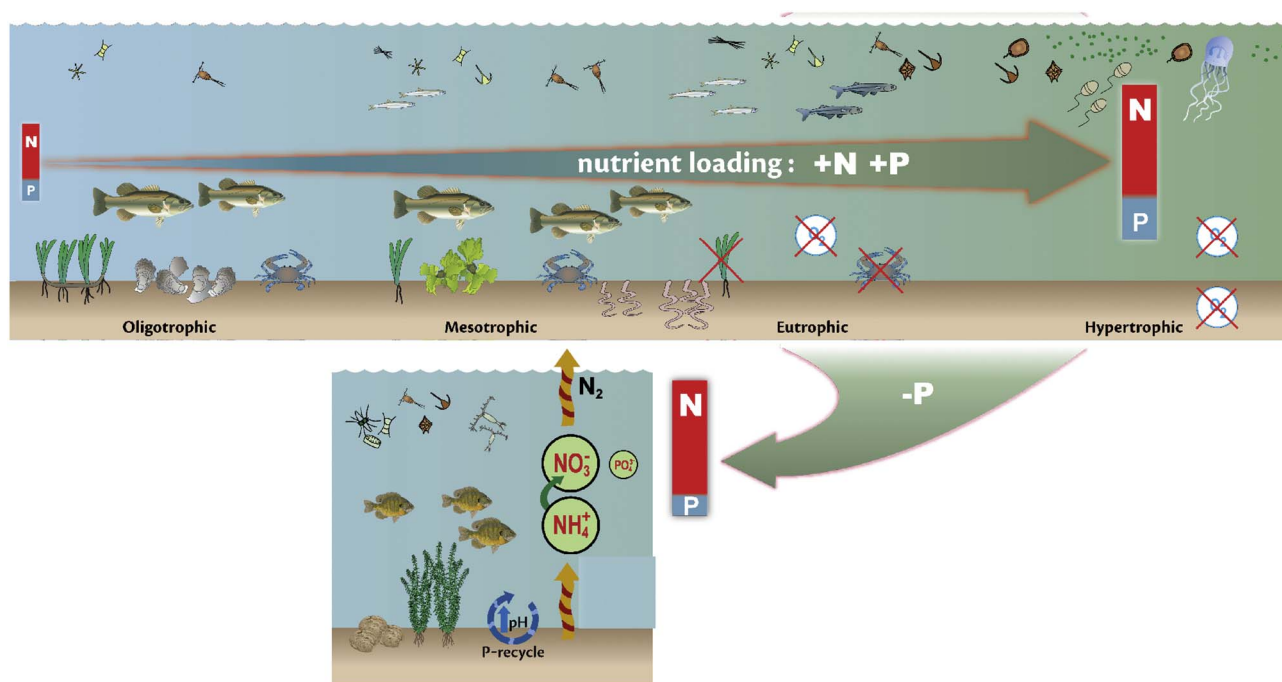


Fig. 1. Conceptual schematic showing the progression of a system towards eutrophication with the increased loading of both nitrogen and phosphorus. The panel below illustrates the conceptual change in the system with an increase N relative to P that may occur from either increased N or decreased P. Biodiversity changes, but so too does biogeochemistry, in turn altering the environmental suitability for certain types of species. Reproduced from Glibert (2015) with permission of the publisher.

submerged grasses), they do not provide an understanding of the mechanisms for how algal biodiversity may change with changing nutrient loads and why HABs may increase (Fig. 1). Without that understanding, management efforts may be misguided. For example, not all nutrient loads result in HABs, and not all nutrient effects that result in HABs cause other eutrophication impacts (i.e., visible scums, hypoxia). The goal of this paper is to review why the eutrophication problem – and especially the relationship between HABs and eutrophication – is complex, why common metrics do not reflect this complexity, how and why biodiversity of algae and other components of the food web may change when nutrients change, and the management actions and research required to tackle the global eutrophication-HAB problem. This paper begins with a review of these complexities of nutrient loads, and then challenges a number of classic paradigms regarding nutrient effects and nutrient control strategies, and concludes with a number of recommendations and suggested ways forward to advance our management approaches as well as our fundamental understanding and predictive capabilities of the grand challenge of nutrient over-enrichment.

2. The complexity of global nutrient loads

Estimating nutrient export to aquatic systems, especially the coastal zone, has been a long-standing challenge. These challenges stem from the multiple sources of nutrients, the spatial disparity by which different sources supply nutrients in different places, the rapid rate of change in nutrient supply, the diversity of nutrient forms that are supplied, and the complex trophodynamic and biogeochemical pathways by which nutrients are transformed. In this section these key challenges are briefly summarized.

2.1. The challenge of estimating nutrient loads

Nutrient sources are many and they are not changing proportionately in different regions nor are these sources contributing equally to eutrophication in all places. Rivers are an important source of anthro-

pogenic nutrients to aquatic systems, and it has been estimated that approximately 60 Tg N (= MT = megatonnes; nitrogen, N) year⁻¹ flow to the world's oceans in rivers under current conditions (Boyer et al., 2006; Howarth, 2008), roughly double the riverine input of N in 1860 (Galloway et al., 2004). In addition to wastewater pollution flowing into rivers, agricultural fertilizers are a particularly important source of nutrient pollution in many parts of the world. Global fertilizer use statistics are well documented and underscore the spatially variable nature of both consumption and supply (FAO, 2015). Where fertilizer use is intensive, inorganic N export to aquatic systems via riverine sources is highest, including Asia, Europe and the USA (Seitzinger and Kroeze, 1998; Dumont et al., 2005; Harrison et al., 2005a, 2005b; Van Drecht et al., 2003).

Globally, the rate of change in use of N fertilizers has eclipsed that of P fertilizers (Sutton et al., 2013; Glibert et al., 2014a). This is due to the large-scale capacity for anthropogenic N synthesis (the Haber-Bosch process; e.g., Smil, 2001), a process for fertilizer production that has no counterpart for P fertilizer. Prior to World War II, the creation of reactive N was largely due to natural processes, including N fixation and lightning, and population expansion kept pace with its creation (Galloway et al., 2002). After the mid-1940s and the commercialization and scaling up of the Haber Bosch process, the manufacture and use of N expanded rapidly, from < 10 MT N yr⁻¹ in 1950 to > 170 MT N yr⁻¹ in 2013, to an expected > 220 MT N yr⁻¹ by 2020 (Fig. 2; Constant and Sheldrick, 1992; FAO, 2012; Heffer and Prud'homme, 2013, 2016). In fact, > 85% of all synthetic N fertilizers have been created since 1985 (Howarth, 2008). In the USA, it has been estimated that there has been at least a 5-fold increase in reactive N use on average compared to pre-industrial time (Houlton et al., 2013), but this increase is spatially variable ranging from negligible to 35-fold in different areas (Sobota et al., 2013). It is expected that China will double its fertilizer production and use in the coming decades (Heffer and Prud'homme, 2016).

Other sources of nutrients are regionally and temporally significant. Animal agriculture is expanding to meet the dietary demands of an increasing population and increasingly animal production is concen-

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