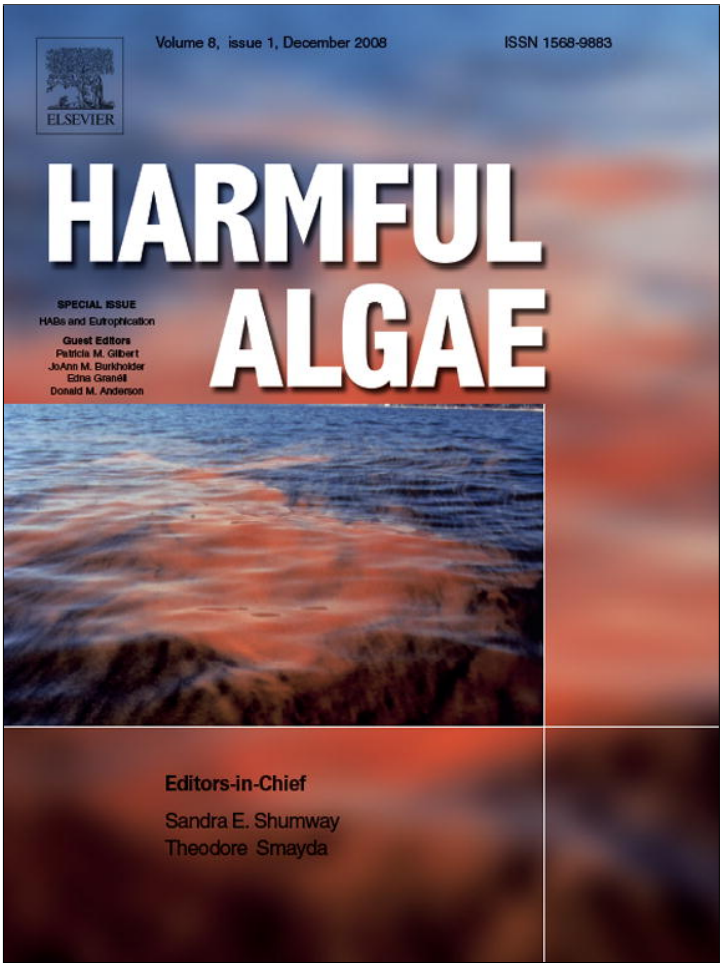
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Prorocentrum minimum tracks anthropogenic nitrogen and phosphorus inputs on a global basis: Application of spatially explicit nutrient export models

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ABSTRACT

Nutrient over-enrichment from land-based sources has degraded estuarine and coastal marine waters worldwide. Linking nutrient loading, in magnitude and form, to specific ecosystem effects, however, has been a challenge on the global scale. The harmful algal species *Prorocentrum minimum* has long been thought to be associated with eutrophication based on several site-specific long-term databases and a previous review of its global spreading. Using recently developed spatially explicit models that quantify global river nitrogen (N) and phosphorus (P) export to the coastal zone and the contribution of natural and anthropogenic sources, as well as a review of the global distribution of *P. minimum*, we show that this HAB species is associated with regions of high dissolved inorganic nitrogen (DIN) and phosphorus (DIP) exports that are strongly influenced by anthropogenic sources (such as fertilizers and manures for DIN). Blooms of this species were also linked to regions with relatively high anthropogenic contributions to dissolved organic N and P export. The global distribution of this species is expected to expand, given that nutrient inputs to watersheds from agriculture, sewage and fossil fuel combustion are projected to more than double by 2050 unless technological advances and policy changes are implemented.

1. Introduction

Global increases in nitrogen (N) and phosphorus (P) usage in the past several decades have been well documented, resulting in part from efforts to meet the food and energy demands by expanding human populations (Galloway et al., 1995, 2003; Vitousek et al., 1997; Howarth et al., 2000; Smil, 2001; Galloway and Cowling, 2002; Glibert et al., 2006). Population growth and economic development, and the production of food (crop and animal production systems) cause dramatic alterations of the landscape, increased nutrient runoff from land as well as large sewage inputs to surface waters (Seitzinger et al., 2002, 2005a). As a consequence, nutrient over-enrichment from land-based sources has degraded estuarine and coastal marine waters worldwide, leading to alterations in ecosystems and the expansion of harmful algal blooms (HABs), among other expressions of eutrophication (e.g., National Research Council, 2000; Smil, 2001; Cloern, 2001; Howarth et al., 2002; Wassmann, 2005).

While estimating nutrient export to the coastal zone remains a challenge, recent progress in spatially explicit modeling of nutrient export from watersheds has advanced understanding of the global variability in nutrients reaching the coastal zone (Seitzinger et al., 2002, 2005a; Boyer et al., 2006). The changing composition of nutrients, both inorganic and organic, discharged to coastal waters is also beginning to be better understood and quantified. Both the rate of N and P use have increased, but use of nitrogenous fertilizers has increased far more so than phosphorus fertilizers (Wassmann, 2005). Moreover, the fraction of total N fertilizer that is composed of organic material and manures is also increasing (Smil, 2001; Glibert et al., 2006). Worldwide use of urea as an N fertilizer and feed additive has increased more than 100-fold in the past 4 decades, and by 50% in the past decade alone (Glibert et al., 2005b, 2006). As of the mid-1990s, about one third of the dissolved N transported by rivers to the coastal ocean was in the form of dissolved organic N (DON; Harrison et al., 2005b), and much of this DON is available for biological utilization by algae as well as bacteria (e.g., Antia et al., 1991; Seitzinger et al., 2002, 2005b; Stepanauskas et al., 2002; Berman and Bronk, 2003; Glibert and Legrand, 2006; Bronk et al., 2007). Furthermore, in many regions of the world, anthropogenic sources account for a substantial portion of the river DON input to the coastal ocean (Harrison et al., 2005b). Linking nutrient loading, in magnitude and form, to coastal ecosystem effects, however, has been a challenge on a global scale.

The relationship between eutrophication and HABs is particularly complex. Increasing nutrient loading to the world's coastal waters is now considered to be one of the major reasons why HABs

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Table 1
Sources for spatially explicit nutrient maps and global *Prorocentrum minimum* distributions

Map	Source	Digital object identifier
Global distribution of *Prorocentrum minimum*	Heil et al. (2005)	doi:10.1016/j.hal.2004.08.003
Dissolved Inorganic N (DIN): yield and dominant source of DIN export	Dumont et al. (2005)	doi:10.1029/2005GB002488
Dissolved Inorganic P (DIP): yield and dominant source of DIP export	Harrison et al. (2005a)	doi:10.1029/2004GB002357
Percent DON and DOP from anthropogenic sources	Harrison et al. (2005b)	doi:10.1029/2005GB002480

are increasing in frequency, duration and harmful properties worldwide (Anderson, 1989; Smayda, 1989, 1990; Hallegraeff, 1993; Anderson et al., 2002; Glibert et al., 2005a,b; Glibert and Burkholder, 2006; Heisler et al., 2008). The establishment of direct links between eutrophication and HABs has often been difficult because not all eutrophic waters support HABs, and not all HABs occur in waters rich in nutrients (Anderson et al., 2002; Glibert et al., 2005a,b). In addition, the sources of nutrients to coastal waters are numerous and the impacts of differing anthropogenic nutrient inputs may well be different, as nutrient sources vary in composition and in rate of delivery, and nutrient transformations can result in greater bioavailability (Heisler et al., 2008).

The purpose of this paper is to apply a set of spatially explicit, global maps of dissolved inorganic and organic N and P yield from the world's rivers and their apportionment to their major sources in relation to the known global distribution of the high-biomass HAB species *Prorocentrum minimum*. This species is a common, neritic, bloom-forming dinoflagellate with a pan-global distribution (Heil et al., 2005). The previous review on this species (Heil et al., 2005) suggested that its apparent recent spreading is indicative of anthropogenic influences, and comparisons between its global distribution and global maps of dissolved inorganic N (DIN) export (Seitzinger et al., 2002) do show a correspondence (Glibert and Burkholder, 2006). The current effort applies recently developed spatially explicit nutrient maps (Seitzinger et al., 2005a) that allow comparison of the distribution of *P. minimum* not only to global DIN export, but also to P export and to the major forms (as inorganic and organic) and anthropogenic sources of N and P. We view the development of these maps as a preliminary step in answering questions posed by the Global Ecology and Oceanography of Harmful Algal Blooms Program (GEOHAB, 2006), "Are there clusters or specific types of HAB species that are indicative of global nutrient increases?" and, "How do anthropogenic changes in land use, agricultural use of fertilizer, and global changes in land cover affect the delivery of nutrients to coastal waters and the resulting incidences of HABs?"

2. Materials and methods

Spatially explicit global maps of dissolved river N and P export and dominant sources were taken from the Global Nutrient Export from WaterSheds (Global NEWS) models (Table 1; Seitzinger et al., 2005a; Dumont et al., 2005; Harrison et al., 2005a,b). The maps depict nutrient export at the mouths of rivers. The nutrient source terms that were considered in the Global NEWS models, based on data from more than 5000 exoreic basins, include natural sources such as N_2 fixation and P weathering, and anthropogenic sources (non-point inputs from fertilizer by crop type, N_2 fixation by crops, atmospheric N deposition, and manure by animal species; point sources from sewage, as estimated by human population and treatment level) (Seitzinger et al., 2005a; Fig. 1). The models also account for hydrological and physical factors including water runoff, precipitation intensity, land use and slope, as well as in-water removal processes such as dams and reservoirs and consumptive water use (Fig. 1). The models were validated with a separate data set that was not used in model formulation, as described by Dumont et al. (2005) and Harrison et al. (2005b). The input databases are at a resolution of $0.5^\circ \times 0.5^\circ$ and the maps represent nutrient export for mid-1990s conditions, using units of nutrient yield (kg N or P km^{-2} of watershed $year^{-1}$), dominant watershed source, and percent contribution from anthropogenic sources.

The global distribution of *P. minimum* was developed by Heil et al. (2005) from a literature survey. It is intended to be a general representation of common occurrence and does not indicate intensity or frequency of occurrence. It should be noted that lack of indication of the presence of the HAB in a particular region may not necessarily mean its absence but, rather, may reflect limited sampling and observation in a particular region.

3. Results and discussion

The global nutrient maps shown here underscore the emerging recognition that global N and P exports throughout the world are

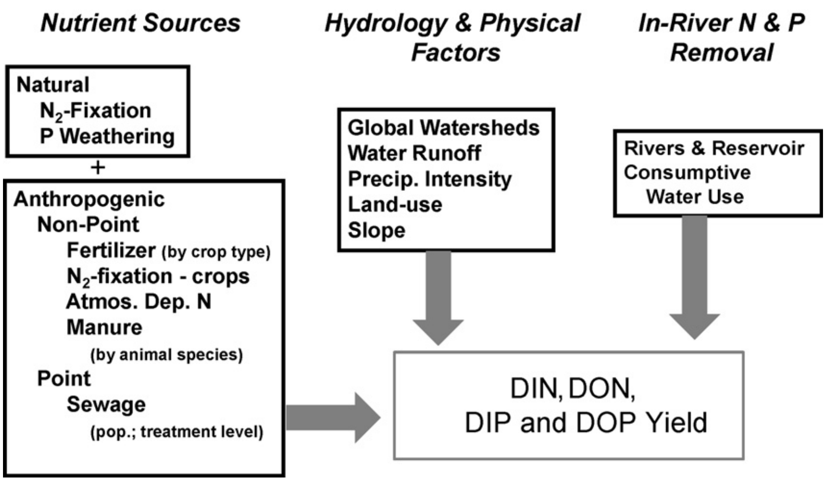

Fig. 1. Schematic of the submodels and parameters used in developing the spatially explicit Global NEWS nutrient maps. Modified from Seitzinger et al. (2005a).

not evenly distributed (e.g., Seitzinger et al., 2005a; Boyer et al., 2006). The Global NEWS models now allow us to explore the relative differences in form of elemental export (as inorganic and organic) as apportioned by source. These differences, in comparison to current understanding of the global distribution of *P. minimum*, reveal several trends.

In terms of a relationship with dissolved inorganic N and P, areas in which *P. minimum* blooms have been documented also generally are areas with high inorganic N and P yields, including eastern Asia, western Europe and eastern North America (Fig. 2A and B). There are, however, a number of exceptions where *P. minimum* is reported from areas with low N or P yields are low, or vice versa. For example, the Indonesian region has high export of DIN and DIP, yet no observations of this HAB species. Several factors may contribute to the lack of observations of *P. minimum* in the Southeast Asia region. First, water temperature in Southeast Asia may exceed the tolerance of *P. minimum* for some period of the year. There have been no reports of *P. minimum* blooms in water exceeding 30 °C for extended periods (Heil et al., 2005). Second, while DIN yield is high, DIP yield is higher compared to other regions with similar high DIN yield; thus, this region may have an ambient N:P stoichiometry that is more favorable to other species than to *P. minimum*. Third, the form of N or P may differ in this region and may not be supportive to growth of *P. minimum*, relative to other global regions where this species is common.

When the dominant sources of dissolved inorganic N or P export are considered, there are large differences globally, and also large differences in the patterns of export between the elements. Throughout much of Asia, western Europe and eastern North America, both fertilizer and manures are the largest sources of inorganic N export (Dumont et al., 2005). Based on the Global NEWS models, agricultural sources of DIN (which include fertilizer, animal manures and agricultural N_2 fixation) collectively contribute about half of the total DIN exported globally (Dumont et al., 2005). On the other hand, for DIP, human sewage is the largest anthropogenic source throughout much of the world, and inorganic P fertilizers and manures are much less significant (Harrison et al., 2005a). Comparing the distribution of *P. minimum* with these sources of N and P, it is apparent that this HAB species proliferates where fertilizers and manures dominate the export of N and where human sources dominate the export of P (Fig. 3A and B). Observations of *P. minimum* are rare where biological N_2 fixation and P weathering are dominant, such as throughout Indonesia, or where human sewage is the dominant source of N, as in northern Africa.

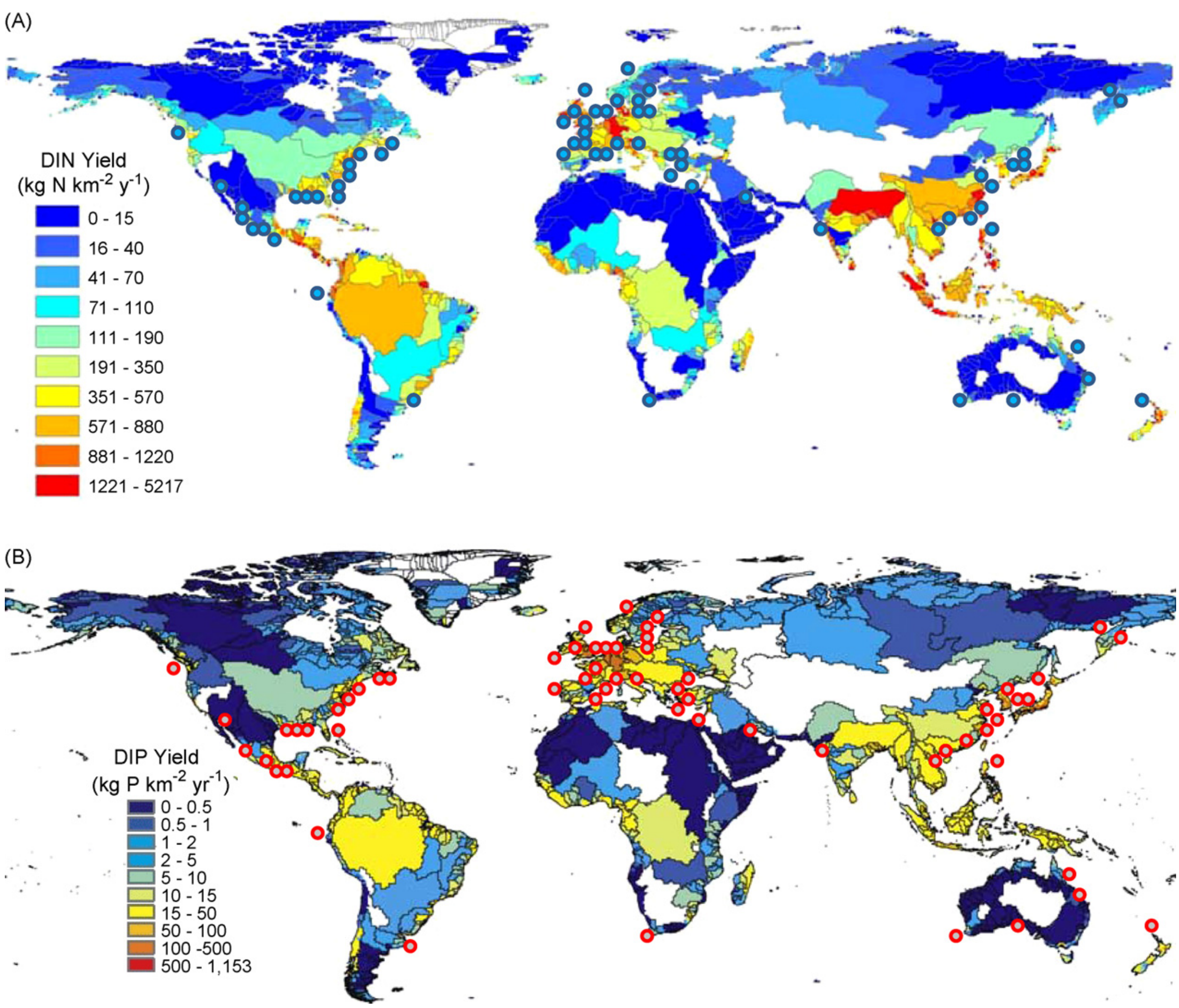

Fig. 2. (A) Global NEWS model of DIN yield by watershed (kg N km^{-2} $year^{-1}$) by exoreic basins (from Dumont et al., 2005), and the global distribution of *P. minimum* indicated by circles (from Heil et al., 2005). (B) As for (A), except for DIP (kg P km^{-2} $year^{-1}$; from Harrison et al., 2005a). Base maps reproduced with permission of the American Geophysical Union.

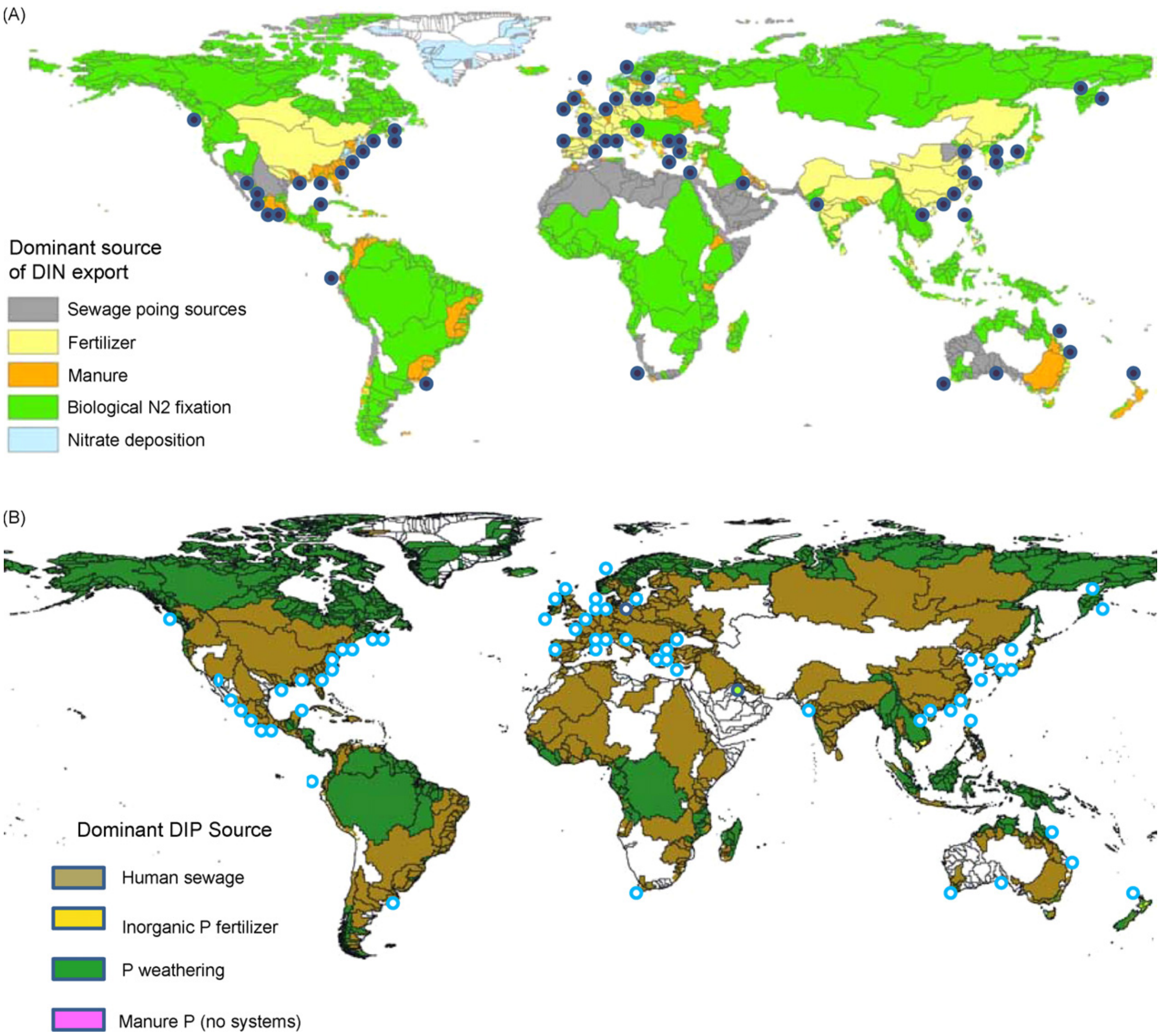

Fig. 3. (A) Dominant source of DIN export in exoreic basins as predicted by the Global NEWS models (from Dumont et al., 2005), and the global distribution of *P. minimum* indicated by circles (from Heil et al., 2005). (B) As for (A), except for DIP (from Harrison et al., 2005a). Base maps reproduced with permission of the American Geophysical Union.

As reported previously, the export of DON and DOP show somewhat different patterns than those of DIN and DIP (Harrison et al., 2005b; DON and DOP yield maps not shown). There is considerable variation, also, in the relative contribution of natural versus anthropogenic sources of DON or DOP export (Harrison et al., 2005b). Anthropogenic sources of DON and DOP are strongly influenced by fertilizer and manure inputs (in contrast to DIP), and are substantial throughout much of southern and eastern Asia, western Europe and North America (Fig. 4A and B). The distribution of *P. minimum* corresponds well with the percent export of anthropogenic N and P, with the exception of northern Africa.

Thus, these maps are considered a first step in our understanding of the relationships between HABs and global nutrient loads and their changes. Efforts to improve the spatially explicit global database of HAB events and magnitudes, such as that being undertaken by the Intergovernmental Oceanographic Commission (IOC) of UNESCO, will further enable the linkage of nutrient exports to HAB occurrence. As has been documented previously, the frequency of blooms of many types of harmful algal species has increased over the past several decades (e.g., Anderson et al., 2002; GEOHAB, 2001; Glibert et al., 2006). Improved maps of HAB occurrence and improved nutrient models based on observations will allow us to test both past and future scenarios with respect to alterations in nutrient loads, and these efforts are now ongoing through both the GEOHAB and the Global NEWS programs.

In interpreting these maps, it should be considered that nutrient yields do not necessarily reflect the nutrient that the cells may "see" at any particular point in time. Nutrient yields are annual averages whereas HABs frequently are ephemeral events, and there has been no effort made to incorporate the event time scale. Thus, there may be a temporal mismatch. Furthermore, the likelihood for a species to bloom depends on a complex suite of factors, not just single nutrient forms and supply levels, such as relative availability (such as N:P, inorganic:organic, or dissolved: particulate nutrient ratios), the retentiveness of the receiving body of water for nutrients relative to the magnitude of nutrient inputs, rates and pathways by which nutrients are consumed and recycled, other physical factors such as temperature, salinity, light intensity, or sediment load, and the relative abundance of competing species or other members of the microbial food web such as viruses, bacteria, or grazers that may affect the survival of a given HAB species (e.g., Glibert et al., 2005a; Turner, 2006; Mitra and Flynn,

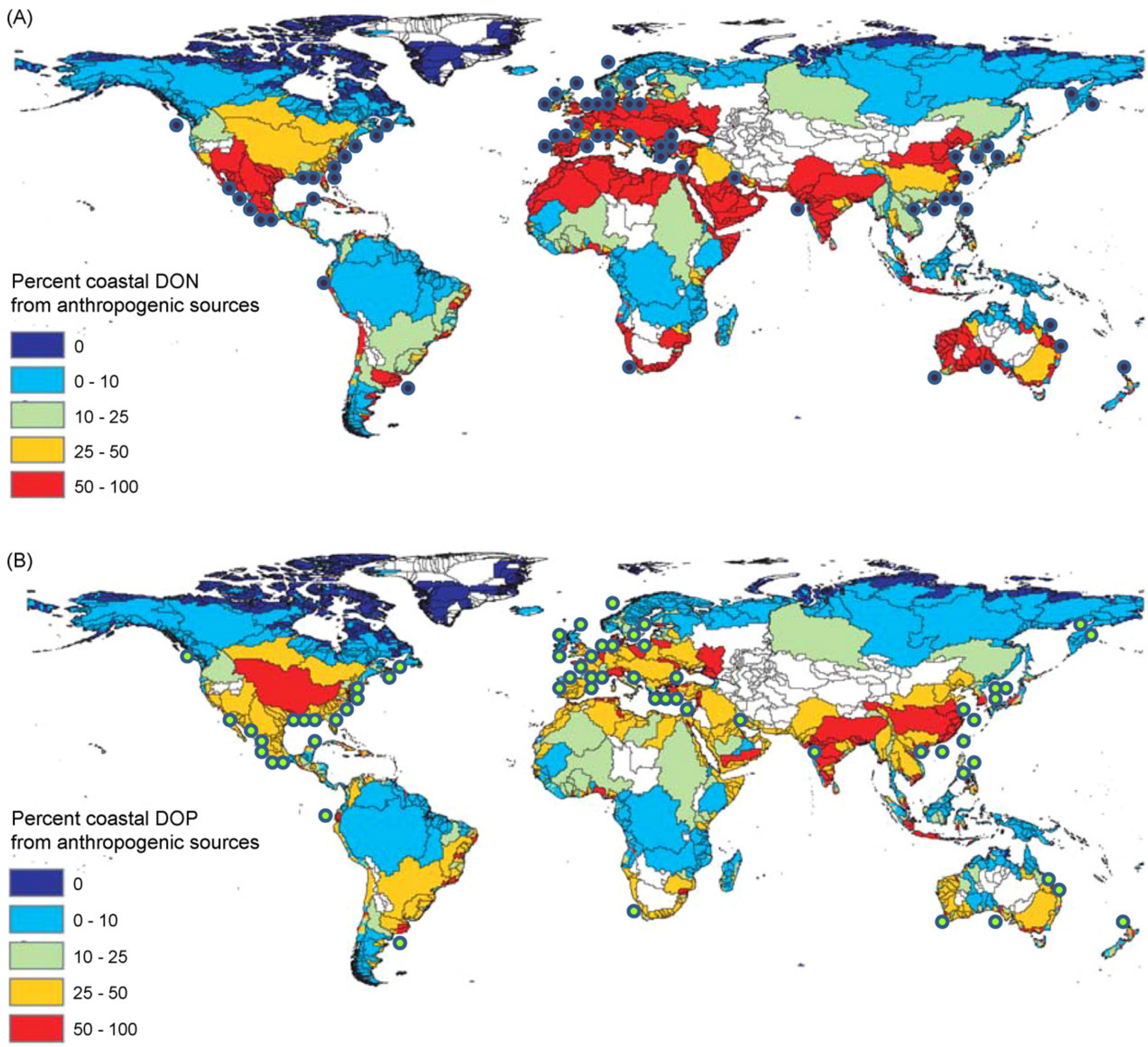

Fig. 4. (A) Percent anthropogenic contribution to DON export from exoreic basins as estimated from Global NEWS models (from Harrison et al., 2005b) and the global distribution of *P. minimum* indicated by circles (from Heil et al., 2005). (B) As for (A), except for DOP (from Harrison et al., 2005b). Base maps reproduced with permission of the American Geophysical Union.

2006; Buskey, 2008). Individual populations may also be composed of genetic variants which may also have different nutrient response capabilites (e.g., Burkholder and Glibert, 2006).

Notwithstanding the inherent limitations of this approach, comparison of these global maps with the known distribution of *P. minimum* has shown that this species proliferates where dissolved N and P yields are high, and where these nutrient sources, whether in inorganic or organic form, have a substantial anthropogenic component. The global expansion of this species, as substantiated by numerous long-term datasets, has been suggestive of a species that proliferates in eutrophic environments (reviewed by Heil et al., 2005). From the Black Sea (Marasović, 1986; Marasović et al., 1990), mid-Atlantic U.S. estuaries such as Chesapeake Bay and the Neuse Estuary (Glibert et al., 2001; Fan et al., 2003; Springer et al., 2005), Oslo Fjord (Paasche et al., 1984), coastal China (Qi et al., 1993; Anderson et al., 2002), and the Baltic Sea (Granéli et al., 1985; Granéli and Moreira, 1990), associations have been drawn between *P. minimum* and nutrient loads. The maps provided herein place these relationships in a global context.

Nutrient inputs (both N and P) to watersheds associated with agriculture, sewage and fossil fuel combustion are projected to more than double by 2050 unless technological advances and policy changes are implemented (Tilman et al., 2001; Millenium Ecosystem Assessment, 2006). The global perspective given here supports the premise that *P. minimum* is a species that may further expand as anthropogenic nutrient loading to the coastal environment continues.

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