



Review

Harmful algal blooms: How strong is the evidence that nutrient ratios and forms influence their occurrence?

Keith Davidson^{a,*}, Richard J. Gowen^b, Paul Tett^a, Eileen Bresnan^c, Paul J. Harrison^d, April McKinney^b, Stephen Milligan^e, David K. Mills^e, Joe Silke^f, Anne-Marie Crooks^b

^a Scottish Association for Marine Science, Scottish Marine Institute, Oban, Argyll PA37 1QA, UK

^b Fisheries and Aquatic Ecosystems Branch, Agriculture Food and Environmental Science Division, Agri-Food and Biosciences Institute, Newforge Lane, Belfast BT9 5PX, UK

^c Marine Scotland Marine Laboratory, P.O. Box 101, 375 Victoria Road, Aberdeen AB11 9DB, UK

^d Department of Earth & Ocean Sciences, University of British Columbia, Vancouver, BC, Canada V6T 1Z3

^e Centre for Environment, Fisheries & Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

^f The Marine Institute, Rinville, Oranmore, Galway, Ireland

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ABSTRACT

There is a perception that anthropogenically-driven changes in nutrient supply to coastal waters influences the abundance, frequency and toxicity of harmful algal blooms (HABs) through a change in the form or ratio of nutrient that limits phytoplankton growth. If nutrient concentrations are not limiting for growth, then ratios do not influence floristic composition. At non-limiting concentrations, evidence that alteration of nitrogen: phosphorus (N:P) ratios has stimulated HABs is limited, and primarily based on hypothesised relationships in relatively few locations (in particular: Tolo Harbour Hong Kong and Dutch Coastal Waters). In all cases, an unequivocal causal link between an increase in HABs (frequency, magnitude or duration) and change in N or P as the limiting nutrient is difficult to establish. The silicon (Si) limitation hypothesis is generally supported by experimental evidence and field data on the nuisance flagellate *Phaeocystis*. We found little evidence that high N:Si ratios preferentially promote harmful dinoflagellates over benign species. Laboratory studies demonstrate that nutrient ratios can influence toxin production, but genus and species specific differences and environmental control make extrapolation of these data to the field difficult. Studies of the role of dissolved and particulate organic nutrients in the growth of HAB species, while limited, demonstrate the potential for organic nutrients (especially organic N) to support the growth of a range of HAB species. There is a clear need for better understanding of the role of mixotrophy in the formation of HABs and for studies of HAB and non-HAB species in competition for environmentally realistic concentrations of organic nutrients.

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1. Introduction

A major factor governing the growth of different species of phytoplankton is the availability of mineral and/or organic nutrients. During the early part of the 20th century, an increase in the human population, industrialisation, and intensification of agriculture has increased the supply of nitrogen (N) and phosphorus (P) to coastal marine waters (Jickells, 1998). Fertilisers, atmospheric inputs, sewage, and agricultural wastes all contribute to this increase. These anthropogenic nutrients have the potential to stimulate phytoplankton production that in turn may have undesirable effects on coastal marine ecosystems and the human use of

them. This is the sequence of eutrophication (Nixon, 1995; Gowen et al., 2008).

A subset of species that make up the phytoplankton may be harmful to human health (e.g. through the production of natural biotoxins), or to human use of the ecosystem (e.g. causing mortality of farmed fish and restricting the harvesting of shellfish). The species that cause harm are widely referred to as “Harmful Algae” and the term “Harmful Algal Bloom” (HAB) is commonly used to describe their occurrence and effects. A link between anthropogenic nutrient supply and the appearance of harmful algae (HABs) has been proposed (Hallegraeff, 1993; Anderson et al., 2002; Heisler et al., 2008; Conley et al., 2009). The view that HABs occur in response to enhanced nutrient loading has recently been reviewed by Gowen et al. (2012) who found that the evidence relating HABs to anthropogenic nutrient enrichment was often equivocal.

* Corresponding author.

E-mail address: kda@sams.ac.uk (K. Davidson).

It is widely accepted that in coastal waters, it is the availability of dissolved inorganic N as ammonium (NH_4^+), nitrate (NO_3^-) and nitrite (NO_2^-) that is most likely to constrain (limit) phytoplankton growth (Ryther and Dunstan, 1971; Howarth and Marino, 2006). However, phosphorus (P) as (PO_4^{3-}) is the limiting nutrient in some parts of the Baltic Sea (Andersson et al., 1996), the Eastern Mediterranean (Krom et al., 2004) and in the Pearl River estuary in southern China (Yin et al., 2001; Xu et al., 2008). A switch from spring P to summer N limitation has also been demonstrated in some locations (Conley, 1999). A meta-analysis of ecosystem response by Elser et al. (2007) suggests that the synergistic effects of combined N and P enrichment are more widespread in marine systems than previously thought. In addition to N and P, the concentration of silicate (Si) in coastal waters is important in governing diatom growth, since diatoms require Si for cell wall (frustule) formation. Hence, rather than being dependent on a simple elevation in coastal nutrient concentrations, the ratios of different nutrients and the form of these nutrients may influence HAB development. Nutrient ratios have also been suggested to influence the amount and rate of toxin generation by biotoxin producing species (Fehling et al., 2004; Granéli and Flynn, 2006).

The potential consequences of changing nutrient ratios for the growth of HAB species are based on the nutrient ratio hypotheses (Officer and Ryther, 1980; Tilman, 1977). These hypotheses purport that a perturbation in the nutrient supply ratio will result in the environmental selection of particular phytoplankters, potentially favouring harmful species (Smayda, 1990; Heisler et al., 2008). As human activity is thought to have increased N and P loads to coastal waters by different proportions (Falkowski, 2000; Conley et al., 2009), resultant changes in the N:P ratio provide a possible mechanism for an anthropogenically mediated increase in HABs.

Generally, Si is less influenced by anthropogenic activity than N and P. Hence in some regions of restricted exchange such as the southern North Sea (Smayda, 1990), the Baltic (Rahm et al., 1996), the Kattegat (Smayda, 1990) and Chesapeake Bay, USA (Conley and Malone, 1992), increases in the coastal inorganic N:Si ratio have been demonstrated. This potentially leads to a switch from diatom to dinoflagellate dominated communities (Officer and Ryther, 1980), the latter containing a greater proportion of HAB species.

The chemical form of nutrients may also be important. Phytoplankton generally exhibit preferential uptake of more reduced forms of N such as NH_4^+ (Dortch, 1990; Flynn et al., 1993; Rees et al., 1995) that may be anthropogenically introduced into coastal waters (Eppley et al., 1979) as well as though *in situ* production within the food web (Davidson et al., 2005). The bioavailability to marine phytoplankton of natural and anthropogenic dissolved organic nutrients is also increasingly recognised, with a number of studies suggesting significant lability (Antia et al., 1991; Carlsson et al., 1993; Bronk, 2002; Lønborg et al., 2009a). The nitrogenous nutrient urea has been linked, through fertiliser runoff, with the development of coastal HABs (Glibert et al., 2006, 2008).

In summary, the hypothesis that HAB species abundance (and toxicity) is related to anthropogenically governed nutrient ratios in coastal waters, and/or the form (quality) of this nutrient, is frequently proposed in the scientific literature (Smayda, 1990; Paerl, 1997; Anderson et al., 2002; Glibert et al., 2005, 2006; Masó and Garcés, 2006; Heisler et al., 2008). However, while conceptually appealing, the nutrient ratio/HAB hypothesis is underpinned by a relatively limited number of studies. Moreover, the hypothesis is being challenged on theoretical grounds, with Flynn (2010) using a modelling to argue that phytoplankton growth on N and P is related to intracellular concentrations. This paper reviews the seminal papers to assess the breadth of evidence that underpin the hypothesis that anthropogenically influenced nutrient ratios and nutrient quality are key to HAB development and toxicity.

2. Nutrient – growth theories

Nutrients may 'limit' both the growth and the yield of phytoplankton populations. The former relates to the rate of increase of biomass, and the latter to the absolute amount of biomass generated per unit of nutrient available. The relationship between nutrients and populations of micro-organisms can be described by a number of theories. Application of these theories typically requires their articulation in mathematical form, for inclusion within modelling frameworks. Such models may then be used to predict the yield or rate of growth of a phytoplankton population given a certain nutrient supply.

The simplest "Monod" theory was developed for organic carbon-limited bacterial growth (Monod, 1942) and was subsequently applied to phytoplankton by Dugdale (1967). The rate of uptake of dissolved nutrient (per unit biomass) is described by a rectangular hyperbolic function of ambient extracellular concentration. Growth rate is directly proportional to uptake rate and increases with increasing ambient nutrient concentration up to a maximum. Both uptake and growth cease when the ambient limiting nutrient is exhausted. The Monod model does not account for cellular storage of nutrients. It is too simple to give a good description of laboratory growth of single species populations but may well be a reasonable approximation for assemblages in the sea (Davidson, 1996).

"Cell-quota" theory (Droop, 1968, 1983) is more sophisticated in that algal growth rates are controlled by cellular concentrations (cell quotas) of nutrients. The cellular quota, Q , of a nutrient (atomic nutrient element (atom organic carbon (C))⁻¹), can vary between limits defined by the minimum or subsistence quota (k_Q) and the maximum cell quota (Q_{max}). The quota allows for cellular storage of a nutrient and so buffers against the effects of ambient change. In marine waters, the ratio of the maximum cell quota: subsistence quota (Q_{max}/k_Q) is typically lower for N and Si (2–4) compared to P (5–90) and is part of the reason why marine phytoplankton tend to be N rather than P limited (Harrison et al., 1990). It also explains why a phytoplankton culture can continue to increase its biomass for many generations after P has been exhausted from the culture medium.

Cell quota based theory, or variants of it, has been used to describe a large range of steady state and transient growth dynamics (Davidson et al., 1993; Davidson and Cunningham, 1996; Tett and Droop, 1988). Most models assume a single limiting nutrient based on a threshold approach (Droop, 1974). The limiting nutrient being the one in least supply relative to cellular chemical composition and the cells' requirements for growth. The ratio k_{Q1}/k_{Q2} determines the relative limitation by nutrients 1 and 2. Thus, if the ratio of ambient nutrients 1 and 2 is $<k_{Q1}/k_{Q2}$ then nutrient 1 may be limiting. However, while conceptually appealing such models are difficult to apply to natural systems because of the difficulties in measuring the cell quota in the field.

While at any one instant there is only a single yield limiting nutrient, the existence of dual nutrient limitation is consistent with the above theory when instantaneous N and P limitation are approximately equal in frequency and severity and hence when increases in phytoplankton biomass require N and P to be added together (Elser et al., 2009).

A further class of models employ complex mechanistic explanations of growth and incorporate more realistic accounts of the main biochemical processes and pools within cells (e.g. Davidson and Gurney, 1999; Flynn and Hipkin, 1999; Flynn, 2001, 2005). These parameter rich models often allowing representation of processes such as surge nutrient uptake (Conway et al., 1976; Mitra et al., 2003), but still retain the approach of the Monod and Quota models of using nutrient ratios to determine 'limitation'.

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