



Complexity in the eutrophication–harmful algal bloom relationship, with comment on the importance of grazing

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ABSTRACT

This article seeks to guide the conceptual development and field application of the eutrophication–HAB hypothesis. After considering the evidence for this hypothesis, the importance of exogenous nutrients as a chemical habitat conditioner and the “family” of nutrient regulated effects that occur are discussed. The various definitions of eutrophication are applied; the conceptual ambiguity over how to perceive eutrophication, and the need to view eutrophication as a process and not as an ecological state are considered. The habitat irradiance–nutrient–flushing gradient regulates the bloom potential in response to exogenous nutrients. There is an apparent species-specific paradox within the eutrophication–HAB hypothesis related to the phycotoxin synthesis–nutrient relationship. Two nutrient–toxin relationships occur: toxin biosynthesis during nutrient sufficiency, and biosynthesis that requires a nutrient limitation. HAB events can be just as much nutrient depletion events as nutrient stimulated events, and whether the former develops depends upon the specific cellular toxicity–nutrient relationship of the bloom species. The importance of grazing in bloom regulation is highlighted. HABs and red tides generally should be viewed as blooms that are regulated by coupled nutrient–grazer processes – nutrient stimulation alone is inadequate, even when exogenous nutrients are not a factor. In assessing the eutrophication–HAB relationship, the collective grazing behavior of the micro-zooplankton, herbivorous copepods, filter feeding benthos, benthic larvae and, when present, omnivorous nekton must be considered. The importance of grazing in the bloom behavior of HAB species is illustrated using field and experimental data during a 5-month brown tide in Narragansett Bay. A cascade in grazing pressure regulated this bloom, with the initial collapse and then restoration of grazing pressure progressing through 7 stages of collective grazing pressure by micro-zooplankton, herbivorous copepods, benthic larvae, benthic filter feeders, and lytic virus infection.

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1. Introduction

The underlying causes of the multi-decadal increase and regional expansion of harmful algal blooms (HABs) and red tides in global coastal waters and epicontinental seas remain enigmatic. The space–time features of HABs suggest that a common driver is operative, indifferent to habitat type, location and bloom species, and is selecting for the flagellate species whose blooms primarily account (see Sournia, 1995) for the HAB phenomenon. The HAB patterns suggest that an anthropogenically disrupted plankton habitat of global proportions – a “changing environment” – may be occurring and underpins this synchronicity, rather than the HAB increase and expansion being the fortuitous space–time coincidence of a series of unrelated, natural and variable regional and

local blooms. Whatever the specific regulatory mechanisms, the community and habitat as a whole – not just the bloom species – are being impacted, with a new trophic equilibrium possibly developing in these disturbed ecosystems.

Two primary HAB-driver hypotheses that apply the “changing environment” view – global climate change and global eutrophication – have been proposed (Smayda, 2002). Ballast water dispersion, which has the required space–time scaling, also has been invoked as a bloom driver. Such emigration-based bloom stimulation is premised to result from the regional and trans-oceanic seedings of propagules and/or the redistribution of bloom species whose assisted dispersal to new and favorable bloom sites overcomes natural geographic barriers. The bloom ecologies of the “changing environment” and ballast water dispersion hypotheses differ fundamentally. Ballast water conveyance is a process – a propagule delivery mechanism – which (as usually applied) does not require changing habitat conditions (see Smayda, 2007). Seedings into recipient habitats do not change the physical and

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chemical factors that affect cellular and population growth, or energy flow (Smayda, 2007). The eutrophication hypothesis, in contrast, posits habitat disturbance as the bloom stimulant – the blooms develop in response to the provisioning of a nutrient that previously was limiting physiologically and/or to biomass accumulation.

The “changing environment” hypotheses are not exclusive, nor preclude ballast water aided blooms, but it is unlikely that there is a singular explanation for the global increase, dynamics and apparent synchrony in HABs – even at a given bloom site – given the ecophysiological (life-form) diversity of the bloom species, the habitat diversity of the bloom localities, and the geographic variations in the importance and type of anthropogenic stressors relative to natural stressors (Smayda and Reynolds, 2001). Yet, the eutrophication–HAB hypothesis is increasingly being invoked, both as the general explanation of the enigmatic HAB phenomenon and to account for local HAB events, to the exclusion of other factors. This application is usually compromised; the data invariably are inadequate to analyze the putative eutrophication–HAB relationship, and the evidence adduced in support of the conclusions is often circumstantial, although more quantitative evidence is beginning to emerge, as outlined in other papers of this special issue.

2. Terms and definitions

This article seeks to guide the conceptual development and field application of the eutrophication–HAB hypothesis, which have been impeded by the multiple definitions and synonyms of eutrophication in use, and the general failure to recognize that eutrophication is a process and not an ecological state. Those issues are considered in greater detail in Section 4.5. In the interim and in an effort to circumvent some definitional problems and confusion as to what eutrophication is, I will use the term *nutrification* (where others might have used *eutrophication*) as a neutral term, i.e. indifferent to the bloom and other ecological consequences of the nutrient enrichment being referenced. Nutrification will mean only that the nutrient levels in the habitat are elevated exogenously (anthropogenically) relative to the intrinsic and naturally occurring concentrations associated with the natural remineralization cycle of the habitat, and its variability, i.e. without reference to biological responses. Further, the influx of exogenous nutrients is considered to chemically disturb the habitat at scales important to plankton populations.

Nutrient will refer to a chemical element essential to metabolism, and when absent the organism dies – that element cannot be substituted by another. The form of the chemical species assimilated and provisioning the essential nutrient, whether inorganic or organic, e.g. as NH_4^+ , NO_3^- , urea or other assimilable nitrogenous compounds, is secondary to its building block (core element), e.g. N, required for growth. Nutrient will be used generically, without reference (unless stipulated otherwise) to a specific macronutrient (N, P, Si, etc.), micronutrient (Fe, Cu, Zn, Co, Mo), essential vitamin, other auxotrophic nutrients, or organic growth factors. The principles of the HAB–eutrophication relationship are of interest, not the metabolism and ecophysiological consequences specific to each of these various nutrient types. Phagotrophic feeding on particulate detritus, bacteria and eukaryotic microalgae is also common among toxic and red tide dinoflagellates, haptophytes and raphidophytes (see Stoecker et al., 2006; Burkholder et al., 2008). This nutritional capacity can help to overcome nutrient limitation and even yield growth rates that exceed those during inorganic nutrient assimilation alone (Stoecker et al., 2006; Burkholder et al., 2008), but in this article it will be considered secondary and supplemental to the

obligate photo-autotrophy of those species, and will not be addressed.

Investigators use different criteria in applying the eutrophication–HAB hypothesis. I define and apply the hypothesis in its simplest terms: anthropogenic nutrients and other chemical products fluxing into coastal waters are disrupting the chemical ecology of these systems. This induces a restructuring of the indigenous phytoplankton assemblages, and leads to the emergence and increased frequency of blooms of HAB and red tide species that previously had been held in check. More specifically, the elevated nutrient concentrations, their altered stoichiometry, and the changes in chemical water quality do not match the nutritional requirements and tolerances of the established phytoplankton assemblage, nor can this assemblage and its grazer-dependent components resist, or recover from this stress (disturbance). As a result, the species' ensemble reorganizes to adjust to the altered habitat chemistry. Whether this behavior becomes an undesirable disturbance, and whether it will be sustained or increase will vary with the specific impact, bloom site (see Glibert and Burkholder, 2006) and the pattern, source and supply rates of the exogenous nutrients being delivered.

Harmful blooms and red tides are distinguished to countervail the tendency of investigators, although it is diminishing, to ignore the relevance of ecophysiological behavior of benign red tide species in evaluations of harmful bloom dynamics. The term red tide is applied to species whose blooms have not been reported to exhibit any of the 10+ types of mortality or other negative impacts that characterize HAB species (Smayda, 1997a). Some species classified as red tide species subsequently have been shown to have negative impacts, but this is not evidence that the other red tide species (a large number) will eventually be reclassified as HAB species. The distinction made between red tides and HABs is partly operational – to emphasize that there are numerous shared and phylogenetically based ecophysiological properties beyond the singular distinction whether a given dinoflagellate species, for example, is a toxin-producer or not. The ecophysiological data for red tide species should not be disregarded in evaluations of eutrophication–HAB behavior. In my view, the eutrophication–HAB relationship is fundamentally one of functional group selection – the phylogeny selected sometimes will be represented by blooms of harmful species, and at other times by benign red tide species (Smayda, 2002). A secondary reason for the HAB–red tide distinction is my growing belief that dinoflagellate bloom behavior, for example, in response to nutrification, may differ between the toxin and non-toxin producing species/strains whose blooms often discolor sea water.

3. Evidence for the eutrophication–HAB hypothesis

The relationships between HABs and eutrophication have been reviewed from various perspectives (Burkholder, 2001; Anderson et al., 2002; Riegman, 1998; Rabalais, 2004; Smayda, 2004; Glibert et al., 2005; GEOHAB, 2006; Glibert and Burkholder, 2006), complemented by the general reviews of Cloern (2001) and Nixon (1995). Glibert et al. (2005), for example, outlined the importance of the changing composition of nutrient pools, the role of physiological state of the organisms, trophic interactions and the emergence of new tools to address this complicated relationship. The evidence for estuarine and marine eutrophication is unambiguous and direct – coastal waters, globally, are becoming enriched with anthropogenic nutrients – a process that Yamamoto (2003) and others before him termed “cultural eutrophication”. The multiple sources and levels of exogenous nutrients fluxing into representative waters, which augment baseline nutrient levels and natural recycling and are leading to nutrient over-enrichment, are

well documented. Exogenous sources include atmospheric deposition, watershed runoff, ground water discharge of nutrients, leaching of agricultural fertilizer, and aquacultural excretion of nutrients (Rabalais, 2004; Turner et al., 2003; Gowen et al., 1990; Glibert et al., 2006; among others). (These inputs do not necessarily increase ambient nutrient levels.) The cultural delivery of inorganic nitrogen and phosphorus has been so great that even in large epicontinental seas, such as the Baltic Sea, Irish Sea and Black Sea, N and P concentrations and their ratios have progressively increased by 2–4-fold or more (Cloern, 2001; Bodeanu, 1993).

Ecosystem changes are occurring in parallel with cultural eutrophication, but the processes and mechanisms are difficult to quantify. Field ecologists must detect, quantify and distinguish specific responses to nutrification from those that occur in response to the natural stresses and habitat variability that natural populations encounter, and seek to mitigate by various physiological acclimation strategies and/or ecological accommodations such as bloom shifts and succession. Where HABs are suspected to be eutrophication-driven, two pertinent questions (relevant also to general application of the eutrophication–HAB hypothesis) must be addressed. Do blooms develop naturally in habitats elsewhere without apparent linkage to nutrient over-supply which correspond in intensity and abundance to eutrophication-driven HABs, i.e. are they the result of some other perturbation? And, where a nutrient linkage is suspected, is the local HAB behavior the direct outcome of a physiological impact – cellular growth – or the indirect (default) consequence – a population accumulation – of other, more primary biological or physical processes activated in response to the altered nutrient and water chemistry? The distinctions between reflected vs. induced events, and between point and threshold departures from baseline dynamics in response to habitat stressors, such as nutrification, are discussed by Smayda (1998).

The first question can be answered affirmatively – prodigious, harmful blooms not traceable to nutrient stimulation are common. Representative examples include the high population density, low biomass bloom (10^9 cells L^{-1}) of the pelagophycean brown tide species, *Aureococcus anophagefferens*, which persisted for 5 months in Narragansett Bay where it was equally abundant in nutrient-rich and nutrient-poor regions (Keller and Rice, 1989, and the 1988 bloom of the haptophyte *Chrysochromulina polylepis* in Scandinavian waters (10^7 cells L^{-1}). Its bloom initially was considered to be induced by pollution, but is now viewed as having been more closely linked to unusual weather patterns (Gjøsæter et al., 2000). Large-scale dinoflagellate blooms that are unrelated to nutrient stimulation occur, such as *Karenia brevis* in pelagic waters of the oligotrophic Gulf of Mexico (Steidinger et al., 1998; but see Brand and Compton, 2007); the precipitous appearance and spreading of *Karenia mikimotoi* in the North Sea (Partensky and Sournia, 1986), and the spreading of *Cochlodinium polykrikoides* in Asian continental shelf waters and frontal zones (Yoon, 2001). The harmful (anoxic) blooms that develop in upwelling regions likewise cannot be attributed to cultural eutrophication (GEOHAB, 2005).

These representative and large-scale examples challenge application of the eutrophication–HAB hypothesis as the general explanation for the global increase in HABs. However, numerous field studies confirming the pioneering studies of Braarud (1945) and Mahoney and McLaughlin (1977) provide solid empirical evidence that HABs and red tides in a variety of regional and local habitats are linked to cultural eutrophication. Representative examples include the long-term increase in abundance of *Prorocentrum minimum* and other species in the Black Sea (Bodeanu, 1995; Moncheva et al., 2001), and raphidophyte and dinoflagellate bloom patterns in the Seto Inland Sea (Imai et al.,

2006). In lesser coastal areas, HABs and red tides have increased with the cultural enrichment of Hong Kong coastal waters (Lam and Ho, 1989); dinoflagellates have bloomed in response to agricultural and aquacultural release of urea (Glibert et al., 2006; Glibert and Terlizzi, 1999), and cyanobacterial blooms have developed in response to atmospheric deposition of nutrients (Paerl and Whittall, 1999), among other examples. The abundance and taxonomic composition of the sedimentary deposits of the cysts of protoperidinium grazers have been used as a general index of water-column eutrophication (Dale, 2001), and some species appear to bloom primarily in chemically disturbed habitats (C-species and Life-form I type in Smayda and Reynolds, 2001). However, these associations have not, as yet, been sufficiently developed to certify the use of these species as reliable indicators of specific habitat chemistries. The search for eutrophication indicator species among HAB and red tide taxa, if they occur, continues six decades after Braarud's (Braarud, 1945) unsuccessful search.

Ecophysiological data support the field evidence that high nutrient levels favor HABs. High K_s (nutrient affinity) coefficients symptomatic of inefficient uptake at low nutrient concentrations generally characterize bloom flagellates (Smayda, 1997a,b), a physiological restraint that should be relaxed by the cultural enrichment of coastal waters. Margalef's Mandala (Margalef, 1978) provides a conceptual framework that HAB and red tide species require an exogenous supply of nutrients above natural recycling in order to bloom, which Sellner et al. (2001) believe they confirmed for a stratified estuary. Thus, although the eutrophication–HAB hypothesis does not explain all of the global HAB phenomenon, there is empirical field and physiological evidence that circumstantially supports the hypothesized linkage in habitats that range in size from the Black Sea, bays, the inner reaches of fjords and estuaries, and coastal lagoons. Definitive evidence is lacking, however, because of the issue juxtaposed in the second question posed earlier – are blooms that are circumstantially linked to eutrophication the direct or indirect consequences of that perturbation? This requires consideration of what eutrophication is, conceptually and mechanistically.

4. Eutrophication: concept, process and effect

4.1. The limnological extrapolation – valid?

The conceptual foundations of eutrophication have been developed primarily by limnologists, initially to depict the “natural aging” of lakes and other land-locked aquatic systems (see Burkholder, 2001), and who demonstrated that the flux of exogenous nutrients into these systems accelerates their natural, long-term progression from an oligotrophic to mesotrophic to eutrophic based metabolism. A similar metabolic aging of coastal marine systems is unlikely since, being more open hydrologically, they are subject to continuous flushing and water mass renewal excluding, perhaps, sea lochs, coastal lagoons, voes, and polls – the closest marine analogues of the land-locked freshwater systems, and whose semi-enclosure and reduced flushing rates increase edaphic impacts and the potential for metabolic stage evolution. This difference in “natural aging” potential may not be relevant to estuarine and marine eutrophication, nor is it evident that freshwater and estuarine/marine phytoplankton communities differ in their responses to eutrophication. Yet, given that eutrophication, as a principle, is extrapolated principally from freshwater behavior, the responses to marine eutrophication at the primary producer level and subsequent ecological consequences possibly differ from freshwater behavior in important ways. Efforts are needed to confirm or nullify this limnetic extrapolation to

marine systems, and to develop a marine-based concept of eutrophication, such as the recent initial efforts of Tett et al. (2007).

4.2. Eutrophication as a chemical habitat conditioner

The eutrophication–HAB hypothesis mechanistically reduces the complex physiological and ecological relationships set into motion by anthropogenic (exogenous) nutrient enrichment (see Section 3) to a simple stimulus–reaction model. Given current knowledge, this over-simplification is acceptable. However, the exogenous enrichment and accumulation of nutrients more than provisions an essential algal nutrient, i.e. an increase in N and P concentrations, with N the focus because coastal ecosystems are generally considered to be N-limited. Exogenous nutrification is (supplies) a polymixture of macro- and micronutrients, humic substances, chelators and chemical inhibitors, and it is also an organic “soup” of diverse nutritional potential and chemical reactivity whose chemical composition varies with the terrestrial source and type of runoff (see Granéli and Moreira, 1990). Nutrification, in its disturbance as a *chemical habitat conditioner*, might be a greater determinant of the HAB response under certain conditions than the accompanying supply of limiting nutrients. The qualitative features of this conditioning are expected to vary seasonally and regionally, and in its capacity to select and support the growth of a given HAB or red tide species. Consequently, the bloom species that respond to nutrient loadings are neither fixed nor similar, even at similar nutrient loading levels, nor should a fixed response be expected. The stochasticity in the composition and concentrations of the chemical water quality ingredients and nutrients during exogenous nutrification, within and among systems, undoubtedly contributes to the stochastic and unpredictable behavior that generally characterizes bloom-species selection during nutrification.

4.3. “Family” of nutrient regulated effects

Investigators increasingly recognize that to focus on increases in nutrients alone as the bloom stimulant is too narrow. There is a “family” of nutrient effects at the cellular and population levels

that influences species selection and bloom behavior, and which must be taken into account – not only are indigenous HAB and red tide species impacted but rather, the whole plankton assemblage is perturbed. This diversity of effects is consistent with the polymixture (chemical) nature of nutrification and its habitat disturbance. At the cellular level, nutrients influence life cycle, nutrient uptake, growth, motility, and nutrient-gathering migrations, among other behavior (Smayda, 1997b). At the population level, species selection, seasonality and abundance are nutrient-linked. The response of HAB and red tide species to exogenous nutrients, therefore, reflects the integrated effect that the changed nutrient levels have on these diverse cellular and population processes. Unpredictable blooms may not only be the result of a species “being in the right place at the right time” (Smayda and Reynolds, 2001). There is a parallel microalgal trait embedded within this maxim which further contributes to the uncertainty with regard to bloom development: *a species will bloom – to some degree – whenever and wherever it can*. This opportunism either will be facilitated or impeded by an increase in nutrients, depending on the extent to which the chemical composition and concentrations of the exogenous nutrient mixture match the nutrient-based ecophysiological needs of the species exposed to this disturbance (see also Glibert and Burkholder, 2006).

The hydraulic properties and hydrodynamic intensity of a habitat modify the potential effect that exogenous nutrients will have on HAB and red tide species responses. Flushing displaces and dilutes the supply of exogenous nutrients and influences the population residence time. The population net growth rate, μ , must exceed the flushing rate, τ , for the population to increase, i.e. $\mu > \tau$ (see Fig. 1). Field studies (see reviews cited earlier) suggest that non-toxic red tide species (i.e. Life-forms I to III in Smayda and Reynolds, 2001) are more likely to bloom than toxic species in nearshore habitats that are less open hydraulically and are nutrient-enriched. And, HABs that occur in estuarine waters tend to be ichthyotoxic, e.g. *Heterosigma akashiwo*, *Prymnesium parvum*. Toxic species cluster primarily in Life-forms IV to VII (Smayda and Reynolds, 2001), and more commonly bloom in open, coastal and continental shelf waters. However, these “mixing-drift” species, which include most of the PST-producers, also periodically bloom

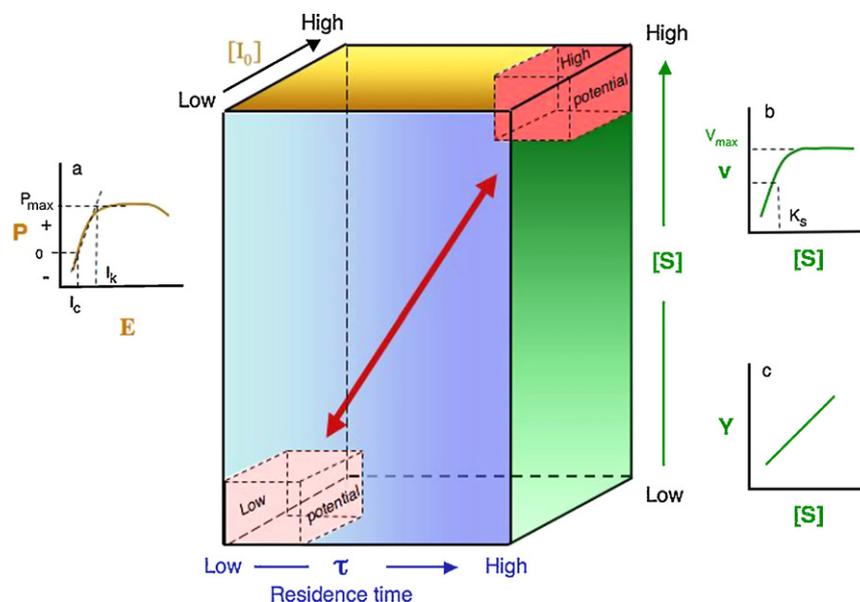


Fig. 1. Harmful algal bloom and red tide potential along a habitat gradient in irradiance, nutrient concentration and flushing rate (expressed as the residence time), and the expected relationships between photosynthesis and irradiance (a), nutrient uptake and nutrient concentration (b), and biomass and nutrient availability–yield–dose relationship (c).

in nutrient-enriched nearshore water where present as autochthonous strains, or advectively seeded. Exogenous nutrients may be more significant in favoring red tide blooms than HABs, but will sustain the latter, once initiated.

4.4. Eutrophication: process and effect

Eutrophication is not an ecological state, it is a process initiated by exogenous nutrient enrichment, which is a disturbance. The microalgal responses – the effects – can be manifested in different ways – by HABs, hypoxia, etc. Unfortunately, process and effect – the two primary components embedded within the term eutrophication – are often conflated. This interchangeable usage has led to conceptual problems and frequent misapplication of the term eutrophication when invoking the eutrophication–HAB hypothesis. An increase in nutrients can initiate an ecologically integrated complex of altered physical, chemical and trophic interactions that induce shifts in phytoplankton abundance, composition and bloom dynamics of the functional groups. These changes impact productivity and modify energy flow; primary production usually increases; the mean standing stock (biomass) is elevated (Fig. 1c), and the ratio of autotrophic to heterotrophic metabolism decreases, e.g. a saprobic shift occurs. These changes and effects are the *consequences* of the process – *eutrophication* – set into motion by the nutrient disturbance; they are not the *process* itself! Eutrophication as a process has properties similar to those in species succession; it proceeds through various stages, each with its own properties operative independently of the overall ecological outcome. And just as there are successional series, there are eutrophication stages arrayed along a continuum of nutrient-enhanced primary production. Historically, these stages have been classified as oligotrophic, mesotrophic, eutrophic and hypertrophic stages, based on freshwater systems. Tett et al. (2007) recently evaluated, from an ecosystem management perspective, various hydrodynamic, chemical and biological reference conditions used as potential indicators of ecosystem metabolic state in temperate marine water bodies undergoing exogenous eutrophication pressure, and being transformed from an oligotrophic to a highly disturbed ecometabolism.

HABs that develop at locations and during periods of nutrient enrichment often are mistaken to be the process when, in fact, they are the consequence. Elevated nutrient concentrations might be more symptomatic of the potential for, rather than direct evidence of, eutrophication. The nutrient increase might be temporary, the result of transitory, natural processes. HABs and red tides that develop then might simply be opportunistic events stimulated, in part, by a transitory nutrient surge, e.g. a storm-driven runoff event (nutrification), rather than a consequence of eutrophication. HABs that are seemingly linked to cultural eutrophication may, in fact, be secondary consequences – reflections (byproducts) – of food web interactions more directly influenced and altered by cultural eutrophication, rather than the direct outcome, i.e. induced by, the eutrophication process (Smayda, 1998). Also relevant to application of the eutrophication–HAB hypothesis, blooms stimulated and sustained by exogenous nutrients alone would be expected to be prolonged, such as developed in Oslofjord (Braarud, 1945) and the Seto Inland Sea (Imai et al., 2006). However, HABs are more often short-lived (several days in duration) – behavior more consistent with nutrient pulsing events than chronic or prolonged nutrient delivery – even in chronically nutrient-enriched habitats, which suggests other controlling factors are operative or interactive with eutrophication. To evaluate eutrophication as a process and to establish its potential and realized effects on HABs and red tides, field measurements of relevant variables and trophic processes carried out at suitable frequency and duration are required and,

ideally, supplemented with suitably designed field experiments. This protocol is much more sophisticated than currently practiced, or within the capacity of standard methodology (see Smayda, 2003). The lack of long-term monitoring data to establish the habitat baseline conditions needed for reference when seeking to assess habitat ecological status and divergence, whether in the past or presently, or projected in response to anthropogenic nutrient exposure is also a handicap. Fortunately, these limitations are being rectified by *in situ* methodology being developed and applied to track the time course of relevant hydrographic parameters, including nutrients (Babin et al., 2005; Glibert et al., 2008), and long-term data sets increasingly are becoming available and being applied.

Nixon (1995) defined eutrophication in terms of the rate of organic carbon supply, and concluded that if the primary production of a system is increasing “we can say that it is undergoing eutrophication”. An increase in nutrients most likely will increase biomass (Fig. 1c), although the relationship between production and ecosystem health is not linear (Tett et al., 2007). Data sets on primary production rates suitable to evaluation of whether Nixon’s (1995) criterion of eutrophication is applicable to HABs, e.g. an increase in HAB frequency would be expected to accompany increased carbon supply, are lacking. The progression of eutrophication through a series of stages (extrapolating from limnetic systems) also poses problems when seeking to relate HABs and red tides to eutrophication. Extant data sets mostly do not provide the detail needed to quantify the extent to which a given system is oligotrophic, mesotrophic or eutrophic. Riegman (1998), based on a multi-species food web model, suggested that eutrophication (his term) would lead to the replacement of competitive specialists by rapidly growing generalists under mesotrophic conditions. Under eutrophic and hypertrophic conditions, generalist species would be replaced by poorly edible species. Confirmation of Riegman’s (1998) nutrient-based selectivity model would strengthen the view that the more relevant consequence of eutrophication in leading potentially to HABs is not the change in the magnitude of primary production. Rather, changes in the rate of supply and trophic routing (vectoring) of organic matter, possibly influenced by allelochemical competition and the degree of prey–predator mismatch, may be more important than the increase in primary production during exogenous nutrient enrichment.

4.5. Eutrophication—its definition

Ambiguity over how to perceive eutrophication, conceptually and practically, is impeding research, data analysis, and ecosystem management. Investigators apply different definitions of eutrophication and use various qualitative descriptors such as eutrophication, over-enrichment and hyper-enrichment synonymously with eutrophication. The Water Framework Directive (WFD) of the European Union (EU) provides a framework for the protection of estuaries and coastal waters, but lacks a definition of eutrophication (Andersen et al., 2006). The boundary between “good”, “moderate” and nutrient-compromised habitat ecological status is usually defined by the environmental management objectives, rather than directly. Richardson and Jørgensen (1996) define eutrophication “as the process of changing the nutritional status of a given water body by increasing the nutrient resources”, which leads to a different eutrophic state. The Urban Waste Water Treatment Directive (UWWTD) of the European Community, which seeks to mitigate the adverse effects of urban waste water discharge, defines eutrophication as “the enrichment of water by nutrients, especially compounds of nitrogen and/or phosphorus, causing accelerated growth of algae and higher forms of plant life to produce an undesirable disturbance to the balance of organisms present and to (water) quality” (Gowen, 1994). The EC Nitrates

Directive focuses on agricultural nitrogen loss in runoff as the enrichment of interest (Andersen et al., 2006). Nixon (1995) defines eutrophication as the increase in the rate of supply of organic matter to an ecosystem; Rabalais (2004) defines it as “the increase in rate of carbon production and carbon accumulation”. Andersen et al. (2006) emphasized that the terms, “accelerated growth”, “undesirable disturbance” and “ecological status”, incorporated into definitions of eutrophication are difficult to apply. They characterized eutrophication as “an unacceptable deviation in structure, function and stability of organisms present in the water and to the quality of water concerned, compared to reference conditions”. They recommended that primary production measurements – “being a sensitive and accurate indicator of eutrophication” – should preferentially be used as a proxy for “growth” over chlorophyll in assessing eutrophication status. Andersen et al. (2006) cautioned against using chlorophyll as an index of eutrophication because “the information inherent in Chl *a* measurements should be interpreted as what it is; a Chl *a* concentration and nothing more” – not biomass, not an indicator of nutrient status, nor of growth rate (see also Tett et al., 2007; Smith, 2007). Tett et al. (2007) pointed out that the term eutrophic, as applied ecologically, has been misapplied historically, based on its Greek etymological root. The etymology of eutrophic refers to a thriving, nourishing, healthy condition – the direct opposite of the condition referenced by current usage of the term eutrophication, i.e. a nutrient-disturbed state suffering from, or en route to habitat and trophic degradation because of an excess – an over enrichment – of exogenous nutrients. Tett et al. (2007) propose a new term – *polutrophic* – to replace eutrophic, and meaning an excess of nourishment, with the terms hypereutrophic, polluted eutrophic and hypertrophism used synonymously.

The differing focus of these definitions – nutrients (chemistry), chlorophyll (“biomass”), primary production (productivity), trophic state (ecosystem) – each a different aspect of the eutrophication–HAB relationship – reveals the complex ecological impacts that eutrophication processes have on communities and ecosystems. Investigators must consider these diverse, interactive effects when seeking to establish whether the floristic outcome of eutrophication is a reflected (indirect) or an induced, direct consequence of enrichment (Smayda, 1998). These diverse effects also make predictions difficult and uniform microalgal responses unlikely. Eutrophication affects N and P cycles, rates and levels of primary production, energy flow, assemblage structure, and species blooms. Each of these impacts moves to different qualitative and quantitative levels as the disturbed ecosystem progresses into, or away from an oligotrophic, mesotrophic or eutrophic stage. The salient feature is that eutrophication is not a fixed condition; it is characterized by different trophic stages whose duration, intensity and chemical nature are driven by the specific eutrophying action.

5. Eutrophication–HABs: a habitat template

The effects of exogenous nutrients on bloom species selection and the specific harmful mode of the HABs that develop are neither predictable nor uniform. This is because of the diversity of the chemical polymixtures that flux into and chemically condition habitats; the “family” of nutrient- and water quality-driven behavior that influences bloom development (Section 4.3), and the variable hydrodynamic features within and among bloom sites. The bloom potential of a habitat is a function of three key, interactive physical–chemical parameters – irradiance (I_0), nutrients (S), and flushing (τ) (Fig. 1). The population level (N) of the bloom species that develops is the sum of its cellular growth rate

(μ) minus the population loss rates due to washout (advection, a), grazing (g) and other mortality (m):

$$N = \mu - [a + g + m] \quad (1)$$

with μ regulated by the irradiance and nutrient conditions.

5.1. Irradiance and the eutrophication–HAB hypothesis

Irradiance must be considered when assessing the eutrophication–HAB relationship. The water-column light field invariably is attenuated during exogenous nutrient delivery; this reduction in irradiance influences the growth rates and toxicity of the species that bloom in response to the nutrient influx (Fig. 1c). There are two primary causes of the increase in water-column turbidity and attenuation of *in situ* irradiance: the seston loading that accompanies the influx of exogenous nutrients, which varies with its source, and the increase in phytoplankton abundance that occurs in response to the nutrient flux. The increase in attenuation has several optical effects: the amount of light available for photosynthesis is decreased; the spectral quality of the transmitted light, which affects motility, is changed (Figuerola et al., 1998); and the euphotic zone depth becomes shallower. These optical changes impact the photosynthetic rate (Fig. 1a), diel phototaxis behavior, and the nutrient-gathering migrations of HAB flagellates (Cullen et al., 1985; Figuerola et al., 1998; Kamykowski, 1981; Kudela and Cochlan, 2000; Nagasoe et al., 2006). The optical properties of the water column vary with the magnitude of exogenous nutrient delivery, whether the delivery is acute or chronic and, particularly, with the seston loading. The resultant stimulation/stress effects on the individual HAB and red tide species differ because of interspecific differences in their irradiance requirements. The relationship between photosynthesis and irradiance – the P – E relationship – illustrates this effect (Fig. 1a). Photosynthesis (P) increases with irradiance (E) up to a saturation level (P_{\max}) and becomes photoinhibited at high irradiance. This P – E relationship has been modeled by the equation (Platt et al., 1980)

$$P = P_{\max} \left[1 - \exp\left(\frac{-\alpha E}{P_{\max}}\right) \right] \left[\exp\left(\frac{-\beta E}{P_{\max}}\right) \right] \quad (2)$$

where α and β are the light-limited and light-inhibited slopes of the P vs. E curve (Fig. 1a), respectively, and α and β may be expressed in terms of carbon fixed per cell, or per unit of chlorophyll relative to E .

The relationship between growth rate, μ , and irradiance follows a similar geometry, and can be modeled using the equation that Kim et al. (2004) applied to *Cochlodinium polykrikoides*:

$$\mu = \mu_m [I - I_0 / I + (I_k - 2I_0)] \quad (3)$$

where μ is the specific growth rate (day^{-1}), μ_m is the maximum specific growth rate (day^{-1}), I is the irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$), I_k is the irradiance at $\mu_m/2$, i.e. half saturation light intensity, and I_0 is the compensation irradiance ($\mu\text{mol m}^{-2} \text{s}^{-1}$).

The irradiance level at which photosynthesis becomes saturated (I_k), and the intensity at which photosynthesis (P) and respiration (R) are equal ($P = R$) and prevent cellular growth – the compensation intensity (I_c) – vary among species. Among dinoflagellates, I_c varies considerably; for example, from $\leq 5 \mu\text{E m}^{-2} \text{s}^{-1}$ for *Akashiwo sanguinea* and other species (Langdon, 1988), to ca. $10 \mu\text{E m}^{-2} \text{s}^{-1}$ for *Karenia mikimotoi*, *Cochlodinium polykrikoides* and *Prorocentrum micans* (Nagasoe et al., 2006); Yamaguchi and Honjo, 1990; Kim et al., 2004). HAB and red tide flagellates compete with diatoms for exogenous nutrients. The I_c for the bloom-diatom *Skeletonema costatum* ($1.1 \mu\text{E m}^{-2} \text{s}^{-1}$) is 9-fold

lower than for the ichthyotoxic raphidophyte *Heterosigma akashiwo* ($9 \mu\text{E m}^{-2} \text{s}^{-1}$) and 32-fold lower than for PSP-producing species *Alexandrium tamarens* (Langdon, 1987). In a competition between these three species at a given nutrient enrichment level, *Skeletonema* would be favored in highly turbid waters, and *Alexandrium tamarens* would be most competitive in clearer waters. Species do not have a fixed I_k or I_c irradiance level; they can photoadapt and physiologically adjust their photosynthesis thresholds. The I_k of four red tide dinoflagellate species decreased 2–4-fold in low light-adapted cultures (Rivkin and Voytek, 1985). This adaptive capacity provides species with physiological flexibility in accommodating to the changes in irradiance quantity and quality that accompany exogenous nutrient/sediment delivery. Species with low I_c and I_k will be advantaged in nutrient-enriched, turbid environments when competing against species having higher photosynthesis saturation and compensation intensities. Irradiance not only affects photosynthesis and growth; it influences cellular toxicity. Toxin production of *Alexandrium catenella* decreased at lower intensities leading Ogata et al. (1989) to conclude that “photosynthesis is essential for toxin production”. In *Alexandrium tamarens*, the influence of irradiance on toxicity also was modified by temperature (Hamasaki et al., 2001), an interaction expected to be common among toxin-producing species.

5.2. Nutrients and the eutrophication–HAB hypothesis

The dissimilar nutritional capacity found among HAB and red tide taxa influences their competitive ability to respond to exogenous nutrients. This contributes to the variable and unpredictable eutrophication–HAB relationship found at the species level. Nutrient uptake and cell growth are related to external and internal (cellular) nutrient concentrations, with the uptake coefficients varying among species (see Smayda, 2006). The dependence of nutrient uptake (v) on the external concentration of a limiting nutrient (S) is described by the Monod model (Fig. 1b)

$$v = V_{\max}S/S + K_s \quad (4)$$

where v is the specific uptake rate per cell, V_{\max} is the maximum velocity of uptake, and K_s the nutrient concentration (the half-saturation coefficient) at which the uptake velocity, v , is one-half V_{\max} , i.e. $V_{\max}/2$. Some investigators treat the growth rate (μ) as a function of external nutrient concentrations and kinetically similar to that of uptake

$$\mu = \mu_{\max}S/(S + K_s) \quad (5)$$

where μ_{\max} is the maximum growth rate. A better approximation of μ is obtained using Droop's cell quota (‘internal stores’) model

$$\mu = \mu_{\max}S(1 - q_0/q) \quad (6)$$

where μ is dependent on the intracellular concentration of the limiting nutrient (“cell quota”, q), and q_0 is the minimal (or subsistence) cell quota, below which the cell is physiologically impaired, and mortality exceeds growth.

The K_s coefficient is an approximate index of a species' competitive ability, i.e. affinity, to take up nutrients in the variable nutrient fields to which they are exposed. The higher a species' K_s , the greater its theoretical dependence on high nutrient concentrations to produce a bloom, while its competitive ability is weakened at low nutrient concentrations when competing against species having a lower K_s and associated greater affinity for nutrient uptake (Smayda, 1997b). The K_s coefficients for inorganic N and P uptake by HAB and red tide species vary by >10-fold, from <1 to >10 μM (see Smayda, 1997; among others).

Since the cellular size of HAB and red tide species varies considerably, the minimal cell quota, q_0 , for N, P and other nutrients also varies among species because q_0 is a function of a species' cellular biovolume. A given nutrient concentration will potentially support a greater population (numerically) of smaller-sized species, i.e. those with a lower q_0 , than larger species. This leads to an effect generally overlooked by investigators: the amount of exogenous nutrient being supplied is, itself, a species selection factor and driver of the bloom magnitude by virtue of the dissimilar K_s and q_0 coefficients found among HAB and red tide species. The diverse nutritional capacity among species also affects the eutrophication–HAB relationship. For example, *Heterocapsa circularisquama* has a broad uptake capacity for dissolved organic phosphorus (DOP) compounds, as does *Karenia mikimotoi*, whereas the ichthyotoxic raphidophytes *Heterosigma akashiwo* and *Chattonella antiqua* apparently cannot use DOP (Yamaguchi et al., 2001). The nitrogen assimilation capacity of HAB dinoflagellates varies interspecifically, both for inorganic N (e.g. Paasche et al., 1984) and urea (Levasseur et al., 1995; Dyrhman and Anderson, 2003), with strain differences occurring (Hosaka, 1992). *Prorocentrum minimum* can assimilate N both in the light and the dark; this enables its diel nutrient gathering strategy, whereas the absolute light requirement of *Karenia mikimotoi* for N uptake precludes such a strategy (Paasche et al., 1984).

5.3. Hydrodynamics and the eutrophication–HAB hypothesis

The flushing characteristics of a habitat undergoing nutrient enrichment influence the potential for HABs and red tides to develop in response (Fig. 1). Bloom potential is dependent on the population residence time, which is determined by habitat flushing rate (a in Eq. (1)). The potential for blooms is lowest when the flushing (washout) rates (τ) are high – the population residence time is low – particularly when low nutrient concentrations and irradiance levels coincide. Bloom potential is greatest when nutrient concentrations and residence time are high (Fig. 1). There is a continuum in the irradiance-flushing combination between these two extremes, along which the prospects of whether a bloom will develop in response to the accompanying influx of exogenous nutrients increase (population $\mu > a$), or decrease (population $\mu < a$).

In summary, in applying the eutrophication–HAB hypothesis it cannot be assumed that the selection and abundance of a species in response to exogenous nutrient is both singularly and directly related to the nutrient supply alone. Bloom potential in response to nutrification is mediated by the accompanying irradiance and flushing characteristics. Further, the toxicity of the bloom will vary with population size, whether the bloom species is N- or P-limited, and the degree and duration of nutrient limitation. It follows that the response of the HAB community to a given nutrient loading will vary among habitats, rather than exhibit uniform and predictable behavior, a consequence readily verified by the collective field evidence.

6. A HAB paradox within eutrophication

Nutrient concentrations not only regulate population abundance (Fig. 1c); they also regulate toxin biosynthesis and cellular toxin levels, but the patterns of regulation differ. At the population level, there is a direct relationship between abundance and nutrient concentration (Fig. 1c), which often leads to a direct relationship between population abundance and toxicity. At the cellular level, the relationship between toxicity and nutrients is more complex, and varies among species. In many species, the relationship is inverse – their cellular toxicity increases with, and is

symptomatic of, nutrient limitation (Flynn and Flynn, 1995; Granéli et al., 1998; Johansson et al., 1996). Both P and N limitation can increase cellular toxin levels, but which nutrient is then more important varies among species. In marked contrast to species whose toxin synthesis is driven by nutrient deficiency, other species synthesize toxins and exhibit high cellular toxicity when nutrient-sufficient (Béchemin et al., 1999; Hamasaki et al., 2001; Johansson et al., 1996; Matsuda et al., 1996; Ogata et al., 1996; among others).

Extrapolated to natural populations, these experimental results suggest that the toxicity and potential impact of HAB species whose cellular toxicity increases with nutrient limitation will progressively increase with population abundance, with toxic impacts expected to develop as a population threshold effect. The population growth rate stimulated initially by the elevated nutrient concentrations begins to wane with the progressive decrease in nutrients being assimilated during population growth and maintenance. The reduced cellular growth rate and, more importantly, the decreased nutrient supply rate relative to population needs can no longer sustain the population, and it becomes physiologically senescent and more toxic. This leads to a eutrophication–HAB paradox. While exogenous nutrients generally stimulate blooms, for some HAB species, given their phycotoxin–nutrient physiology, it is the depletion and physiological limitation of nutrients following nutrient sufficiency that induces and/or accelerates their cellular synthesis of phycotoxins, elevates cellular and population toxicity, and brings about their harmful bloom impacts. *Toxic HAB events can be just as much nutrient depletion events as nutrient-stimulated events, and whether the former develops is dependent on the specific cellular toxicity–nutrient relationship of the bloom species!* For some species, growth and toxicity are stimulated by nutrient enrichment; for other species, nutrient enrichment stimulates their growth, but their toxicity is stimulated by nutrient depletion.

HAB species that grow well, bloom, synthesize toxins, and are competitive at high nutrient concentrations fall within the classical eutrophication–HAB paradigm, unlike HAB species whose toxic blooms are nutrient depletion events. For the latter species, a two-step nutrient control sequence regulates their toxic blooms. There is an initial phase of accelerated cellular and population growth stimulated by elevated nutrient concentrations; this stage is followed by a reduced growth and increased toxin synthesis phase that is induced by nutrient limitation, during which the toxicity of the residual bloom population is elevated. The complex relationship between N and P concentrations, their proportions, the population size and physiological state of the species in bloom, and the toxicity of the blooming strain must be taken into account in local applications of the eutrophication–HAB relationship. A species whose toxicity is induced by N or P limitation may never reach its toxic potential during a given bloom, if its bloom is terminated because of physical disturbance (advection; increased turbulence) or grazing while nutrient levels remain non-limiting.

7. Grazing and the eutrophication–HAB hypothesis

HABs that develop in habitats enriched with exogenous nutrients should not *a priori* be considered to be solely or primarily stimulated by this enrichment when and where facilitated by favorable gradients in the habitat irradiance–flushing template (Fig. 1), i.e. the blooms should not then be considered to be under exclusive physical–chemical regulation. Blooms are also under biological control – particularly by grazers – which must be taken into account in the eutrophication–HAB relationship. Grazing experiments using micro-zooplankton, copepod and benthic filter-feeders (too extensive to review here; see Turner,

2006, in part) extrapolated to natural populations provide strong evidence that red tides and HAB outbreaks reflect, if not require, reduced grazing pressure. The strength of the relaxation in grazing pressure needed to produce a bloom – mindful of the multiple, concurrent sources of grazing pressure – is determined by the balance between the growth (μ) and grazing (g) rates, which are influenced by the overall ecological conditions. The balance between μ and g also determines whether exogenous nutrients or grazing primarily control the HABs and red tides that develop, and which of the potential bloom species present will benefit – be selected to bloom – based on their individual μ – g relationships. In some instances, and for some species, a collapse in grazing pressure may be required; for others, a significant reduction may be needed, and for still other species a modest release in grazing pressure will facilitate blooms. The production of anti-grazing substances will enhance the ability of a species to escape, or otherwise diminish grazer control of its blooms, particularly if it is a slow-grower. If it lacks an allelopathic capacity or a superior growth rate, or does not benefit from a size-based predator–prey mismatch, some other grazing depressant will be essential if it is to bloom competitively in response to exogenous nutrients. The collective evidence prompts the hypothesis that grazers play a major and general role in regulating red tide and HAB outbreaks, and not only in the eutrophication–HAB relationship. Sunda et al. (2006) and Mitra and Flynn (2006) have argued that HAB species promote and sustain blooms through positive feedback, and even by self-propagating regulation of zooplankton grazing activity that shunts nutrients away from competing species. Their models impose an ecophysiological uniformity on HAB species and predatory behavior that is inconsistent with the diversity found. Their provocative models may apply more to selected HAB species, rather than generally, and are possibly vitiated during eutrophication processes.

7.1. Illustration of HAB regulation by grazers

The capacity of grazers to affect the eutrophication–HAB relationship and the complexities of this grazing control are manifested by the progressive cascade in the collapse of grazing pressure and its subsequent restoration that facilitated a 5-month brown tide bloom (*Aureococcus anophagefferens*) in Narragansett Bay (Fig. 2). *Aureococcus anophagefferens* reached a recorded population maximum of 1.2×10^9 cells L^{-1} . This high-density, low-biomass bloom was not a demonstrable effect of eutrophication – the population maxima were similar in the nutrient-rich and nutrient-poor regions of the bay. However, the apparent bloom control features exhibited by the grazer communities are consistent with their hypothesized generic role in bloom regulation, and thereby relevant to the eutrophication–HAB hypothesis.

Seven stages of grazer influence are recognizable during the brown tide bloom (May–September), characterized by a sequence (Fig. 2) of three grazer-breakdown stages (Stages I–III) and three grazer-restoration stages (Stages V–VII), with the restoration sequence preceded by a viral infestation stage (Stage IV). The first breakdown in grazing occurred in May, prior to which the combined advection (a) and grazing (g) rates exceeded, or were in balance with the *Aureococcus* growth (μ) rate, i.e. $a + g > \mu$, and thwarted bloom inception. The diverse community of ciliates and heterotrophic flagellates, normally abundant at that time, was sparse (Smayda and Villareal, 1989b). This microbial community has been shown, both in natural populations and when in culture, to feed avidly on *Aureococcus anophagefferens* (Caron et al., 1989; Sieburth et al., 1988). Depression of micro-zooplankton grazing on *Aureococcus* brown tides also frequently has been shown (Gobler et al., 2002, 2004; Caron et al., 2004; Deonaraine et al., 2006; among

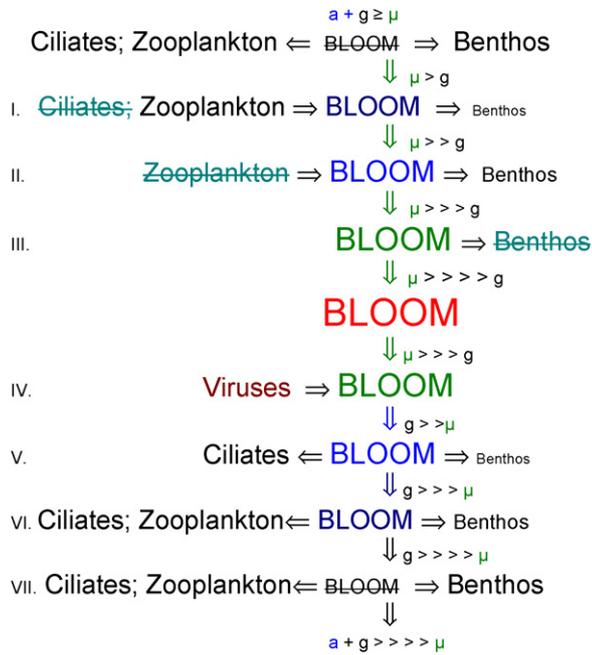


Fig. 2. The cascade in the progressive collapse of grazing pressure that initially facilitated a brown tide bloom (*Aureococcus anophagefferens*) in Narragansett Bay, followed by the progressive restoration and increase in grazing pressure leading to bloom termination, and the 7 stages in this grazing control. The symbols μ designate *Aureococcus* population growth rate; g is the summed grazing rate of the grazer communities; the population loss due to advection. Where stricken through, grazing by that functional groups designated to be impeded by *Aureococcus* [see text for further details].

others). Failure of the microbial grazer community to contain the inception and initial progress of the brown tide bloom, i.e. the net population growth rate exceeded grazing rates ($\mu > g$), was followed by a second, broad-based breakdown in control by zooplankton grazers, which propelled the bloom (Fig. 2). The abundance of *Acartia tonsa*, the dominant herbivorous copepod in Narragansett Bay, decreased with increasing brown tide abundance; the allochthonous cladoceran community (*Evadne nordmanni* and *Podon* sp.), normally present and abundant at this time, conspicuously failed to develop; and benthic invertebrate larval abundance was reduced below normal levels. Each of these zooplankton elements exhibited a strong, statistically significant inverse relationship with *Aureococcus* abundance (Smayda and Fofonoff, 1989; Smayda and Villareal, 1989b). The inimical effect of *Aureococcus* on *Acartia tonsa* suggested by the field data was confirmed in grazing experiments (Durbin and Durbin, 1989). Adult female *Acartia tonsa* fed *Aureococcus* exhibited lower feeding rates, reduced egg production, reduced body growth and weight, and poor general physiological conditioning. The reduction in the collective zooplankton grazing pressure contributed to the continued increase found in *Aureococcus* abundance, i.e. $\mu \gg g$ (Fig. 2). Deonarine et al. (2006) found meso-zooplankton (copepod nauplii, polychaete larvae) avoided *Aureococcus* during intense blooms and preferentially grazed other species, but resumed grazing on *Aureococcus* when at low population levels.

The third, and greatest, breakdown in grazer control was the failure in benthic grazing, specifically the cessation of filter feeding by the mussel (*Mytilus edulis*) population (Fig. 2). The reduction in *Mytilus* filtering rate was scaled to the abundance of *Aureococcus*; in experimental mesocosms, *Mytilus* ceased filtering in mid-June at a threshold *Aureococcus* population of ca. 250 million cells L^{-1} (Tracey, 1988; Tracey et al., 1988). Given this influence of *Aureococcus* abundance, the temporal pattern in the progressive

reduction in mussel filtration during the bloom cycle and the time when filtration failed completely are obscure. Hence, although benthic grazer failure is treated as sequential Stage III in the breakdown of grazer control (Fig. 2), it most likely overlapped and progressed with the suppression in microbial and zooplankton grazing. The progressive breakdown in benthic grazing on *Aureococcus* leading to its cessation is signified in Fig. 2 by the increased font size labeling Benthos proceeding from Stages I to III. The *Mytilus* filter feeding threshold of ca. 250 million *Aureococcus* cells L^{-1} was exceeded from May through July (Smayda and Villareal, 1989b), and led to ca. 99% mortality of the abundant mussel beds in Narragansett Bay. The bay-wide mortality of *Mytilus* resulted from starvation following the utilization and exhaustion of glycogen reserves during the prolonged period when *Mytilus* ceased to filter-feed on the phytoplankton (Tracey, 1988; Tracey et al., 1988). The northern quahog *Mercenaria mercenaria* is a major species in Narragansett Bay attaining population densities up to 190 animals m^{-2} (Rice et al., 1989). Mesocosm studies with vs. without *Mercenaria* have shown that it avidly grazes *Aureococcus*, and brown tides failed to develop when *Mercenaria* was present at high densities (Cerrato et al., 2004, and references therein). Mortality of the bay scallop *Argopecten irradians* also followed cessation of its filter feeding during a *Aureococcus* brown tide elsewhere (Bricelj et al., 1987). The combined reduction in grazing by the microbial, zooplankton and benthic grazers in Narragansett Bay led to a huge excess of the *Aureococcus* net population growth over grazing losses ($\mu \gg g$) (Fig. 2) at the time when *Aureococcus* reached its maximal abundance.

Aureococcus abundance began to decline in August (Smayda and Villareal, 1989a,b). This decline may have been set into motion by the lytic virus infection of *Aureococcus* cells (Stage IV) detected in mid-July (Sieburth et al., 1988). Milligan and Cosper (1994) isolated *Aureococcus*-specific virus that are fully lytic and cause complete mortality in days. However, viruses have also been shown to promote growth of *Aureococcus* during blooms, possibly by regeneration of DOM, which has been shown to increase population growth (Gobler et al., 2004; MacIntyre et al., 2004). Initially, despite the probable reduction in the net population growth rate of *Aureococcus*, i.e. from $\mu \gg g$ to $\mu > g$ resulting from viral infection (Fig. 2), *Aureococcus* abundance remained high, but the population was now in a senescent and declining state, and the balance between μ and g shifted in favor of grazers. During this period of viral infection, in mid-August the micro-zooplankton grazer community, particularly ciliates, rebounded in abundance (Stage V) (Smayda and Villareal, 1989b). In addition, ingestion of *Aureococcus* by phagotrophic flagellates was revealed in electron micrographs of samples collected earlier in late July (Sieburth et al., 1988). *Aureococcus* abundance continued to decrease until its demise in late September (Smayda and Villareal, 1989b), during which zooplankton and benthic grazing presumably increased (Stages VI and VII) because of the release of inimical *Aureococcus* abundance effects on their ingestion rates and reproductive physiology. Copepod and benthic grazing further decimated the declining *Aureococcus* population as the summed microzooplankton, copepod, benthic larvae, and benthic filter feeder grazing losses progressed from $g > \mu$ to $g \gg \mu$, and complemented also by advective losses, i.e. $a + g \gg \mu$ (Fig. 2).

The inimical effects of the *Aureococcus* bloom on the grazer communities were both direct and indirect. For example, *Aureococcus* physiologically, i.e. directly, impaired *Acartia tonsa* fecundity and growth, and its inhibition of the ciliate population, on which *A. tonsa* feeds, indirectly affected its abundance. The bay anchovy (*Anchoa mitchilli*) suffered reproductive failure during the brown tide (Smayda and Villareal, 1989b). This also was probably an indirect effect because the abundance of tintinnids, copepods,

and benthic larvae, the bay anchovy's preferred food items (Detwyler and Houde, 1970), was reduced during the *Aureococcus* bloom.

The well-established grazing of *Aureococcus* by micro- and mesozooplankton and shellfish (clams, mussels and scallops) usually has been considered only in the context that each trophic category functioned in isolated top-down control. The *Aureococcus* – grazing relationships (Fig. 2) suggest each specific type of top-down control is embedded within a greater, overarching grazing cascade that regulates *in situ* eutrophication–HAB behavior to a greater extent than any individual top-down control mechanism. Evidence for a trophic cascade from mesozooplankton to *Aureococcus* passing through the nanoplankton and picoplankton has been discussed by Deonaraine et al. (2006). MacIntyre et al. (2004) present a conceptual model for the initiation of *Aureococcus* blooms regulated by nutrients and irradiance in the absence of grazing, and in which DON is recognized as an important nutrient. The mixotrophy of *Aureococcus* is expected to influence the extent to which its putative husbandry of blooms through grazer feedback control mechanisms (Sunda et al., 2006) is realized. The principal products of excretion among crustacean zooplankton are inorganic nutrients (Parsons et al., 1984), which are elevated during exogenous nitrification.

In summary, and with regard to the role of grazers in the eutrophication–HAB relationship: HABs that are “true” population increases, i.e. are not physically aggregated swarms in which the abundance and toxicity of sparse populations are amplified, require, more often than not, a reduction in grazing pressure. HABs and red tides, generally, should be viewed as blooms that are regulated by coupled nutrient-grazer processes – nutrient stimulation alone is inadequate to trigger a bloom, whether nitrification is a factor or not. There must be an accompanying relaxation in grazing pressure resulting in $\mu > g$ and leading to population growth. Blooms that develop in response to exogenous nutrients require a community-level analytical approach when dealing with the role of grazers in the eutrophication–HAB relationship. Investigators should not restrict interest to a single functional group – the collective grazing behavior of the microzooplankton, herbivorous copepods, filter feeding benthos, benthic larvae and, when present, omnivorous nekton must be considered, although it is recognized that this can be logistically difficult. The balance between a bloom-species growth rate (μ) and the summed grazing rates (g) is an important determinant of whether that species will bloom. This balance, which controls the strength (magnitude) and duration of the bloom, varies spatially and temporally because the respective growth and grazing rates vary with nutrient levels, grazer community composition and abundance. “Normal” grazing processes are disrupted prior to or during HABs; this grazing failure potentially can sequentially and additively progress up the grazer ladder, and influence bloom species selection, bloom duration, and bloom impacts.

It cannot be excluded that at chronically nutrient-enriched bloom sites where HABs may have become more frequent, some grazer populations increasingly exposed to toxic species inhibitory to their grazing may be evolving toxin-resistant cohorts that can feed above the toxic species. The acquisition of resistance by *Acartia hudsonica* fed *Alexandrium tamarense* has been demonstrated experimentally (Colin and Dam, 2007). Teegarden et al. (2008) found copepod feeding responses to natural prey populations did not follow a predictable relationship proportional to prey toxin levels and concluded “copepod grazers do not follow predictable feeding rules throughout a continuum of conditions”. Clearly, the complex issue of grazer regulation of HABs must be addressed, combining field and experimental investigations in efforts to quantify the varieties of bloom behavior accompanying the nitrification–HAB relationship, and bloom ecology generally.

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References

- Andersen, J., Schlüter, L., Ærtebjerg, G., 2006. Coastal eutrophication: recent developments in definitions and implications for monitoring strategies. *J. Plankton Res.* 28, 621–628.
- Anderson, D.M., Glibert, P.M., Burkholder, J.M., 2002. Harmful algal blooms and eutrophication: nutrient sources, composition and consequences. *Estuaries* 25, 704–726.
- Babin, M., et al., 2005. New approaches and technologies for observing harmful algal blooms. *Oceanology* 18, 210–227.
- Béchemin, C., Grzebyk, D., Hachame, F., Hummert, C., Maestrini, S.Y., 1999. Effect of different nitrogen/phosphorus nutrient ratios on the toxin content of *Alexandrium minutum*. *Aquat. Microb. Ecol.* 20, 157–165.
- Bodeanu, N., 1993. Microalgal blooms in the Romanian area of the Black Sea and contemporary eutrophication conditions. In: Smayda, T.J., Shimizu, Y. (Eds.), *Toxic Phytoplankton Blooms in the Sea*. Elsevier, Amsterdam, pp. 203–209.
- Bodeanu, N., 1995. Algal blooms in Mamaia Bay (Romanian Black Sea coast). In: Lassus, P., Arzul, G., Erard-Le Denn, E., Gentien, P., Marcaillou-Le Baut, C. (Eds.), *Harmful Marine Algal Blooms*. Lavoisier Publishing, Paris, pp. 127–132.
- Braarud, T., 1945. A phytoplankton survey of the polluted waters of inner Oslo Fjord. *Hvalraadetets Skrifter* 28, 1–142.
- Brand, L.E., Compton, A., 2007. Long-term increase in *Karenia brevis* abundance along the southwest Florida coast. *Harmful Algae* 6, 232–252.
- Bricelj, V.M., Epp, J., Malouf, R.E., 1987. Intraspecific variation in reproductive and somatic growth cycles of Bay scallop *Argopecten irradians*. *Mar. Ecol. Prog. Ser.* 36, 123–137.
- Burkholder, J.M., 2001. Eutrophication and oligotrophication. In: *Encyclopedia of Biodiversity*, 2, pp. 649–669.
- Burkholder, J.M., Glibert, P.M., 2008. Skelton, H. A. Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae* 8, 77–93.
- Caron, D.A., Lim, E.L., Kunze, H., Cosper, E.M., Anderson, D.M., 1989. Trophic interactions between nano- and microzooplankton and the “brown tide”. In: Cosper, E.M., Carpenter, E.J., Bricelj, V.M. (Eds.), *Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms*. Springer-Verlag, Berlin, (Coastal and Estuarine Studies No. 35), pp. 265–294.
- Caron, D.A., et al., 2004. Microbial herbivory on the brown tide alga, *Aureococcus anophagefferens*: results from natural ecosystems, mesocosms, and laboratory experiments. *Harmful Algae* 3, 439–457.
- Cerrato, R.M., Caron, D.A., Lonsdale, D.J., Rose, M.M., Schaffner, R.A., 2004. Effect of the northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide alga *Aureococcus anophagefferens*. *Mar. Ecol. Prog. Ser.* 281, 93–108.
- Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. *Mar. Ecol. Prog. Ser.* 210, 223–253.
- Colin, S.P., Dam, H.G., 2007. Comparison of the functional and numerical responses of resistant versus non-resistant populations of the copepod *Acartia hudsonica* fed the toxic dinoflagellate *Alexandrium tamarense*. *Harmful Algae* 6, 875–882.
- Cullen, J.J., Zhu, M., Davis, R.F., Pierson, D.C., 1985. Vertical migration, carbohydrate synthesis, and nocturnal nitrate uptake during growth of *Heterocapsa niei* in a laboratory water column. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), *Toxic Dinoflagellates*. Elsevier, Amsterdam, pp. 189–194.
- Dale, B., 2001. Marine dinoflagellate cysts as indicators of eutrophication and industrial pollution: a discussion. *Sci. Total Environ.* 264, 235–240.
- Deonaraine, S.N., Gobler, C.J., Lonsdale, D.J., Caron, D.A., 2006. Role of zooplankton in the onset and demise of harmful brown tide blooms (*Aureococcus anophagefferens*) in US mid-Atlantic estuaries. *Aquat. Microb. Ecol.* 44, 181–195.
- Detwyler, R., Houde, E.D., 1970. Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacola* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchelli* (Pisces Engraulidae). *Mar. Biol.* 7, 214–222.
- Durbin, A.G., Durbin, E.G., 1989. Effect of the “Brown Tide” on feeding, size and egg laying rate of adult female *Acartia tonsa*. In: Cosper, E.M., Carpenter, E.J., Bricelj, V.M. (Eds.), *Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms*. Springer-Verlag, Berlin, (Coastal and Estuarine Studies No. 35), pp. 625–646.

- Dyrhman, S.T., Anderson, D.M., 2003. Urease activity in cultures and field populations of the toxic dinoflagellate *Alexandrium*. *Limnol. Oceanogr.* 48, 647–655.
- Figuerola, F.L., Neill, F.X., Figueiras, F.G., Villarino, M.L., 1998. Diel migrations of phytoplankton and spectral light field in the Ria de Vigo (NW Spain). *Mar. Biol.* 130, 491–499.
- Flynn, K.J., Flynn, K., 1995. Dinoflagellate physiology: nutrient stress and toxicity. In: Lassus, P., Arzul, G., Erard-Le Denn, E., Gentien, P., Marcaillou-Le Baut, C. (Eds.), *Harmful Marine Algal Blooms*. Lavoisier Publishing, Paris, pp. 541–550.
- GEOHAB, 2005. Global ecology and oceanography of harmful algal blooms. In: Pitcher, G., Moita, T., Trainer, V., Kudela, R., Figueiras, P., Probyn, T. (Eds.), *GEOHAB Core Research Project: HABs in Upwelling Systems*. IOC and SCOR, Paris, 74 pp.
- GEOHAB, 2006. Global ecology and oceanography of harmful algal blooms. *Harmful Algal Blooms in Eutrophic Systems*. IOC and SCOR, Paris, 82 pp.
- Gjøsaeter, J., et al., 2000. A long-term perspective on the Chrysochromulina bloom on the Norwegian Skagerrak coast 1988: a catastrophe or an innocent incident? *Mar. Ecol. Prog. Ser.* 207, 201–218.
- Glibert, P.M., Burkholder, J.M., 2006. The complex relationships between increases in fertilization of the Earth, coastal eutrophication and proliferation of harmful algal blooms. In: Granéli, E., Turner, J.T. (Eds.), *Ecology of Harmful Algae*. Springer, Berlin, pp. 341–354.
- Glibert, P.M., Harrison, J., Heil, C., Seitzinger, S., 2006. Escalating worldwide use of urea—a global change contributing to coastal eutrophication. *Biogeochemistry* 77, 441–463.
- Glibert, P.M., Kelly, V., Alexander, J., Codispoti, L.A., Boicourt, W.C., Trice, T.M., Michael, B., 2008. *In situ* nutrient monitoring: A tool for capturing nutrient variability and the antecedent conditions that support algal blooms. *Harmful Algae* 8, 175–181.
- Glibert, P.M., Seitzinger, S., Heil, C., Burkholder, J.A., Parrow, M.W., Codispoti, L., Kelly, V., 2005. The role of eutrophication in the global proliferation of harmful algal blooms. *Oceanography* 18, 198–209.
- Glibert, P.M., Terlizzi, D.E., 1999. Co-occurrence of elevated urea levels and dinoflagellate blooms in temperate estuarine aquaculture ponds. *Appl. Environ. Microbiol.* 65, 5594–5596.
- Gobler, C.J., Deonarine, S., Leigh-Bell, J., Gastrich, M.D., Anderson, I.R., Wilhelm, S.W., 2004. Ecology of phytoplankton communities dominated by *Aureococcus anophagefferens*: the role of viruses, nutrients, and microzooplankton grazing. *Harmful Algae* 3, 471–483.
- Gobler, C.J., Renaghan, M.J., Buck, N.J., 2002. Impacts of nutrients and grazing mortality on the abundance of *Aureococcus anophagefferens* during a New York brown tide bloom. *Limnol. Oceanogr.* 47, 129–141.
- Gowen, R.J., 1994. Managing eutrophication associated with aquaculture development. *J. Appl. Ichthyol.* 10, 242–257.
- Gowen, R.J., Rosenthal, H., Mäkinen, T., Ezzi, I., 1990. Environmental impact of aquaculture activities. In: DePauw, N., Billard, R. (Eds.), *Aquaculture Europe 89 – Business Joins Science*. Bredene, Belgium, (European Aquaculture Society, Spec. Publ. No. 12), pp. 257–283.
- Granéli, E., Johansson, N., Panosso, R., 1998. Cellular toxin contents in relation to nutrient conditions for different groups of phycotoxins. In: Reguera, B., Blanco, J., Fernández, M., L., Wyatt, T. (Eds.), *Harmful Algae*, Xunta de Galicia and Intergovernmental Oceanographic Commission of UNESCO 1998, pp. 321–324.
- Granéli, E., Moreira, M.O., 1990. Effects of river water of different origin on the growth of marine dinoflagellates and diatoms in laboratory cultures. *J. Exp. Mar. Biol. Ecol.* 136, 89–106.
- Hamasaki, K., Horie, M., Tokimitsu, S., Toda, T., Taguchi, S., 2001. Variability in toxicity of the dinoflagellate *Alexandrium tamarense* isolated from Hiroshima Bay, western Japan, as a reflection of changing environmental conditions. *J. Plankton Res.* 23, 271–278.
- Hosaka, M., 1992. Growth characteristics of a strain of *Heterosigma akashiwo* (Hada) Hada isolated from Tokyo Bay, Japan. *Bull. Plankton Soc. Jpn.* 39, 49–58.
- Imai, I., Yamaguchi, M., Hori, Y., 2006. Eutrophication and occurrences of harmful algal blooms in the Seto Inland Sea, Japan. *Plankton Benthos Res.* 1, 71–84.
- Johansson, N., Granéli, E., Yasumoto, T., Carlsson, P., Legrand, C., 1996. Toxin production by *Dinophysis acuminata* and *D. acuta* cells grown under nutrient sufficient and deficient conditions. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*. Intergovernmental Oceanographic Commission of UNESCO, pp. 277–280.
- Kamykowski, D., 1981. Dinoflagellate growth rate in water columns of varying turbidity as a function of migration phase with daylight. *J. Plankton Res.* 3, 357–367.
- Keller, A.A., Rice, R.L., 1989. Effects of nutrient enrichment on natural populations of the brown tide phytoplankton *Aureococcus anophagefferens* (Chrysophyceae). *J. Phycol.* 25, 636–646.
- Kim, D.-I., Matsuyama, Y., Nagasoe, S., Yamaguchi, M., Yoon, Y.-H., Oshima, Y., Imada, N., Honjo, T., 2004. Effects of temperature, salinity and irradiance on the growth of the harmful red tide dinoflagellate *Cochlodinium polykrikoides* Margalef (Dinophyceae). *J. Plankton Res.* 26, 61–66.
- Kudela, R.M., Cochlan, W.P., 2000. Nitrogen and carbon uptake kinetics and the influence of irradiance for a red tide bloom off southern California. *Aquat. Microb. Ecol.* 31, 31–47.
- Lam, C.W.Y., Ho, K.C., 1989. Red tides in Tolo Harbour Hong Kong. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides Biology, Environmental Science and Toxicology*. Elsevier, New York, pp. 49–52.
- Langdon, C., 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. Part 1. A comparative study of the growth-irradiance relationship of three marine phytoplankton species: *Skeletonema costatum*, *Olisthodiscus luteus* and *Gonyaulax tamarensis*. *J. Plankton Res.* 9, 459–482.
- Langdon, C., 1988. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton II. A general review. *J. Plankton Res.* 10, 1291–1312.
- Levasseur, M., Gamache, T.St., Pierre, I., Michaud, S., 1995. Does the cost of NO₃ reduction affect the production of harmful compounds by *Alexandrium excavatum*? In: Lassus, P., Arzul, G., Erard-Le Denn, E.P., Gentien, P., Marcaillou-Le Baut, C. (Eds.), *Harmful Marine Algal Blooms*. Lavoisier Publishing, Paris, pp. 463–468.
- MacIntyre, H.L., Lomas, M.W., Cornwell, J., Suggett, D.J., Gobler, C.J., Koch, W.W., Kana, T.M., 2004. Mediation of benthic-pelagic coupling by microphytobenthos: an energy- and material-based model for initiation of blooms of *Aureococcus anophagefferens*. *Harmful Algae* 3, 403–437.
- Mahoney, J.B., McLaughlin, J.J.A., 1977. The association of phytoplankton blooms in Lower New York Bay with hypertrophication. *J. Exp. Mar. Biol. Ecol.* 23, 53–65.
- Margalef, R., 1978. Life forms of phytoplankton as survival alternatives in an unstable environment. *Oceanol. Acta* 1, 493–509.
- Matsuda, A., Nishijima, T., Fukami, K., 1996. Effects of nitrogen deficiency on the PSP production by *Alexandrium catenella* under axenic cultures. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*. Intergovernmental Oceanographic Commission of UNESCO, pp. 305–308.
- Milligan, K.L.D., Cosper, E.M., 1994. Isolation of virus capable of lysing the brown tide microalga *Aureococcus anophagefferens*. *Science* 206, 805–807.
- Mitra, A., Flynn, K.J., 2006. Promotion of harmful algal blooms by zooplankton predatory activity. *Biol. Lett.* 2, 194–197.
- Moncheva, S., Doncheva, V., Kamburska, L., 2001. On the long-term response of harmful algal blooms to the evolution of eutrophication off the Bulgarian Black Sea coast: are the recent changes a sign of recovery of the ecosystem—the uncertainties. In: Hallegraef, G.M., Blackburn, S.I., Bolch, C.J., Lewis, R.J. (Eds.), *Harmful Algal Blooms 2000*. Intergovernmental Oceanographic Commission of UNESCO, pp. 177–181.
- Nagasoe, S., Kim, D.-I., Shimasaki, Y., Oshima, Y., Yamaguchi, M., Honjo, T., 2006. Effects of temperature, salinity and irradiance on the growth of the red tide dinoflagellate *Gyrodinium instriatum* Freudenthal et Lee. *Harmful Algae* 5, 20–25.
- Nixon, S.W., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. *Ophelia* 41, 199–219.
- Ogata, T., Kodama, M., Ishimaru, M., 1989. Effect of water temperature and light intensity on growth rate and toxin production of toxic dinoflagellates. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides Biology, Environmental Science and Toxicology*. Elsevier, NY, pp. 423–426.
- Ogata, T., Koike, K., Nomura, S., Kodama, M., 1996. Utilization of organic substances for growth and toxin production by *Alexandrium tamarensis*. In: Yasumoto, T., Oshima, Y., Fukuyo, Y. (Eds.), *Harmful and Toxic Algal Blooms*. Intergovernmental Oceanographic Commission of UNESCO, pp. 343–346.
- Paasche, E., Bryceson, I., Tangen, K., 1984. Interspecific variation in dark nitrogen uptake by dinoflagellates. *J. Phycol.* 20, 394–401.
- Paerl, H.W., Whittall, D.R., 1999. Anthropogenically-derived atmospheric nitrogen deposition, marine eutrophication and harmful algal bloom expansion: is there a link? *Oceanology* 28, 307–311.
- Partensky, F., Sournia, A., 1986. Le Dinoflagellé *Gyrodinium* cf. *aureolum* dans le plancton de l'Atlantique nord: identification, écologie, toxicité. *Cryptogamie Algologie* 7, 251–276.
- Parsons, T.R., Takahashi, M., Hargrave, B., 1984. *Biological Oceanographic Processes*, 3rd Edition. Pergamon Press, Oxford, 330 pp.
- Platt, T., Gallegos, C.L., Harrison, W.G., 1980. Photoinhibition of photosynthesis in natural assemblages of marine phytoplankton. *J. Mar. Res.* 38, 687–701.
- Rabalais, N.N., 2004. Eutrophication. In: Robinson, A.R., Brink, K.H. (Eds.), *The Sea*, 13Harvard Univ. Press, pp. 821–866 (Chapter 21).
- Rice, M.A., Hickox, C., Zebra, I., 1989. Effects of intensive fishing pressure on the population structure of quahogs, *Mercenaria mercenaria* (Linnaeus 1758) in Narragansett Bay. *J. Shellfish Res.* 8, 345–354.
- Richardson, K., Jørgensen, B.B., 1996. Eutrophication: definition, history and effects. In: Richardson, K., Jørgensen, B.B. (Eds.), *Eutrophication in Coastal Marine Systems*. Coastal and Estuarine Studies, No. 52, American Geophysical Union, pp. 1–19.
- Riegman, R., 1998. Species composition of harmful algal blooms in relation to macronutrient dynamics. In: Anderson, D.M., Cembella, A.D., Hallegraef, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. NATO ASI Series. Springer-Verlag, Berlin, pp. 474–488.
- Rivkin, R.B., Voytek, M.A., 1985. Photoadaptations of photosynthesis by dinoflagellates from natural populations: a species approach. In: Anderson, D.M., White, A.W., Baden, D.G. (Eds.), *Toxic Dinoflagellates*. Elsevier, Amsterdam, pp. 97–102.
- Sellner, K.G., Sellner, S.G., Lacouture, R.V., Magnien, R.E., 2001. Excessive nutrients select for dinoflagellates in the stratified Patapsco River estuary: Margalef reigns. *Mar. Ecol. Prog. Ser.* 220, 93–102.
- Sieburth, J.M., Johnson, P.W., Hargraves, P.E., 1988. Ultrastructure and ecology of *Aureococcus anophagefferens* gen. et sp. nov. (Chrysophyceae): the dominant picoplankton during a bloom in Narragansett Bay, Rhode Island, summer 1985. *J. Phycol.* 24, 416–425.
- Smayda, T.J., 1997a. What is a bloom? A commentary. *Limnol. Oceanogr.* 42, 1132–1136.

- Smayda, T.J., 1997b. Harmful algal blooms: their ecophysiology and general relevance to phytoplankton blooms in the sea. *Limnol. Oceanogr.* 42, 1137–1153.
- Smayda, T.J., 1998. Patterns of variability characterizing phytoplankton, with examples from Narragansett Bay. *ICES J. Mar. Sci.* 55, 562–573.
- Smayda, T.J., 2002. Adaptive ecology, growth strategies, and the global bloom expansion of dinoflagellates. *J. Ocean.* 58, 281–294.
- Smayda, T.J., 2003. Environmental monitoring, with examples from Narragansett Bay. In: Hallegraeff, G.M., Anderson, D.M., Cembella, A.D. (Eds.), *Manual on Harmful Algal Blooms*. UNESCO Monographs on Oceanographic Methodology 11, pp. 595–625.
- Smayda, T.J., 2004. Eutrophication and phytoplankton. In: Wassmann, P., Olli, K. (Eds.), *Drainage Basin Nutrient Inputs and Eutrophication: an Integrated Approach*. University of Tromsø, Norway. ISBN 82-910866-34-2 [An e-book available at: www.ut.ee/~olli/eutr/], pp. 89–98.
- Smayda, T.J., 2006. Autecology of bloom-forming microalgae: extrapolation of laboratory results to field populations and the Redfield–Braarud debate revisited. In: Subba Rao, D. (Ed.), *Algal Cultures, Analogues of Blooms and Applications*. Science Publishers, Enfield, NH, pp. 215–270.
- Smayda, T.J., 2007. Reflections on the ballast water dispersal-harmful algal bloom paradigm. *Harmful Algae* 6, 601–622.
- Smayda, T.J., Fofonoff, P., 1989. An extraordinary, noxious “brown-tide” in Narragansett Bay II. Inimical effects. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier, NY, pp. 133–136.
- Smayda, T.J., Reynolds, C.S., 2001. Community assembly in marine phytoplankton: application of recent models to harmful dinoflagellate blooms. *J. Plankton Res.* 23, 447–461.
- Smayda, T.J., Villareal, T.A., 1989a. An extraordinary, noxious “brown-tide” in Narragansett Bay I. The organism and its dynamics. In: Okaichi, T., Anderson, D.M., Nemoto, T. (Eds.), *Red Tides: Biology, Environmental Science and Toxicology*. Elsevier, NY, pp. 129–132.
- Smayda, T.J., Villareal, T., 1989b. The 1985 “brown-tide” and the open phytoplankton niche in Narragansett Bay during summer. In: Cosper, E.M., Carpenter, E.J., Bricej, V.M. (Eds.), *Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms*. Springer-Verlag, Berlin, (Coastal and Estuarine Studies No. 35), pp. 159–187.
- Smith, V., 2007. Using primary productivity as an index of coastal eutrophication: the units of measurement matter. *J. Plankton Res.* 29, 1–6.
- Sournia, A., 1995. Red-tide and toxic marine phytoplankton of the world ocean: an inquiry into biodiversity. In: Lassus, P., Arzul, G., Erard-Le Denn, E., Gentien, P., Marcaillou-Le Baut, C. (Eds.), *Harmful Marine Algal Blooms*. Lavoisier Publishing, Paris, pp. 103–112.
- Steidinger, K.A., Vargo, G.A., Tester, P.A., Tomas, C.R., 1998. Bloom dynamics and ecophysiology of *Gymnodinium breve*, with emphasis on the Gulf of Mexico. In: Anderson, D.M., Cembella, A.D., Hallegraeff, G.M. (Eds.), *Physiological Ecology of Harmful Algal Blooms*. NATO ASI Series. Springer-Verlag, Berlin, pp. 133–153.
- Stoecker, D., Tillmann, U., Granéli, E., 2006. Phagotrophy in harmful algae. In: Granéli, E., Turner, J.T. (Eds.), *Ecology of Harmful Algae*. Springer, Berlin, pp. 177–188.
- Sunda, W.G., Granéli, E., Gobler, C.J., 2006. Positive feedback and the development and persistence of ecosystem disruptive algal blooms. *J. Phycol.* 42, 963–974.
- Teegarden, G.J., Campbell, R.G., Anson, D.T., Ouellet, A., Westman, B.A., Durbin, E.G., 2008. Copepod feeding response to varying *Alexandrium* spp. cellular toxicity and cell concentration among natural plankton samples. *Harmful Algae* 7, 33–44.
- Tett, P., Gowen, R., Mills, D., Fernandes, T., Gilpin, L., Huxham, M., Kennington, K., Read, P., Service, M., Wilkinson, M., Malcolm, S., 2007. Defining and detecting undesirable disturbance in the context of marine eutrophication. *Mar. Poll. Bull.* 55, 282–297.
- Tracey, G., 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 “brown tide” in Narragansett Bay Rhode Island. *Mar. Ecol. Prog. Ser.* 50, 73–81.
- Tracey, G.A., Johnson, P.A., Steele, R., Hargraves, P.E., Sieburth, J.M., 1988. A shift in photosynthetic picoplankton composition and its effect on bivalve mollusc nutrition: the 1985 “brown tide” in Narragansett Bay Rhode Island. *J. Shellfish Res.* 7, 671–675.
- Turner, J.T., 2006. Harmful algae interactions with marine planktonic grazers. In: Granéli, E., Turner, J.T. (Eds.), *Ecology of Harmful Algae*. Springer-Verlag, Berlin, pp. 259–270.
- Turner, R.E., Rabalais, N.N., Justic, D., Dortch, Q., 2003. Future aquatic nutrient limitations. *Mar. Poll. Bull.* 46, 1032–1034.
- Yamaguchi, M., Honjo, T., 1990. Effects of temperature, salinity and irradiance on the growth of the noxious red tide flagellate *Gymnodinium nagasakiense* (Dinophyceae). *Nippon Suisan Gakk.* 55, 2029–2036.
- Yamaguchi, M., Itakura, S., Uchida, T., 2001. Nutrition and growth kinetics in nitrogen- or phosphorus-limited cultures of the ‘novel red tide’ dinoflagellate *Heterocapsa circularisquama* (Dinophyceae). *Phycologia* 40, 313–338.
- Yamamoto, T., 2003. The Seto Inland Sea – eutrophic or oligotrophic. *Mar. Poll. Bull.* 47, 37–42.
- Yoon, Y.H., 2001. A summary of the red tide mechanisms of the harmful dinoflagellate, *Cochlodinium polykrikoides*, in Korean coastal waters. *Bull. Plankton Soc. Japan* 48, 113–120.