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Biol. Lett. 2006 **2**, 194-197
doi: 10.1098/rsbl.2006.0447

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doi:10.1098/rsbl.2006.0447

Promotion of harmful algal blooms by zooplankton predatory activity

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The relationship between algae and their zooplanktonic predators typically involves consumption of nutrients by algae, grazing of the algae by zooplankton which in turn enhances predator biomass, controls algal growth and regenerates nutrients. Eutrophication raises nutrient levels, but does not simply increase normal predator–prey activity; rather, harmful algal bloom (HAB) events develop often with serious ecological and aesthetic implications. Generally, HAB species are outwardly poor competitors for nutrients, while their development of grazing deterrents during nutrient stress ostensibly occurs too late, after the nutrients have largely been consumed already by fast-growing non-HAB species. A new mechanism is presented to explain HAB dynamics under these circumstances. Using a multi-nutrient predator–prey model, it is demonstrated that these blooms can develop through the self-propagating failure of normal predator–prey activity, resulting in the transfer of nutrients into HAB growth at the expense of competing algal species. Rate limitation of this transfer provides a continual level of nutrient stress that results in HAB species exhibiting grazing deterrents protecting them from top-down control. This process is self-stabilizing as long as nutrient demand exceeds supply, maintaining the unpalatable status of HABs; such events are most likely under eutrophic conditions with skewed nutrient ratios.

Keywords: predator–prey; harmful algal bloom; zooplankton; eutrophication

1. INTRODUCTION

Algal blooms occur when biomass accumulation exceeds dispersal through biological and physical processes. For bloom development in immature ecosystems (e.g. during the spring bloom) grazer mismatch is important, but within mature ecosystems, for growth to exceed grazing losses, an alternative mechanism is required (Irigoien *et al.* 2005). Many such blooms inevitably disrupt the flow of energy and elements through trophic levels; we use the term harmful algal bloom (HAB) to describe any ecosystem-disrupting bloom. Only certain algal species form blooms and there is no universal explanation in their physiology for their success (Smayda 1997; Irigoien *et al.* 2005). However, they appear intrinsically more capable than other species of producing secondary metabolites (e.g. toxins), structural or other defences (e.g. mucus) that render them less palatable to grazers (Teegarden 1999; Tillmann & John 2002; Irigoien *et al.* 2005) or which adversely affect the growth of competitor algal species (allelopathic interactions, e.g. Legrand *et al.* 2003). Development of such mechanisms is often enhanced by unbalanced growth during nutrient stress (John & Flynn 2002; Cembella 2003; Legrand *et al.* 2003). Importantly, these algae are not always ungrazed; if they are of good nutritional status and thus palatable then they will be grazed, especially from thin algal suspensions where predators may have little choice (Nejstgaard *et al.* 1995; Turner *et al.* 1998). Not only does algal nutrient status affect the likelihood of top-down control of these organisms, but any negative impact on predator growth will decrease nutrient regeneration, further enhancing algal nutrient stress and unpalatability (Flynn & Davidson 1993; Jones & Flynn 2005; Mitra & Flynn 2005). It is this process that forms the basis for the mechanism for HAB development presented here.

The electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2006.0447 or via http://www.journals.royalsoc.ac.uk.

2. MATERIAL AND METHODS

Figure 1 shows a sequence of interactions leading to the formation of a HAB. Here, algal population A_1 grows more rapidly than A_2 ($\mu_1 > \mu_2$), removes more nutrients and is more important as a prey item for zooplankton ($g_1 > g_2$). A_2 is initially palatable and depending on the level of grazing (i.e. if $g_2 > \mu_2$) may not form a bloom at all. However, if nutrient removal by algal activity exceeds addition (from physical processes as well as from bacterial and zooplanktonic regeneration processes, *r*), then algal populations (A_1 and A_2) become nutrient limited. Population A_2 also becomes less palatable and g_2 decreases accordingly (figure 1*b*). Zooplankton continue to consume A_1 and increasingly also each other (g_Z; Flynn *et al.* 1996; Bonnet *et al.* 2004) as community structure changes. Nutrients regenerated primarily via g_1 and g_Z support μ_1 and μ_2, but there is a progressive shift in the fate of this nutrient as A_2 exceeds A_1. Through predatory activity, the nutrients formally within A_1 (figure 1*b*) are shunted into A_2, which forms a large, essentially ungrazed, HAB (figure 1*c*).

To illustrate the dynamics of these events, we have employed a dual nutrient (nitrogen (N) : carbon (C)) predator model with a multi-species prey model developed from that of Mitra (2006). The zooplankton model can, in addition to simulating the normal stoichiometric consequences of feeding on prey of varying elemental composition, display prey switching (variable selectivity) to optimize feeding and also reject prey as quality deteriorates (see figure EA1 of the electronic supplementary material). These capabilities are not typically displayed in zooplankton models, but are of crucial importance in order to simulate the processes correctly. In most experiments, algal nutrient status is not determined, despite its potential to have a profound impact on the interaction (Flynn & Davidson 1993; Jones & Flynn 2005) and promoting deterrence development (Granéli *et al.* 1998; Tillmann & John 2002; Irigoien *et al.* 2005). In the simulated system (Flynn & Davidson 1993; Flynn *et al.* 1996), an outwardly poorly competitive phytoplankter ends up dominating a predator–prey system containing two algal species through it becoming *de facto* a HAB species, disrupting the normal trophic interactions. Additionally, the non-HAB species adversely affects the growth rate of the HAB species through an allelopathic interaction (Davies & Leftley 1985; Flynn *et al.* 1996) described here by a sigmoidal function of the non-HAB species C-biomass.

3. RESULTS

The model correctly simulates the observations that when the HAB species grows alone with the predator, the outcome of the predator–prey interaction differs depending on whether or not the prey exhausts the limiting nutrient. If the prey becomes nutrient-stressed and hence unpalatable, the predator resorts

Received 9 November 2005
Accepted 25 January 2006

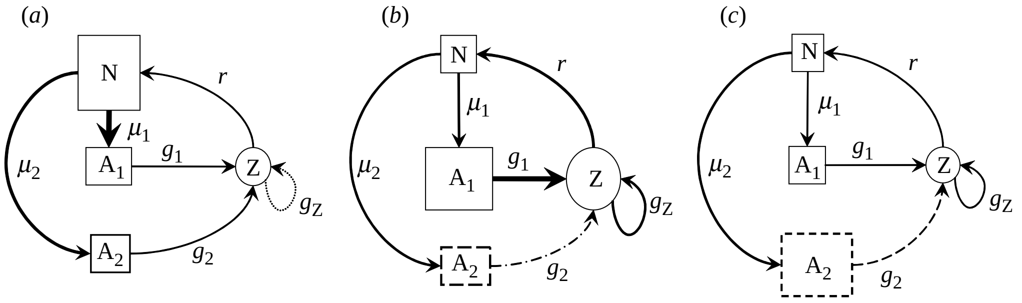

Figure 1. Sequence of interactions in harmful algal bloom (HAB) formation promoted by predator activity. Algal species A_1 and A_2 consume limiting nutrient (N) at rates μ_1 and μ_2 with grazing rates g_1 and g_2, respectively, supporting zooplankton (Z) growth and nutrient remineralization (*r*, including associated bacterial activity) with inter/intra zooplankton grazing rate g_Z. Thickness of arrows denotes relative rate. Decreasing box-line thickness in A_2 denotes decreasing palatability and/or increasing toxicity; size of boxes indicates relative concentration. (*a*) Start conditions. (*b*) Bloom of A_1 (non-HAB species). (*c*) Bloom of A_2 (HAB formation).

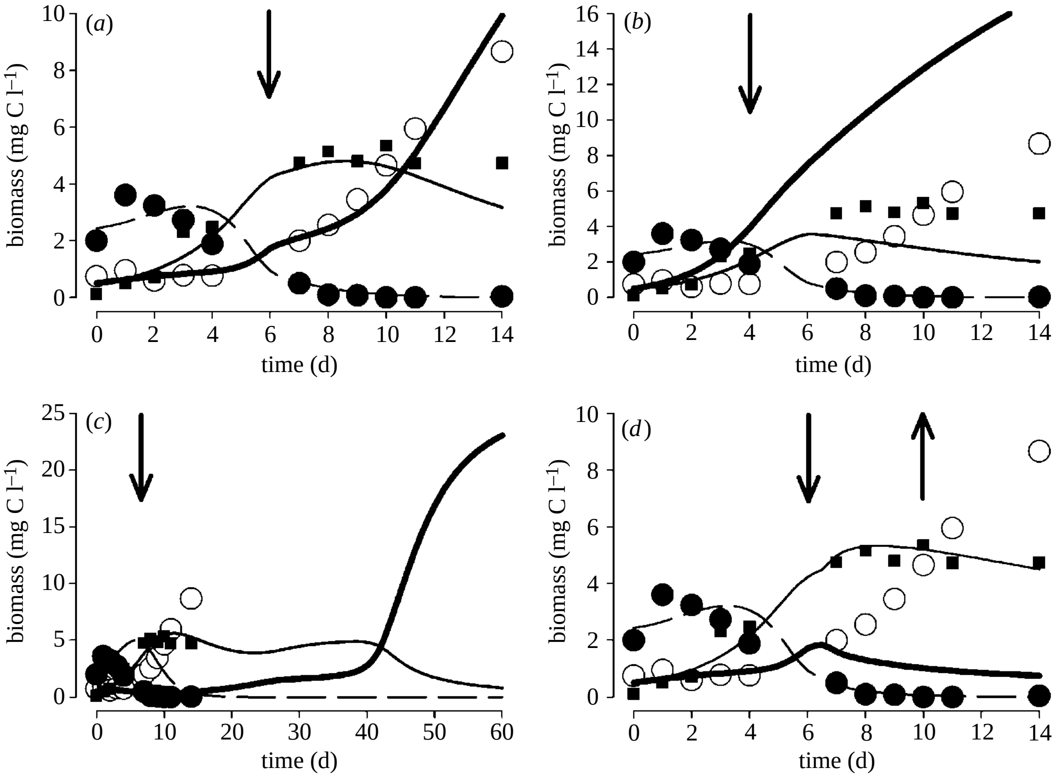

Figure 2. Simulation of interactions in algal bloom formation promoted by predator activity. Experimental data (symbols) and model output (lines) describe the predator–prey interactions. The HAB species (open circles, thick line) becomes unpalatable (harmful) to the predator (closed squares, thin line) when nutrient-stressed and thence not predated. The non-HAB species (closed circles, dashed lines) remains palatable when nutrient-stressed. (*a*) Original fit to data. (*b*) Allelopathic interaction turned off. (*c*) Prey-switching function turned off. (*d*) Prey-rejection function turned off. Down arrows indicate where prey quality (palatability) for the HAB species has declined by 25%; up arrow indicates converse; see figure EA1 of the electronic supplementary material.

to cannibalism and the HAB population is ungrazed (see figure EA2 of the electronic supplementary material).

In the absence of the predator, the non-HAB species may not only outgrow the HAB species, but inhibit its growth (see figure EA3 of the electronic supplementary material; Flynn *et al.* 1996). However, the presence of the predator completely overturns this event (figure 2*a*) by grazing out the non-HAB species, for which it demonstrates a preference. By the time the predator switches to the HAB species, the N-source is exhausted and this prey item is no longer palatable (see figures EA1 and EA4 of the electronic supplementary material). The predator turns to consuming faecal material and cannibalism (cf. figure 1*c*). Nutrients that are remineralized by the predatory activity are used primarily by the HAB species, enhancing its biomass formation (figure 2*a*, cf. figure 1*c*) but critically not its nutritional status as nutrient-demand exceeds supply (N : C, and hence palatability, remains low; see figure EA4 of the electronic supplementary material).

The best fit of the model to experimental data is given by inclusion of descriptions of allelopathy, prey switching and prey rejection linked to prey quality (figure 2*a*). Removal of the allelopathic control of the HAB species prompts an earlier HAB event (figure 2*b*). Removal of prey switching, that normally results in predation being directed primarily towards the most favoured prey item, prompts a later event (figure 2*c*, also see figure EA5 of the electronic supplementary material). However, the most important feature is prey rejection associated with changed algal palatability as nutrient status of the HAB species declines. Removal of this feature results in a failure of the model to simulate the HAB event (figure 2*d*; see figure EA6 of the electronic supplementary material).

4. DISCUSSION

While algal bloom formation requires the decoupling of grazing from phytoplankton growth (Irigoien *et al.* 2005), the impact of grazing deterrence on bloom dynamics has hitherto not been linked to variable nutrient status and hence to the scenario we describe in figure 1. The dynamics of regeneration of the limiting nutrient versus nutrient consumption by algae is critical for bloom formation through this mechanism, as is the role of predators that exhibit prey selectivity and hence the balance of bottom-up versus top-down control (Glibert 1998). Demand for the limiting nutrient must exceed supply (in figure 1*c*, $r<\mu_1+\mu_2$). Thus, the HAB biomass increases but nutrient status and palatability remain depressed (figure 1*b*,*c*). Ironically, a low-competitive advantage in nutrient acquisition by the HAB species would ultimately favour their growth in these circumstances (with nutrient stress occurring at relatively high-nutrient levels) through earlier promotion of the development of grazing deterrents. The initial presence of faster growing, more palatable algal prey can thus actually favour the development of the HAB. Indeed, typically HAB events follow the bloom of non-HAB species (figure 1*b* versus *c*, Smayda 1997; Gobler & Sanudo-Wilhelmy 2001).

Although the importance of the mechanism described here will vary between ecosystems, the basic concept is likely to have universal applicability and not to be confined to just HAB events as typically defined (Smayda 1997). Thus, similar trophic processes would promote the growth of other algal species to give blooms through the development of grazing deterrents under nutrient rate limitation of growth (Irigoien *et al.* 2005). However, for various reasons, the mechanism is most likely to develop under eutrophic conditions in which nutrient ratios are skewed (Officer & Ryther 1980), especially in ecosystems subjected to high N eutrophication where production becomes phosphorus (P) rather than N-limited (Conley 1999). The development of deterrents is commonly promoted by P-stress (Granéli *et al.* 1998; John & Flynn 2002; Cembella 2003) a condition likely to promote the described trophic feedback process more strongly than N-stress; P-regeneration by zooplankton is less likely than N-regeneration (Mitra & Flynn 2005), thus algal demand for P will more likely exceed P regeneration. Allelopathic interactions will be most effective at the high-biomass densities and nutrient stress levels (Cembella 2003; Legrand *et al.* 2003) achieved under such conditions. Larger algal populations also allow for greater prey selectivity by grazers (figure 1*a*, $g_1>g_2$) because of the ready availability of good quality prey of different species during the nutrient-replete phase of bloom growth. Finally, the carrying capacity of the system for zooplankton is more likely to be attained under eutrophic conditions, setting a limit to the concentration of predators and hence to top-down control of algae as zooplankton turn to intra- and inter-guild consumption between and within micro- and meso-zooplankton (g_Z in figure 1, Glibert 1998; Bonnet *et al.* 2004).

It is not just grazing activity that is important here; the heterotrophic activity of the whole microbial loop, consuming the products of the first (non-HAB) bloom, acts as a vector for the transfer of nutrients to the HAB species (figure 1*b*,*c*). Any mixotrophic capabilities (Nygaard & Tobiesen 1993; Martin-Cereceda *et al.* 2003) will further advantage the HAB species, helping to shunt nutrients from the previous non-HAB event into their own biomass. While environmental factors such as temperature (affecting predation and nutrient regeneration), light (affecting algal growth), and the entry of new nutrients into the system, will alter the timing of the event, once the trophic feedback has commenced (figure 1*b*,*c*), the occurrence if not the magnitude of the bloom is assured unless environmental conditions deteriorate significantly.

This work was supported by the Natural Environment Research Council, UK.

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