Resource fluctuation patterns influence emergent properties of phytoplankton assemblages and their resistance to harmful algal blooms

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Abstract. Recent advances in phytoplankton modelling have used species-rich, self-organising assemblages. These models have shown that phytoplankton with complementary life-history traits related to resource exploitation assemble into stable states of lumpy coexistence when resources fluctuate where species' niches occur in clusters along resource gradients. They have also shown that a high degree of competitive dissimilarity between clusters arises, and that this relates to the incidence of monospecific blooms of allelochemical-producing taxa, i.e. some harmful algal bloom (HAB) species. These findings further suggest that the mode (sudden v. gradual changes) under which limiting resources fluctuate plays an important role in determining the emergent properties of the assemblage. For example, productivity, biodiversity and the number of species clusters (and, therefore, resistance to HABs) are all enhanced when switches in resource supplies are gradual, compared with when they are sudden. These theoretical findings, as well as others discussed herein, are of particular interest in watersheds where human activities, such as dam construction, have the capacity to dramatically alter natural-resource fluctuation patterns.

Additional keywords: competition, HABs, inflows, inorganic nutrients, lumpy coexistence.

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Introduction

Many aquatic systems experience alternating periods of reproductive growth limitation where one resource limits productivity during a period of the year and a different resource limits productivity in another (Murrell et al. 2007; Kolzau et al. 2014). In systems influenced by pulsed inflows (Tamvakis et al. 2012; Roelke et al. 2013; Roy et al. 2013; Morse et al. 2014) or wind-driven mixing events (Lares et al. 2009; Hu et al. 2011; Chen et al. 2013), switches between these periods can be sudden. Contrastingly, in systems influenced by slower, seasonally developing wet and dry periods or annually occurring periods of upwelling (Anabalon et al. 2014; Zhou et al. 2014), gradual switching between periods might occur. In the Anthropocene, hydraulically less dynamic systems can result from human activities. For example, construction of reservoirs has led to smaller-magnitude flooding events and extended periods of flow above that of the historical baselines in systems downstream from dams (Magilligan and Nislow 2005; Poff et al. 2007). Such altered flows might cause downstream systems to shift from experiencing sudden to gradual resource-supply switches. Globally, impoundment construction is ongoing in many watersheds (Winemiller et al. 2016) and the question of how such human activities might influence emergent properties of phytoplankton assemblages, most notably the incidence of harmful algal blooms (HABs), is worth exploring.

In the present perspectives paper, we examine classic and recent theories that employ the same mechanistic modelling framework. Our focus is on relationships among resource-supply concentrations (here, inorganic nutrients), the nature of environmental fluctuations (here, driven by quick or slow changes in the resource supply) and emergent properties of phytoplankton assemblages. The emergent properties on which we focus are productivity, biodiversity and resistance to HABs. Some of the more enticing theoretical findings from these modelling studies, and how they might be applied in best management practices, are discussed.

Availability of multiple resources

The influence of multiple resource availabilities in complex biological systems has long been of interest to ecologists and ecosystem scientists. Resources receiving the greatest attention
have been organic carbon (C), nitrogen (N) and phosphorus (P), because those elements are commonly limiting for organisms. Through many decades of study, generalised patterns were realised. For example, terrestrial and freshwater aquatic systems generally show a degree of stoichiometric mismatch between primary producers and consumers, where plants and microalgae tend towards higher C : N and C : P, reflecting primary-producer growth limitation by N and P. In turn, these mismatched C : N and C : P ratios influence the strength of herbivory and the flux of organic matter through foodwebs (Strong 1992; Cyr and Pace 1993; Cebrian 1999; Elser et al. 2000).

Generalised patterns were also learned regarding the N : P ratio. Productivity, species interactions, species composition and diversity, grazing, proliferation of parasites and pathogens, and activity of microbes were all shown to associate with N : P ratio (Sterner and Hessen 1994; Elser and Urabe 1999; Smith 2002; Sterner and Elser 2002; Güsewell 2004). In aquatic systems, and specifically in regards to microalgae, an expansion in the distribution of HABs has been documented, with shifts in the N : P ratio (Smyady 1990; Hallegraeff 1993; Anderson et al. 2002; Fu et al. 2012; Davidson et al. 2014; Gilbert and Burkholder 2018). Mechanisms underpinning HAB proliferation with shifts in the N : P ratio are diverse, and, in some cases, not well understood. Examples where the mechanism is understood include selection towards N-fixing species with N : P decreases where some of the N-fixers are toxic (Smith 1983; Vahtera et al. 2007). Selection towards other toxic species has been observed with N : P increases where the toxic species are able to up-regulate genes responsible for production of P-binding proteins and the enzyme alkaline phosphatase, which aids in the breakdown of dissolved organic P (Harke et al. 2012; Gobler et al. 2016).

Ecological theories for recurrently fluctuating environments

Phytoplankton biodiversity

Just as resource ratios can influence ecosystem form and functioning, so can environmental fluctuation. Focusing again on microalgae, specifically the species of phytoplankton of large water bodies, Hutchinson (1961) wrote on ‘how it is possible for a number of species to coexist in a relatively isotropic or unstructured environment all competing for the same sorts of materials’ (p. 137). In other words, he addressed how it might be possible for so many plankton species to co-exist on so few limiting resources. As suggested by Hutchinson, this ‘paradox of the plankton’ might be solved by considering non-equilibrium systems, or systems that environmentally change, of which he mentioned several drivers of change. These included light and chemical gradients experienced by phytoplankton with vertical turbulent diffusion, symbiotic and commensal relationships among plankton, selective predation, multiple life stages of phytoplankton, and transitory invasion of littoral species into open waters. When considered as biodiversity-sustaining mechanisms, each of these sources of environmental change has limitations regarding how much of the phytoplankton diversity can be explained, as noted by Hutchinson (1961).

However, environmental changes in lakes and coastal-zone systems arising from inflows were not addressed in Hutchinson’s seminal paper. Inflows can have profound effects on species diversity and succession in phytoplankton assemblages, and have long been of interest to aquatic ecologists (Ketchum 1951, 1954; Brook and Woodward 1956). The primary mechanisms acting on phytoplankton during an inflow event include hydraulic displacement of cells, followed by recovery of species at differential rates, and changed ion (conductivity and salinity) and nutrient concentrations differentially influencing species’ growth rates. However, when inflows are periodically recurrent (or at least near-so), they can lead to repeating patterns of environmental fluctuation, particularly with resource concentrations. These resource fluctuations are of great interest as recent theoretical studies suggest that they are foundational to emergent properties of phytoplankton assemblages (Roelke and Spatharis 2015a, 2015b; Sakavara et al. 2018), including their resistance to HABs (Muhl et al. 2018). How this comes about can be mechanistically explained using a surprisingly simple mathematical function embedded into a competition-modelling framework.

Monod equation and R*

Resource concentration can be used to estimate a species’ growth rate when two life-history traits of the species are known, which are the maximum growth rate and the half-saturation coefficient for resource-limited growth. The mathematical function used for this estimation is called the Monod equation (Monod 1950), and it can be embedded into differential equations that depict phytoplankton population and resource concentration change (Box 1). In those equations, the maximum growth rate (μmax) and half-saturation coefficient for resource-limited growth (k50) predict growth rate (μ) instantaneously from the resource concentration (S). The Monod function shows that μ increases practically linearly with increases in S over the low range of S (Fig. 1). At high S concentrations, the Monod function shows μ to asymptotically approach μmax. When the population loss rate is also considered, the concentration of S, above which a population will grow and below which it will decrease, can be predicted. This concentration of S is coined R* (Tilman 1977, 1982; Grover 1997), the point where the summed rate of losses to a population equals the population μ (Fig. 1). The R* can be calculated by assuming that Eqn 1 (see Box 1) equals zero (no population change), substituting μ for the Monod equation, then solving for S.

When considering phytoplankton assemblages, knowledge of species-specific Monod functions and R* values can be embedded into competition models and used to predict competitive outcomes, species succession, and even the incidence of HABs (discussed further below). Competition models take different forms depending on how environmental change comes about. For example, if fluctuation in all resource supplies occurs in-phase and of proportional magnitudes all phytoplankton may be limited by a single resource. Alternatively, if fluctuation in resource supplies occurs out-of-phase or in disproportional magnitudes, over time, multiple resources will likely play a role in phytoplankton growth limitation.

Single resource-limited systems: resource saturation–limitation model

When a single resource is responsible for phytoplankton growth limitation over time, the resource saturation–limitation (RSL)
**Box 1. Equations of the models**

The simple multispecies, multi-nutrient model (Eqn 1, 2) has resources loading from an external source (inflows) and dilution of ambient resources and uniform cell loss to all phytoplankton species (hydraulic displacement). The differential equations have the following form:

\[
\frac{dS_j}{dt} = v(S_{j,\text{Source}} - S_j) - \sum_{i=1}^{n} Q_{S,j} \mu_i N_i (i = 1, \ldots, n) (j = 1, 2)
\]

(1)

\[
\frac{dN_i}{dt} = \left [ \mu_{\text{max},i} \left ( \min \left [ \frac{S_j}{S_j + K_{S,j}}, \frac{S_{j+1}}{S_{j+1} + K_{S,j+1}} \right] \right ) - v \right ] N_i (i = 1, \ldots, n)
\]

(2)

where Eqn 1 is used to determine the rate of resource concentration change for the jth resource (Sj, μM) and Eqn 2 is used to determine the rate of population density change for the ith species (Ni, cells L\(^{-1}\)). In Eqn 1, v is hydraulic flushing (defined as the inflow divided by the system volume (day\(^{-1}\)), S\(_{j,\text{Source}}\) is the concentration of the jth resource (μM) in the source, Q\(_{S,j}\) is the fixed cellular content of the jth resource (μmol cell\(^{-1}\) in the jth species, and \(\mu_i\) is the specific growth rate (day\(^{-1}\)) of the ith species. In Eqn 2, \(\mu_{\text{max},i}\) is the maximum specific growth rate (day\(^{-1}\)) of the ith species, and K\(_{S,j}\) is the half-saturation coefficient for resource-limited reproductive growth (μM) for the ith species and jth resource, ‘min’ is a function that considers only the minimum value of the two Monod functions following the ‘law of the minimum’ (von Liebig 1855, as reviewed in de Baar 1994), and other parameters are the same as previously defined.

Using Eqn 2 and assuming steady-state conditions, meaning Ni is neither growing or declining, S\(_j\) (the amount of unused resources at steady-state for the limiting resource) can be solved for, which is also referred to as \(R^*_j\), as follows:

\[
R^*_j = \frac{v K_{S,j}}{\mu_{\text{max},i} - v}
\]

(3)

The complex multispecies, multi-nutrient model (Eqn 4, 5) is the simple model, with effects of preferential grazing, algal pathogens and self-shading added. The differential equations have the following form:

\[
\frac{dS_j}{dt} = v(S_{j,\text{Source}} - S_j) - \sum_{i=1}^{n} \left [ \mu_i \left ( 1 - \frac{N_{\text{Total}}}{N_{\text{Total}} + \chi} \right ) - \alpha_i m - \frac{N_i}{N_i + \beta} \right ] Q_{S,j} N_i (j = 1, 2)
\]

(4)

\[
\frac{dN_i}{dt} = \left [ \mu_{\text{max}} \left [ \min \left [ \frac{S_1}{S_1 + K_{S1}}, \frac{S_2}{S_2 + K_{S2}} \right] \right ] \right ] \left ( 1 - \frac{N_{\text{Total}}}{N_{\text{Total}} + \chi} \right ) - v - \alpha_i m - \frac{N_i}{N_i + \beta} m \right ] N_i (i = 1, \ldots, n)
\]

(5)

where Eqn 4 is used to determine the rate of resource concentration change for the jth resource and Eqn 2 is used to determine the rate of population density change for the ith species. For these equations, \(N_{\text{Total}}\) is the cell density of all species combined (cells L\(^{-1}\)), \(\chi\) is a coefficient that describes how quickly phytoplankton populations become light limited as the total phytoplankton biomass increases (cells L\(^{-1}\)), \(m\) is the maximum mortality rate coefficient among all species present before self-organisation (day\(^{-1}\)), \(\alpha_i\) is a number between 0 and 1 specific to the ith species (dimensionless), representing vulnerability to grazing, \(\beta\) is a coefficient that describes the efficiency with which a pathogen propagates through a host population (cells L\(^{-1}\)), and all other symbols are the same as previously defined.

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model serves as a competition-modelling framework. In the RSL model, the species with the greatest \(\mu_{\text{max}}\) will have the highest \(\mu\) when \(S\) is high (Fig. 2a). If a uniform loss term is introduced, such as a non-selective grazer or hydraulic displacement from inflows, and resource concentrations remain high, the species with the greatest \(\mu_{\text{max}}\) will eventually competitively exclude other species in the assemblage. At low \(S\), and again applying a uniform loss term, both \(\mu_{\text{max}}\) and \(k_S\) life-history traits can be used to predict the superior competitor. Here, the species with the greatest \(\mu_{\text{max}} / (2 \times k_S)\) (initial slope of the species-specific Monod curve) will have the highest \(\mu\) (Fig. 2a).
The RSL model can be used to illustrate how high species diversity can persist when the system is not at equilibrium; in this case, the concentration of $S$ fluctuates over time. For example, as $S$ goes from high to low concentration, a succession of species will occur. The succession will be from the species with the highest $\mu_{\text{max}}$ through species with intermediate $\mu_{\text{max}}$ and $k_S$ (2 × $k_S$), eventually to the species with the greatest $\mu_{\text{max}}$ and $k_S$ (2 × $k_S$). Succession occurs because negative population growth for a species occurs after its $\mu$ drops below its $R^*$ (the point where the summed rate of losses to a population equals the population $\mu$). This sequence of succession is Species 1 to Species 2 to Species 3 in Fig. 2a. A succession of species will occur in the opposite sequence (Species 3 to Species 2 to Species 1) when $S$ changes from low to high concentration, provided that Species 2 and Species 1 are not locally extinct. When $S$ fluctuates recurrently, that is, going from high to low to high concentrations, and so on, co-existence of many species of varying life-history traits ($\mu_{\text{max}}$ and $k_S$ combinations) becomes possible (Kilham and Kilham 1980; Smayda 1980; Sommer 1989).

**Systems with multiple limiting resources: resource-ratio model**

As mentioned previously, the resource that limits growth changes over time in many systems, limiting the utility of the RSL model. For such systems the resource-ratio (RR) model serves better as a competition-modelling framework. For this, knowledge of a species optimal resource ratio is required. This is defined as the $R^*$ for one resource divided by the $R^*$ for another. The species’ optimal resource ratio influences its resource consumption vector in regards to the two resources. The varied consumption vectors of species comprising an assemblage, in turn, influence the boundaries between resource-ratio regions where one species gains a competitive advantage over others (Fig. 2b). Competitive exclusion will occur should the concentrations of resources remain fixed for an extended period of time. For example, in the assemblage shown in Fig. 2b, Species 1 gains a competitive advantage at a low ratio of Resource 1 to Resource 2 ($S_1 : S_2$). If $S_1 : S_2$ remains low for an extended period of time, Species 1 will exclude the other species. Conversely, Species 3 gains a competitive advantage over other species in the assemblage at a high $S_1 : S_2$. If $S_1 : S_2$ remains high for an extended period of time, only Species 3 will survive. If the resource ratio fluctuates over time, that is, the system is a non-equilibrium system, co-existence of many species in a RR model framework becomes possible (Tilman 1977, 1982; Sommer 1989; Grover 1997). For the assemblage shown in Fig. 2b, a succession sequence will occur from Species 1 to Species 2 to Species 3 as $S_1 : S_2$ changes from low to high. A succession sequence will occur in the opposite order (Species 3 to Species 2 to Species 1) as $S_1 : S_2$ changes from high to low. Co-existence of...
species of varying life-history traits ($\mu_{max}$ and multiple nutrient-specific $k_S$ values) becomes possible when $S_1:S_2$ fluctuation is recurrent. Fascinatingly, when species-rich pools are permitted to self-organise under such fluctuating resource-ratio conditions, the resource gradient still gets partitioned into near-evenly spaced niches, but the distribution of species along the resource gradient is not even. Instead, species organise into a ‘lumpy’ form of coexistence (Sakavara et al. 2018).

**Lumpy coexistence**

‘Lumpy coexistence’ describes an emergent state of biological systems where species’ niches occur in clusters along an environmental gradient (Holling 1992; Scheffer and van Nes 2006; Scheffer et al. 2018). In this state, species comprising a cluster are almost competitive equivalents, with nearly complete niche overlap among members. This results in competitive exclusion rates among members of a cluster being much longer than periods relevant to ecology. For example, in an aquatic system, planktonic exclusion rates might occur over many thousands of days when competitors are near-neutral, whereas other ecological processes important to those competitors, such as grazing, pathogen effects and migration, might occur over periods of days to weeks. Another feature of lumpy coexistence is that competition between clusters is reduced. This occurs because members of one cluster are sufficiently dissimilar from members of another cluster so as to reduce niche overlap between the clusters. Similar to before, this results in exclusion rates between clusters along a resource gradient being much longer than periods relevant to ecology. A combination of the neutrality within clusters and low niche overlap between clusters, the hallmark signature of lumpy coexistence, results in high and stable diversity. The concept is appealing because it reconciles conflicts arising from classic niche theory (Hardin 1960; MacArthur and Levins 1967) and neutrality (Hubbell 2001), accommodating both conceptual frameworks when explaining coexistence and biodiversity (Fig. 3).

The notion that lumpy coexistence is an emergent state of biological systems has been met with skepticism primarily because the first simulations showing species-rich pools self-organising into species clusters were based on the abstract Lotka–Volterra model (Scheffer and van Nes 2006). Since then, the much more mechanistic RR model has been used to show that, indeed, species-rich pools self-organise into species clusters when resources fluctuate (Sakavara et al. 2018). Sakavara et al. (2018) showed that during the period of phytoplankton assemblage self-organisation, the way in which the ambient resource ratio changes over time is influenced by the periodicity of resource-supply fluctuation. This is true regardless of the resource-supply magnitude. Furthermore, Sakavara et al. (2018) showed that some resource-ratio conditions occur much more frequently along the trajectory than do others during the period of self-organisation and species clusters form about these higher-frequency resource-ratio conditions (Fig. 4). Sakavara et al. (2018) went on to show that the emergence of lumpy coexistence is robust over a wide range of resource-loading periodicities, phase differences and magnitudes.

It is unrealistic to attempt to measure the values of $\mu_{max}$ and $k_S$ of all species comprising a natural phytoplankton assemblage. Consequently, it is not practical to directly measure lumpy coexistence on the basis of these life-history traits. However, if we assume that organism size is a proxy for life-history traits and that size distributions of co-occurring species indicate niche partitioning, a practice commonly employed by ecologists (Marquet 2000; Litchman et al. 2007; Maury et al. 2007; Sommer et al. 2017), then there is strong evidence of lumpy coexistence in phytoplankton systems, because it has been observed in both inland and marine systems (Havlicek and Carpenter 2001; Scheffer and van Nes 2006; Segura et al. 2011, 2013; Muhl et al. 2018). Furthermore, the occurrence of lumpy coexistence appears generalisable, because it has been observed in zooplankton, corals reef, bird, beetle and mammal communities (Drost et al. 1992; Holling 1992; Havlicek and Carpenter 2001).

**Emergent properties of phytoplankton in fluctuating aquatic systems**

**Productivity and resource use**

Autotrophic biomass is often used as a proxy for productivity in aquatic systems. How well autotrophs utilise resources for
productivity is reflected in various metrics, which include overyielding and resource-use efficiency (RUE). The productivity of an assemblage relative to the performance of individual species comprising the assemblage when in isolation (monoculture) defines overyielding, where higher values reflect a greater relative resource exploitation by the assemblage (Fridley 2001; Hooper et al. 2005). So, in regards to phytoplankton assemblages, the summed biomasses of all species comprising an assemblage when grown together would be greater than the biomass of the most productive member of that assemblage when grown in monoculture under the same conditions (in this case, overyielding is called transgressive). The RUE is defined by the autotrophic biomass relative to the concentration of the limiting resource, where again higher values indicate a greater ability of the assemblage to exploit the limiting resource (Sheriff et al. 1995; Ptacnik et al. 2008).

Using the RR model and employing recurrently fluctuating resource supplies, recent research has shown that after a period of self-organisation, assemblages are always overyielded (Roelke and Spatharis 2015a) and RUE is high (Smeti et al. 2018). As mentioned earlier, high biodiversity can be sustained when resources recurrently fluctuate. This ensures that species of varied optimal RR survive and enables greater resource exploitation through time by the assemblage. These theoretical findings suggest that in natural systems characteristic of recurrent resource fluctuations, when competition for these resources is the primary assemblage-shaping mechanism, phytoplankton will self-organise into a species-rich assemblage that is better able to exploit resources.

However, observations from natural systems show that resource exploitation by phytoplankton is strikingly different. Whereas we are unaware of attempted measurements of overyielding in naturally occurring phytoplankton assemblages (likely because species-level evaluations of monoculture performance are prohibitively challenging), estimations of RUE are common (measurements of biomass and limiting resource are easy). Comparison of RUE in some natural systems has shown an ~200-fold range (Ptacnik et al. 2008). So, clearly something more than recurrent resource fluctuations and competition is influencing autotrophic production. Other factors are likely to include production limitation by grazing (Gaul and Antia 2001; Katechakis et al. 2002; Winder et al. 2012), pathogens (Bratbak et al. 1993; Fuhrman 1999; Mayali et al. 2008) or light (Townsend et al. 1994; Mellard et al. 2012).

Interestingly, in natural systems, RUE shows a positive relationship with species richness (Ptacnik et al. 2008, 2010; Striebel et al. 2009). However, the relationship varies in strength. For example, in some of the natural-system comparisons, RUE changes with changes in richness are less pronounced when richness is high. This suggests a stabilising effect of richness on RUE (Ptacnik et al. 2008). However, at low richness, RUE changes with changes in richness are more pronounced (Ptacnik et al. 2008). As noted by Ptacnik et al. (2008), factors that impair microbial biodiversity might also affect RUE. Using the RR model and employing recurrently fluctuating resource supplies, Smeti et al. (2018) demonstrated that species richness–RUE relationships reported in Ptacnik et al. (2008) can occur following a species deletion from a self-organised assemblage, where, during assemblage, re-organisation extinction cascades can occur that sometimes lead to reduced RUE.

Resistance to HABs

Competitive dissimilarity within an assemblage is important when examining HABs, as recent research has shown (Muhl et al. 2018). In that study, species’ R* values are plotted in multidimensional space and distances between the HAB species and other species are quantified using the Pythagorean theorem and orthogonal triangles. Muhl et al. (2018) coined the sum of these distances as the allelopathy R* composite distance, where ‘allelopathy’ is appended to the name because the focus is on HAB species that suppress growth of competitors through production of growth-inhibiting chemicals. Through simulation analysis employing self-organised phytoplankton assemblages (from Roelke and Eldridge 2008, Muhl et al. 2018) mapped diversity over ranges of allelochemical production rates and sensitivities to allelochemicals of resident species (see representative simulation, Fig. 5a). From such diversity maps, transition boundaries are obvious where the multispecies assemblage gives way to a monospecific bloom of the HAB species. Assemblages characteristic of steeper transition boundary slopes are more resistant to HABs because they require greater allelochemical production rates or increased sensitivities to allelochemicals before monospecific blooms can occur. Muhl et al. (2018) showed that this assemblage resistance to HABs is positively related to the assemblage’s allelopathy R* composite distance (Fig. 5b), thus elucidating a competition-based mechanism (through RR theory with added allelopathy) that might help explain HAB incidence.
Effect of resource supply-switching mode

As mentioned before, switching between limiting resources in aquatic systems may be sudden or gradual, depending on the physical forcing mechanisms acting on the system. Recent modelling studies have suggested that switching mode in the resource supply is critical to emergent properties of phytoplankton systems, which include biodiversity, productivity and resistance to HABs (see Table 1).

Biodiversity

Regarding biodiversity, simulation analyses have shown that species evenness and diversity are higher in systems characteristic of gradual resource-supply switches than in systems with sudden switches (Roelke and Spatharis 2015a). As reported, this occurs because gradual resource-supply switches lead to slower-changing ambient resource ratios. This, in turn, enables species of intermediate competitive ability to persist in self-organised assemblages. It is further shown that the magnitude of the biodiversity enhancement in gradually changing resource-supply scenarios is influenced by the degree of complementarity in the assemblage (a measure of to-what-extent species are able to utilise resources in the presence of each other, which is a function of the species-specific resource requirements). At high degrees of complementarity, species clusters form only at the extremes of the resource gradient, whereas at low degrees of complementarity, species clusters form across the breadth of the resource gradient (Roelke and Spatharis 2015a; Sakavara et al. 2018). In the former, species richness is reduced because only species with life-history traits enabling superior competitive abilities for one resource survive. In the latter, species richness is higher because species with intermediate competitive abilities co-exist along with species with superior competitive abilities.

Through further simulation analyses of an enhanced RR model (added grazing, pathogens and light factors, see Box 1), Roelke (2018) showed that an interaction occurs among the mode of switching, algal pathogens and self-shading, where much higher species richness and diversity occur when changes in resource loadings are gradual. Regarding pathogens, this finding is consistent with the ‘killing the winner’ hypothesis, where more abundant species experience greater pathogen effects, thereby maintaining higher diversity (Thingstad 2000; Weeks and Hoffmann 2008; Winter et al. 2010). Regarding self-shading effects, when light limitation is high, resources are no longer limiting and so it stands to reason that resource-driven competitive exclusion will occur to a lesser extent.

Productivity

Regarding productivity, simulation analysis of the RR model showed that autotrophic biomass and overyielding are higher in systems characteristic of gradual switches in resource supply (Roelke and Spatharis 2015a). Furthermore, simulation analysis of the enhanced RR model showed that the suppressing effect of grazers, pathogens and shelf-shading on productivity are lessened in systems characteristic of gradual switches in resource supply (Roelke 2018). Here, the slower-changing ambient resource ratios and persistence of species with intermediate competitive abilities allow the assemblage to exploit resources more fully over time. Whereas overyielding has not been studied

![Fig. 5. Using resource-ratio (RR) theory with added allelopathy to relate characteristics of self-organised assemblages to the incidence of harmful algal blooms (HABs). (a) Employing biodiversity maps, here a function of allelochemical production rate and sensitivity to allelochemicals of assemblage members, a transition boundary (red line) is observed where the assemblage gives way to a monospecific bloom of the HAB species. The slope of this line reflects the resistance of the assemblage to HABs that, when plotted against the dissimilarity between the HAB species and the rest of the assemblage, (b) shows a clear ranking, with lumpy assemblages being more resistant to HABs than are neutral assemblages. Intrinsically assemblages, not addressed in the present paper, are the most resistant to HABs. Reproduced from Muhl et al. (2018).](image)
in naturally occurring phytoplankton systems, it has been studied in plant systems. There the development of overyielding is believed to occur as communities mature (Tilman et al. 2001; Cardinale et al. 2007; Marquard et al. 2009), a notion with which these observations from plankton modelling are consistent. As before, model simulations suggested that the degree of complementarity in the assemblage plays a role, where the formation of species clusters only at the extremes of the resource gradient leads to much higher assemblage biomass, but also lower overyielding. This occurs because nearly all members of a self-organised assemblage with a high degree of complementarity perform well in monoculture.

**Resistance to HABs**

In systems characterised by gradual resource-supply switches, resistance to HABs might also be increased. This is likely because the number of species clusters emerging from self-organisation is greater when resource-supply switches are gradual than when they are sudden (Table 1; Roelke and Spatharis 2015a; Sakavara et al. 2018). As described previously, the number of species clusters emerging from self-organisation in fluctuating environments is a function of the resource ratio trajectory during each fluctuation period (Sakavara et al. 2018). The mechanisms underpinning the relationship between resource-ratio trajectory and the nature of the fluctuation (periodicity, phase difference, magnitude, switching mode) has yet to be explored.

**Other emergent properties**

Other attributes of self-organised phytoplankton assemblages influenced by the mode of switching in resource supply include the amount of species interactions, magnitude of resource drawdown, breadth of the resource gradient exploited, and the type of succession pattern expressed over the fluctuation period. As richness is greater with gradual switches in the resource supply than it is with sudden switches, it is not surprising that the amount of species interactions is also greater (Roelke and Spatharis 2015a). However, with self-shading, species interactions are reduced (Roelke 2018). Because biomass is greater with gradual switches in the resource supply than it is with sudden switches, it is also not surprising that the magnitude of resource drawdown is also greater. Interestingly, the breadth of the resource gradient exploited is reduced when resource-supply switches are gradual. This occurs because species with extreme life-history traits do not survive self-organisation as well when ambient resource-ratio change is slower (Roelke and Spatharis 2015a). This is true regardless of the complementarity level. Finally, the alternating succession states observed when resource-supply switches are sudden, which are commonly observed in natural plankton systems (Sommer et al. 1986; Sommer 1989), are not observed when resource-supply switches are gradual. This occurs because species with extreme life-history traits do not survive self-organisation as well when ambient resource-ratio change is slower (Roelke and Spatharis 2015a).

**Table 1. Comparison between emergent properties of phytoplankton self-organised in systems characteristic of sudden and gradual switches in the resource-supply mode when fluctuation periodicity is 365 days**

Numbers shown are the percentage difference in the gradual switching mode relative to the sudden switching mode (positive numbers mean that gradual switching mode is greater). HAB, harmful algal bloom

<table>
<thead>
<tr>
<th>Property</th>
<th>RR model with fluctuating resource supply</th>
<th>With added preferential grazing</th>
<th>With added algal pathogens</th>
<th>With added self-shading</th>
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<tr>
<td>Biodiversity</td>
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<td>Richness (%)</td>
<td>10</td>
<td>14</td>
<td>63</td>
<td>59</td>
</tr>
<tr>
<td>Evenness (%)</td>
<td>22</td>
<td>9</td>
<td>2</td>
<td>–8</td>
</tr>
<tr>
<td>Diversity (%)</td>
<td>26</td>
<td>20</td>
<td>21</td>
<td>31</td>
</tr>
<tr>
<td>Productivity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Biomass (%)</td>
<td>26</td>
<td>28</td>
<td>28</td>
<td>23</td>
</tr>
<tr>
<td>Overyielding (%)</td>
<td>14</td>
<td>9</td>
<td>–7</td>
<td>–104</td>
</tr>
<tr>
<td>HAB resistance</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of species clusters (%)</td>
<td>33</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Competition</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species interactions (%)</td>
<td>12</td>
<td>26</td>
<td>6</td>
<td>–35</td>
</tr>
<tr>
<td>Resource use</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unused Resource 1 concentration (%)</td>
<td>–212</td>
<td>–185</td>
<td>–416</td>
<td>–29</td>
</tr>
<tr>
<td>Unused Resource 2 concentration (%)</td>
<td>–242</td>
<td>–158</td>
<td>–432</td>
<td>27</td>
</tr>
<tr>
<td>Resource gradient used (%)</td>
<td>–5</td>
<td>–14</td>
<td>–1</td>
<td>–25</td>
</tr>
<tr>
<td>Succession</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species sequence</td>
<td>Alternating states (sudden)</td>
<td>Mirror image (gradual)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 2. Hypotheses stemming from recent theoretical research that employs the resource-ratio (RR) model with fluctuating resource supplies

<table>
<thead>
<tr>
<th>Number</th>
<th>Hypothesis</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>The number of species clusters in an assemblage is proportional to the assemblage resistance to take-over by allelochemical-producing bloom species.</td>
</tr>
<tr>
<td>2</td>
<td>The number of species clusters occurring in an assemblage is related to the mode of switching in resource supplies.</td>
</tr>
<tr>
<td>3</td>
<td>With strong algal pathogens or shelf-shading effects, species richness will dramatically increase as resource-supply transitions become more gradual.</td>
</tr>
<tr>
<td>4</td>
<td>Reduced productivity that occurs with preferential grazing, pathogens and self-shading will lessen when resource-supply transitions become more gradual.</td>
</tr>
<tr>
<td>5</td>
<td>Species extinctions strengthen the relationship between biodiversity and resource-use efficiency.</td>
</tr>
<tr>
<td>6</td>
<td>Complementarity must be known before diversity and productivity in recurrently fluctuating environments can be predicted.</td>
</tr>
<tr>
<td>7</td>
<td>Mirror-image succession in plankton will occur when resource fluctuations are gradual.</td>
</tr>
</tbody>
</table>

Discussion

Sociopolitical and economic forces coupled to large human populations have resulted in significant changes to drivers that shape aquatic-ecosystem form and functioning. Often of focus have been hydrological processes and associated loadings or redistributions of sediments, nutrients, salts and pollutants (Schmeller et al. 2018; Shadrin et al. 2018; Nordhaus et al. 2018), or sometimes simply the extreme change in the chemical environment through application of limiting resources (e.g., Sweeney 2014). The way in which aquatic systems experience environmental fluctuation has received less attention. As mentioned in our opening, continued construction of dams worldwide (Winemiller et al. 2016) will lead to hydraulically less dynamic aquatic systems. This will occur because construction of reservoirs leads to smaller-magnitude flooding events and extended periods of flow above that of the historical baselines in systems downstream from dams (Magilligan and Nislow 2005; Poff et al. 2007). In turn, and in regards to systems characteristic of limitation by multiple resources that switch through time, this may lead to a shift from downstream systems being shaped by sudden switches in resource loadings, to systems being shaped by gradual switches.

How resource loadings changing from sudden to gradual switches might affect natural phytoplankton systems can be surmised by comparing emergent properties of simulated phytoplankton assemblages self-organised under these conditions of resource supply. The theoretical work summarised in the present paper suggests that productivity and biodiversity are greater in systems characteristic of gradual switches in resource supply (Roelke and Spatharis 2015a; Roelke 2018), biodiversity is sustained through lumpy coexistence (Sakavara et al. 2018) and is positively related to the resistance of an assemblage to HABs (Muhl et al. 2018), and, consequently, assemblages self-organised under conditions of gradual resource-supply switches are more resistant to HABs because they are lumperier (Table 1; Roelke and Spatharis 2015a; Sakavara et al. 2018). These theoretical observations provide fundamental and mechanistic insights into the form and functioning of phytoplankton systems.

The theoretical work presented here also suggests intriguing relationships between resource-loading switching mode and the stability of ecosystem functions. The influence of algal pathogens and self-shading on phytoplankton richness was much greater when resource-loading switches were gradual (Roelke 2018). With an increased species richness, an increased stability of ecosystem function is expected, especially in regards to productivity (Ptacnik et al. 2008, 2010; Striebel et al. 2009). Indeed, the theoretical results summarised here show that the production-suppressing effects of common plankton processes, i.e., grazing, pathogens and self-shading, were lessened when resource-loading switches were gradual (Roelke 2018).

There are other ecological principles suggested by the theoretical research summarised here as well. These are as follows: the strength of the RUE relationship with species richness increases following local species-extinction events (Smeti et al. 2018); complementarity among members of an assemblage strongly relates to how productivity and biodiversity will respond to altered modes of resource-supply switches (Roelke and Spatharis 2015a), and ‘mirror-image’ succession might result following a change from sudden to gradual switching modes in resource loadings (Roelke and Spatharis 2015b).

All of these theoretical findings are intriguing notions (summarised in Table 2), because they would increase fundamental understanding of not just plankton systems, but terrestrial plant systems as well. They also elucidate a path for future research aimed at development and field-testing of best management practices attempting to maintain or improve environmental quality, e.g., lessening the impact or even circumventing HABs. Whereas it is unrealistic to manage the environmental fluctuation regime of large systems, managing smaller water bodies is realistic (e.g., see Lundgren et al. 2013; Grover et al. 2017). Smaller water bodies would include embayments and coves characteristic of limited water exchanges with adjacent larger systems. In the case of HABs, if invasion of the HAB species could be prevented into smaller water bodies, then these embayments and coves might serve as refuge habitat and accelerate ecosystem recovery after HABs subside. If the smaller water body is the source of HAB species propagation, then the HAB might be prevented altogether. There is much empirical testing of the notions listed in Table 2 that needs to occur. In addition, testing of how recurrently fluctuating resource supplies and modes of resource-supply switching interact with other factors common to the Anthropocene, such as eutrophication, salinification, pollution and climate change, is needed.
Conflicts of interest
The authors declare that they have no conflicts of interest.

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References


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