# Predictability of plankton communities in an unpredictable world

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## SUMMARY

1. Plankton ecology contributes significantly to ecological theory building, because plankton organisms are relatively easy to manipulate and have short generation times and a relatively small set of traits making them an ideal experimental model system for addressing both general ecological questions as well more system-specific questions.

2. Since the environment is changing at an unprecedented rate, there is an ongoing demand for predictions from plankton ecology on the consequences of global change.

3. In 2010, a colloquium was held on three subjects: chaos versus predictability in plankton dynamics, global patterns versus regional differences in plankton dynamics and climate-induced changes in plankton dynamics.

4. Papers in this Special Issue propose a new model of plankton dynamics under climate change in different climate zones; offer increased attention to the role of winters in resetting population dynamics; discuss the effects of climate change on ecological stoichiometry and efficiency of trophic transfer; describe the relative and interacting effects of changes in temperature and hydrology on plankton; and analyse the effects of climate change on host–parasite dynamics.

5. Important research gaps include increased monitoring of understudied climatic zones, adaptation of plankton organisms to altered environmental conditions, interactions of climate change with legacy nutrients, interactions with other anthropogenic pressures and interactions with the infochemical network.

*Keywords*: Anthropocene, global change, plankton dynamics, plankton periodicity, seasonality

## Introduction to the special issue

Plankton ecology is a core discipline of limnology and marine biology and encompasses all aspects of the interactions that determine the abundances and distribution of plankton organisms. Since plankton plays a central role in the functioning of open-water systems, and worldwide the environment is changing at an unprecedented rate, an interesting challenge lies ahead in assessing how seasonal plankton dynamics will alter in the light of global change. Therefore, we brought together creative minds in plankton ecology in a colloquium 'Predictability of Plankton Communities in an Unpredictable World' to invoke discussion on three subjects: chaos versus predictability in plankton dynamics, global patterns versus regional differences in plankton dynamics and climate-induced changes in plankton dynamics. The meeting was held in Amsterdam from the 7th to the 9th of April 2010, as a SIL (Societas Internationalis Limnologiae) – Plankton Ecology Group activity, under the auspices of the Royal Dutch Academy of Arts and Sciences (KNAW). This special issue is composed of the proceedings of the meeting and addresses many aspects of plankton ecology in a changing world. The majority of the contributions are related to climate change, but climate change is only the tip of the iceberg of the human impacts on the Earth system (Steffen *et al.*, 2011). Human activity is a major factor in altering the landscape (Price *et al.*, 2011), and over the past few centuries, its impacts on the global environment have escalated to such an extent that Earth's ecosystems depart significantly from their trajectories in a world without humans (Crutzen, 2002). Recently, the

formal geologic term *Anthropocene* has been proposed, marking the significant human global impact on the Earth's ecosystems (Crutzen, 2002).

One important consequence of this human activity has been an increase in the frequency and intensity of harmful algal blooms in continental fresh and coastal marine waters worldwide (Van Dolah, 2000; de Figueiredo *et al.*, 2004; O'Neil *et al.*, 2012). Dinoflagellate blooms appear to have caused death of birds and fish from the late Pliocene, 3.5 to 2 million years ago (Emslie *et al.*, 1996). In fact, global warming events corresponded with all five mass extinctions in the Phanerozoic eon (Mayhew, Jenkins & Benton, 2008; Castle & Rodgers, 2009), and the current-day link between harmful algal blooms and warming has led to the hypothesis that toxin-producing algae played a major role in each of the five mass extinctions (Castle & Rodgers, 2009). Toxic cyanobacterial blooms are suspected of having caused the mass death of a large Pleistocene mammal assemblage (Braun & Pfeiffer, 2002), and also in recent times, many cases have been described of animal deaths associated with cyanobacterial blooms (e.g. Francis, 1878; O'Donoghue & Wilton, 1951; Stewart, Seawright & Shaw, 2008). Eutrophication is considered the major driver of recent increases in harmful algal blooms (Smith & Schindler, 2009). Climate change is expected to further aggravate directly and indirectly these symptoms of eutrophication (Paerl & Huisman, 2008; Moss *et al.*, 2011; de Senerpont Domis *et al.*, 2013b).

## Contributions to the special issue

The seasonal succession of plankton organisms in lakes from the arctic to the tropics was analysed in this issue by de Senerpont Domis *et al.* (2013b), who built on the traditional PEG model (Sommer *et al.*, 1986) and its recent modifications (Sommer *et al.*, 2012). Their paper includes predicted climate change scenarios for the various climate regions. The review concludes that warming-induced increases in nutrient loading, enhanced water column stability and shifts in the fish community structure can alter food-web functioning and trophic transfer by increasing the number of bacterivores, enhancing the risk of cyanobacterial dominance and shifting the zooplankton community to small-bodied zooplankton. This is further corroborated by Özen *et al.* (2013), who showed that nutrient enrichment and warming act together to have a stronger effect on microbial, phytoplankton and zooplankton communities than either of them alone. More specifically, nutrient enrichment and warming led to higher bacterioplankton, phytoplankton, heterotrophic nanoflagellates and rotifer biomass (Özen *et al.*, 2013).

An important caveat in the original formulation of the PEG model was the assumption that winter effectively resets the plankton dynamics in temperate lakes. Climate change research has improved our understanding of the role winter conditions play in setting the stage for the following seasons. Mild winters, associated with a positive value of the North Atlantic Oscillation, positively influence the abundance of some overwintering species, such as the copepod *Eudiaptomus* (George, 2000). In their analysis of 205 small, mainly oligotrophic Swedish lakes along a latitudinal gradient, Weyhenmeyer, Peter & Willen (2013) found that the duration of the ice-free period was best related to phytoplankton species richness and biomass.

There is evidence that higher temperatures promote the share of cyanobacteria in the phytoplankton (Kosten *et al.*, 2012), which might be explained as a direct temperature effect on growth rates, as it has been hypothesised that at higher temperatures, growth rates of eukaryotic taxa decline, whereas cyanobacterial growth rates reach their optima (Paerl & Huisman, 2008). However, Lürling *et al.* (2013) revealed that, based on the literature data and a controlled experiment with eight cyanobacteria and eight chlorophytes, optimum growth temperatures and growth rates at the optimum temperature were similar for both cyanobacteria and chlorophytes. Nonetheless, extrapolation from laboratory cultures to nature should be made critically unless the experiments include the complete species assemblage of interest (Lehman & Sandgren, 1985) and the factors that promote/control cyanobacterial blooms in freshwater ecosystems. de Senerpont Domis *et al.* (2013a) exemplified this with a population-level study indicating that the combined effect of toxic cyanobacteria and warmer temperatures on *Daphnia* populations might be additive rather than synergistic.

Changes in hydrology, rather than temperature, may determine cyanobacterial dominance. Romo *et al.* (2013) pointed out that water residence time, as influenced through precipitation, can control seasonal dominance, toxicity and colony size of noxious *Microcystis aeruginosa* in a Mediterranean lake. The contribution of Segura *et al.* (2013) confirms these observations: their mechanistical model shows that, compared to other functional groups, the competitive ability of large cyanobacteria with gas vesicles was highest under low flushing rates.

Anthropogenic activity has already increased atmospheric $CO_2$ by more than 100 $\mu$atm (Tyrrell, 2011). In a laboratory mesocosm study, Verschoor *et al.* (2013) demonstrated that elevated atmospheric $CO_2$ concentrations have the potential to relieve phytoplankton

communities from carbon limitation, and the concomitant shift towards nutrient limitation (N, P) drives changes in phytoplankton community structure. The altered biochemical composition of the phytoplankton reflected in changed C : P and C : N ratios (Verschoor *et al.*, 2013) could also affect energy flow over the phytoplankton–zooplankton boundary and reduce zooplankton growth (Lürling & Van Donk, 1997; van de Waal *et al.*, 2009). The effects of stoichiometric alterations might spread via changed plankton community composition to higher trophic levels (van de Waal *et al.*, 2009).

At higher trophic levels, planktivorous fish might strongly shape plankton communities through size-dependent predation (Brooks & Dodson, 1965; Carpenter *et al.*, 2001). These fish appear to exert stronger top-down forcing in lakes than initially projected in the PEG model (Sommer *et al.*, 2012). In temperate lakes, fish predation may be high even in winter (Jeppesen *et al.*, 2004). In warmer climate and low latitude lakes, early and enhanced reproduction of fish results in strong predation pressure on large-bodied zooplankton and thereby promotes turbid water (van Leeuwen *et al.*, 2007; Meerhoff *et al.*, 2007; Jeppesen *et al.*, 2010). Lacerot *et al.* (2013) provided experimental evidence for an uncoupling of the phytoplankton–zooplankton interaction in a subtropical pond, even in the absence of fish predation. The contribution by Wagner *et al.* (2013) on warming-induced changes in trophic coupling between the key herbivore *Daphnia* and both a vertebrate and invertebrate predator further underlines the importance of a mechanistic understanding of temperature-driven changes in trophic interactions.

Whereas the role of planktivorous fish in shaping plankton communities through effects on the more vulnerable large zooplankton has received considerable attention, far less information exists on the role of parasites in shaping plankton communities (Decaestecker *et al.*, 2005; Ibelings *et al.*, 2011). Gsell *et al.* (2013) demonstrated that parasite (the fungal chytrid *Zygorhizidium planktonicum*) growth and invasion success are not solely controlled by host density (the diatom *Asterionella formosa*), but that environmental variability affects parasite transmission. This particular host–parasite system formed the basis for an eco-epidemiological model including dependence of parasite reproduction on host nutrient status (Gerla *et al.*, 2013). The modelling exercises showed that host–parasite cycles may be a prominent feature in plankton communities, but also that parasite populations may collapse suddenly (Gerla *et al.*, 2013).

Accelerated human activities in the 20th century have resulted in damming of rivers, construction of reservoirs and creation of small impoundments (Rosenberg, McCully & Pringle, 2000; Havel, Lee & Vander Zanden, 2005; Downing *et al.*, 2006). Many of these standing waters suffer from an over-enrichment of the water with nutrients (Smith & Schindler, 2009) that has increased the incidence and intensity of harmful algal blooms (de Figueiredo *et al.*, 2004). Those blooms form only when building blocks (e.g., light, nutrients) to fuel their proliferation are sufficient, and concomitantly, the energy transfer at the algae–grazer interface is blocked. In general, high-density cyanobacteria blooms imply that the founder population was successful in avoiding their main predators along with their main competitors, that is, faster-growing phytoplankton species. Understanding the factors that determine the abundance and distributions of nuisance phytoplankton is one of the main research themes within the field of plankton ecology.

Inasmuch as the current world population is projected to reach 9.3 billion in 2050 and more than 10 billion in 2100 (United Nations, 2011), there is no reason to assume that ongoing changes will soon reverse. In contrast, the blend of techno-demographic growth and climate change will demand more water, food and energy (Meybeck, 2003). Hence, anthropogenic drivers such as demographic growth, agriculture, industrialisation, urbanisation and water engineering will continue to stimulate the creation of stagnant waters and eutrophication. Thus, we predict that the incidence and intensity of such harmful algal blooms will further increase in near future (Fig. 1). However, probably here our predictive capacities end. It might be virtually impossible to predict the composition of future plankton communities, because of innumerable unknown factors creating the unpredictable world. We should realise that communities are abstractions made for our own convenience, but that selection takes place at the level of the individual. Here, the new environmental factors will select for individuals tolerant to these new conditions and open niches for invading organisms.

As Ellis, Antill & Kreft (2012) pointed out, 'humans appear to have altered plant species richness in regional landscapes by causing moderate loss of native species coupled with related but larger gains in exotic species, mostly by invasions'. Instead of focusing on plankton community composition of which predictability might be poor in systems in transition, we can predict effects on processes far more accurately (Moss *et al.*, 2011). Indeed, Bauer, Sommer & Gaedke (2013) indicated that knowledge on internal feedback mechanisms can make plankton succession more predictable.
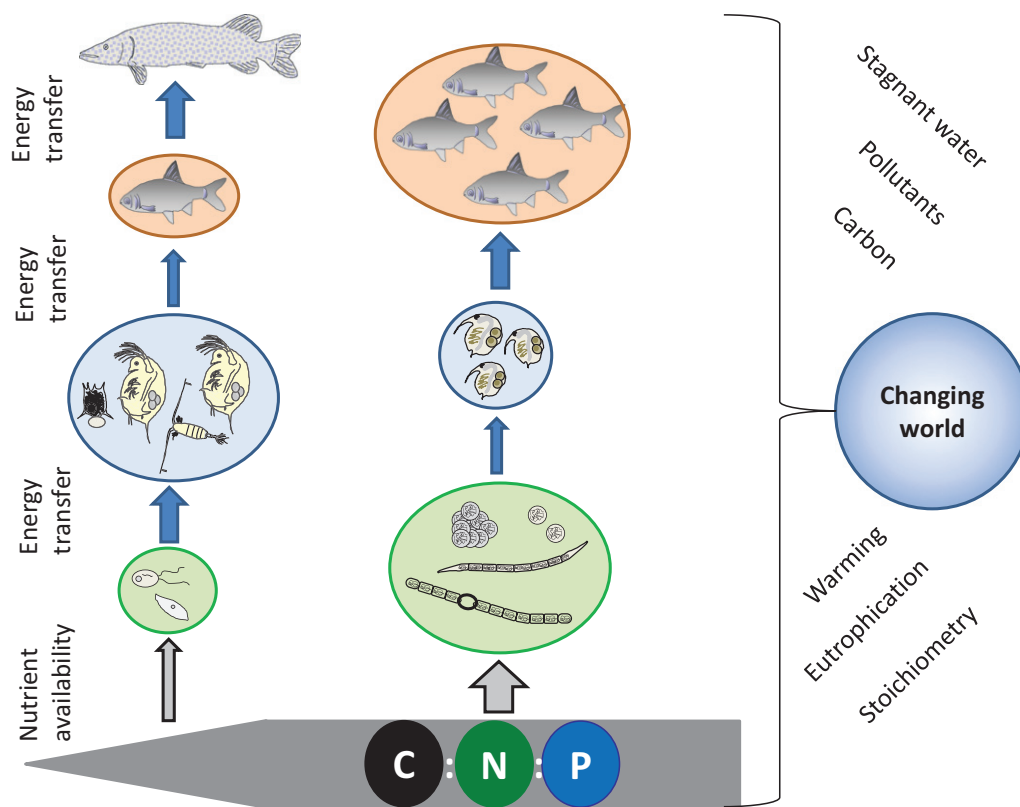
**Fig. 1** Key factors resulting from anthropogenic activities in a changing world (right) causing changes in trophic state, structure and energy flow in a simplified, schematic pelagic food chain.

## The virtual supplement to this special issue: key earlier contributions to the topic

*Freshwater Biology* has published several key papers on plankton dynamics, which are freely available at http://bit.ly/VI2012 in association with this special issue. A precursor for this introductory paper was written by Harris (1994), who pointed out the problems underlying the predictability of plankton dynamics, including chaos, complex dynamics and nonlinear interactions. The seminal paper by Reynolds (1984) brought a deeper understanding on the role that phytoplankton functional traits play in determining periodic cycles in temperate lakes and thus paved the way for the contributions of de Senerpont Domis *et al.* (2013b) and Segura *et al.* (2013) in this issue. Freshwater food webs seem to be characterised by high levels of redundancy making it more important what species do rather than who they are (Woodward, 2009). With their morphological classification based on 700 species from 200 lakes across multiple climate zones, Kruk *et al.* (2010) made a compelling first step towards capturing functional variation in phytoplankton (Reynolds, 1984). Implementation of such a morphology-based function grouping into a mechanistic model accurately predicted seasonal succes-

sion of a subtropical lake (Segura *et al.*, 2013). Such a trait-based approach can be useful for zooplankton communities as well (Barnett, Finlay & Beisner, 2007).

One of the first papers to acknowledge the role that climate change can play in determining plankton dynamics was George *et al.* (1990). Through the seminal work of this group on climate warming, we also gained a better understanding of the link between winter conditions and plankton succession (George, 2000), allowing plankton ecologists to revise their paradigm on the winter as a period of resetting of biomass. Adrian *et al.* (1999) showed that after milder, wetter winters, several plankton species advanced the timing of their peak biomass. The study by Romare *et al.* (2005) on deep Lake Washington showed that milder winters are associated with a larger overwintering *Daphnia* community and early onset of population increase in spring. In shallow lakes, the effect of winter conditions on plankton succession seems to be short-lived, as a result of low heat storage capacity, and is soon overtaken by prevailing weather conditions and biotic interactions (Adrian *et al.*, 1999). However, the study by Hülsmann *et al.* (2012) showed that the effect of winter conditions can be nuanced; while not affecting the population peak of *Daphnia* in spring, milder winters did reduce the contribu-

tion of resting eggs to population development, which may alter the genetic composition of populations.

The interplay between climate change and changes in nutrient loading, and the problems associated with disentangling these effects when looking at plankton time series, was addressed by George *et al.* (1990), Anneville, Gammeter & Straile (2005) and Battarbee *et al.* (2005). Mesocosm experiments looking at the combined effect of nutrient loading and warmer temperatures provide a more mechanistic understanding of how these different pressures act upon aquatic systems (Mckee *et al.*, 2002; Liboriussen *et al.*, 2011).

## Further research on plankton dynamics

Long-term monitoring will remain essential in determining climate impacts on plankton dynamics. Interregional comparisons are needed; temperate areas will not simply change to resemble present-day tropical systems, which themselves do not experience 'eternal summers', but are subjected to strong seasonalities, and which might change at rates even faster than predicted for higher latitude regions. Certainly, plankton organisms could adapt to changes in their environment, which more plastic species might do faster than others. Whether such adaptation will help plankton in surviving predicted catastrophes (high salinities, complete drying-up of waters) remains to be seen. Besides monitoring and adaptation, we can also identify a few other urgent research gaps.

### Legacy effects

Past excessive agricultural applications of manure and fertilisers have over-enriched phosphorus in catchment soils that may continue to be a major source of phosphorus to surface waters for hundreds of years (Carpenter, 2005; Keatley *et al.*, 2011). How altered climate conditions will interact with this legacy requires intensive research. A complication will be that the interplay between legacy and present-day physicochemical forcing might differ among lakes, thereby leading to different responses of the plankton communities to changes in climate (Roberts *et al.*, 2004).

### Interaction between anthropogenic pressures

Since the onset of the chemical revolution, the global environment has been loaded with pollutants like heavy metals and a myriad of synthetic chemicals, such as polychlorinated hydrocarbons, pesticides, plasticisers and surfactants. Environmental factors, such as high temperature, low oxygen concentration and high or low pH, can influence the effects those chemicals exert on plankton organisms (Holmstrup *et al.*, 2010). For example, cadmium toxicity to *Daphnia magna* was increased at higher temperatures (Heugens *et al.*, 2010), while carbaryl and low oxygen levels had synergistic effects on *Daphnia pulex* (Hanazato & Dodson, 1995). A synergistic effect between the natural stressor and the toxicant was observed in almost 80% of studies that included heat stress and 60% that included oxygen depletion (Holmstrup *et al.*, 2010). Hence, stronger synergistic effects of toxicants and changed environmental conditions might be expected in the near future. However, the magnitude of synergisms probably depends on a complex of changing factors, such as synthetic chemical production, discharge, persistence, hydrology, plankton organisms' sensitivity and climate effects on physiological processes, where, for example, higher temperature might result in higher toxicant uptake, but also in increased detoxification and elimination rates. How this complex changing environment might influence the abundance and distribution of plankton poses a key challenge to scientists from ecology and toxicology.

### Infochemistry

Organisms intensively use chemical messengers to locate food, find a mate, recognise close kin, mark a territory and detect enemies. The sea of chemical messengers forms a complex infochemical web that includes both chemically mediated trophic and indirect non-trophic interactions. Hence, infochemicals influence the temporal and spatial distribution of organisms creating a tight connection between the information network and food-web functioning (Dicke, 2006). In planktonic bi- and tritrophic food chains, infochemicals played a major role in stabilising dynamics preventing extinctions on higher trophic levels (Verschoor, Vos & van der Stap, 2004). Alterations in environmental conditions (pH, salinity, humic acids, temperature, etc.) could influence the natural chemical information networks by affecting synthesis and excretion of messenger molecules, as well as the chemical characteristics of the messengers. How climate changes might influence the intricate aquatic infochemical network is difficult to predict. More research is needed to resolve the chemical nature of messenger molecules and study their fates under altered environmental conditions.

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