nature

NEWS & VIEWS

ECOLOGY

Production in pristine lakes

Jonathan J. Cole

An investigation of lakes in Sweden has delivered results that run counter to the idea that primary production is generally limited by the availability of nutrients. There are lessons for limnologists in this.

On page 506 of this issue, Karlsson *et al.*[1] show that, in lakes, the primary production of algae and the growth of bottom-dwelling (benthic) invertebrates and fishes is not controlled by nutrients. Rather, the determining factor is the light climate, which is itself determined by dissolved organic matter from the watershed. This conclusion is both intriguing and likely to prove controversial.

Primary production is the rate at which organic matter is synthesized from raw materials — carbon dioxide, water, inorganic nutrients — and light energy, and forms the base of the food web in most environments. In aquatic systems, excessive primary production — known as eutrophication and taking the form of algal blooms — has a host of undesirable effects, including bottom-water anoxia, loss of fish species and large-scale production of algal toxins[2]. The main cause of eutrophication in lakes is the input of phosphorus and nitrogen, which tend to be the limiting nutrients in that demand for them by algae often exceeds supply[3,4]. If you add enough phosphorus and nitrogen, most lakes will experience blooms. If the nutrient input is reduced, these blooms abate.

In lakes with modest to high nutrient levels, there is also a good correlation[5] between total phosphorus (TP) and the amount of algal biomass (which is usually expressed in terms of the concentration of the photosynthetic pigment, chlorophyll *a*; this is not a direct measure of primary production but makes for a good surrogate). The TP–chlorophyll correlation is driven by the fact that phosphorus is usually the primary limiting nutrient: unless there are other complications, such as deep mixing or food-web changes, much of the available phosphorus is assimilated by algae.

All in all, there is firm evidence on multiple scales and using multiple approaches[4] that nutrients control eutrophication. But what is the story for lakes in the pristine, low-nutrient (oligotrophic) state? When nutrients are added, not only does primary production increase, but the entire community of primary producers and consumers is also altered, often drastically. Thus, nutrient additions stimulate primary production and select for species that respond to nutrients. The question here is what limits the ambient community in nutrient-poor lakes.

JENNY ASK

Figure 1 | Clear difference. This example of a subarctic lake is nutrient-poor but productive because of a high-light climate stemming from the clear and shallow water[1].

The somewhat surprising answer to emerge from Karlsson and colleagues' study[1] is that the light climate, and not nutrients, is the main factor controlling both primary production and secondary production of benthic invertebrates and fishes in pristine lakes (Fig. 1). Furthermore, the light climate is controlled largely by the input of highly coloured dissolved organic matter (CDOM) that enters lakes from surrounding forests. This organic matter, rich in dark-brown humic substances, gives lake water its characteristic tea-like colour, which can be very weak in some lakes but extremely dark in others.

So what limits productivity in nutrient-poor lakes, according to Karlsson *et al.*, is the input of dissolved organic matter from the surrounding watershed. Their evidence comes from a well-crafted correlation analysis of a series of 12 Swedish lakes that varied in CDOM and nutrients. Neither primary production nor the secondary production of fishes or invertebrates was positively correlated with nutrients; all were inversely correlated with the fraction of surface light that reached the mean depth of the lake, a combined effect of CDOM and depth.

Why this difference? There are strong correlations between nutrients and primary production (or rather chlorophyll *a*) and fish biomass[6] in lakes in general. But the conclusion of this new study[1] is that the absorbance of light by CDOM is the limiting factor.

Karlsson *et al.*[1] point out that many lakes are small, nutrient-poor, rather shallow and have significant amounts of benthic primary production in addition to the phytoplankton production that occurs in the open water above the lake bottom. Indeed, globally, most lakes are like those studied here rather than the high-nutrient lakes that dominate most TP–chlorophyll data sets. Moreover, the TP–chlorophyll relationship includes only the planktonic component, and that just in the surface water. The strength of the relationship is driven largely by eutrophic lakes — lakes with high TP, such as those already experiencing anthropogenic eutrophication. For pristine lakes there is much more variation in CDOM than there is in TP (ref. 7). Unless there is some large external input of phosphorus, CDOM will explain more of the variation in primary production than will TP.

Should we thus conclude that we need not worry about nutrient inputs to lakes? The answer is 'no'. If large amounts of nutrients were added to oligotrophic lakes, the lakes would, in all likelihood, also experience algal blooms, as do other humic lakes[8,9]. The study[1] does suggest that the anthropogenic and climatic factors that are affecting the concentrations of CDOM in many parts of the world[10] will probably have an effect on primary production in small lakes. But although the authors' conclusions are both bold and reasonable, the data come from only a handful of lakes, and all of them in Sweden. The idea that light and CDOM limit primary production will remain controversial until it is tested against a larger and more diverse array of lakes.

There are, however, lessons for limnologists in this paper. Pay attention to CDOM. Consider both benthic and pelagic production of the whole lake (not just the surface water). And do not assume that the well-known principle of nutrient limitation[11] can be applied in general — most of the world's lakes contain only low quantities of both nitrogen and phosphorus, and many have lots of CDOM. ■

Jonathan J. Cole is at the Cary Institute of Ecosystem Studies, Millbrook, New York 12545-0129, USA.
e-mail: colej@caryinstitute.org

1. Karlsson, J. *et al. Nature* **460,** 506–509 (2009).
2. Rabalais, N. N., Turner, R. E. & Wiseman, W. J. Jr *Annu. Rev. Ecol. Syst.* **33,** 235–263 (2002).
3. Likens, G. E. *Limnol. Oceanogr. Spec. Symp.* **1,** 1–328 (1972).
4. Smith, V. H. in *Successes, Limitations, and Frontiers in Ecosystem Science* (eds Pace, M. L. & Groffman, P. M.) 7–49 (Springer, 1998).
5. Smith, V. H. *Limnol. Oceanogr.* **27,** 1101–1111 (1982).
6. Hanson, J. M. & Leggett, W. C. *Can. J. Fish. Aquat. Sci.* **39,** 257–263 (1982).
7. Carpenter, S. R., Cole, J. J., Kitchell, J. F. & Pace, M. L. *Limnol. Oceanogr.* **43,** 73–80 (1998).
8. Schindler, D. W. *et al. Proc. Natl Acad. Sci. USA* **105,** 11254–11258 (2008).
9. Smith, V. H. & Schindler, D. W. *Trends Ecol. Evol.* **24,** 201–207 (2009).
10. Monteith, D. T. *et al. Nature* **450,** 537–540 (2007).
11. Sterner, R. W. *Int. Rev. Hydrobiol.* **93,** 433–445 (2008).

QUANTUM MECHANICS

Hidden context

Boris Blinov

The idea that physical phenomena might be described by a more down-to-earth theory than quantum physics has met with resistance from many physicists. Indeed, it seems that nature is not as simple as we would like.

Quantum mechanics is weird, there is no doubt about that. Efforts to demystify this theory and reconcile it with the laws of classical physics have led to the development of theories of hidden local variables — the hypothetical parameters of a quantum system that govern the seemingly random outcomes of quantum measurements. As it turns out, these theories require quantum mechanics to be non-contextual: the results of measurements on a quantum system should not depend on the act and specific properties (the context) of the measurement process itself; they should be set prior to it. But on page 494 of this issue, Kirchmair and colleagues[1] report the results of an experiment on a system of trapped ions and demonstrate that quantum mechanics conflicts with non-contextuality regardless of the quantum state of the system. This is a significant advance, coming on the heels of recent tests of quantum contextuality performed with photons[2] and neutrons[3] in very special quantum states.

The concept of non-contextuality can be understood in simple terms. Imagine you shake a pair of dice in a cup and then flip the cup bottom-up on a table. The dice are hidden from you, but they have stopped rattling around and the values of their top faces are now set. These values are random (given that the dice are fair), but from the moment you place the cup on the table they are fixed (Fig. 1a). If you now remove the cup and see the outcome, it will be the same as the value hidden inside the cup (Fig. 1b). You could do the same exercise tomorrow, or you could look at one die first and at the other die next, or vice versa, and the outcome would still be the same. This 'classical' measurement process is thus non-contextual.

But 'quantum dice' behave differently. Until the moment you observe them, the values of the quantum dice are not set, even though they have stopped rattling. The top face of each die is a superposition of the one-, two-, three-, four-, five- and six-dot faces (Fig. 1c). It is only when the cup is removed and the quantum dice are observed that a certain value is assigned to the top face (Fig. 1d). What's more, the observed values depend on the way you measure their states — that is, on how you look at them: it may be different if you look at the dice one after another or at the same time. The values are revealed only in the particular context of the measurement.

The celebrated Bell's inequality[4], the violation of which by quantum systems has been used to refute hidden-variable theories, requires the preparation of a very specific quantum state called the entangled state. But, in general, other types of quantum state (there are many!) do not violate this inequality. A definitive test of non-contextuality would involve demonstration of the violation of a Bell-like inequality for any quantum state, not just the entangled state. Such a test entails many more sequential operations and measurements on the quantum states than Bell-inequality tests. Moreover, the measurements themselves must be compatible, which means that they must be done simultaneously or, if done sequentially, should be unaffected by the order in which they are performed.

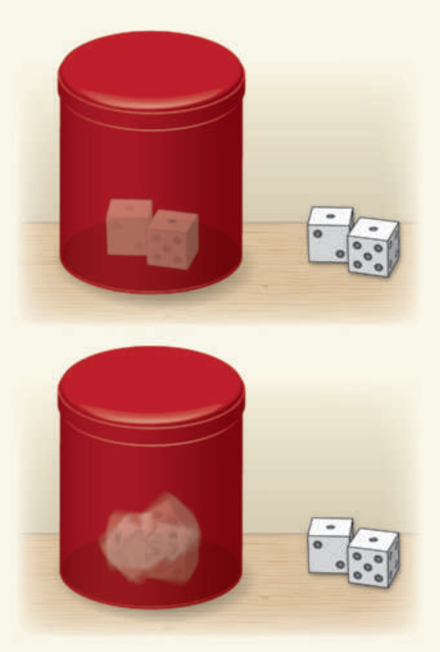

Figure 1 | Quantum dice. a, b, If a pair of dice is shaken in a cup, the dice stop spinning as soon as the cup is turned over on a table. The values observed on the top faces of the dice when the cup is lifted from the table are the same as the values hidden inside the cup. These 'classical' dice are non-contextual — that is, their values are predetermined, and are unaffected by the way we look at them, whether we observe them simultaneously or sequentially. **c, d,** By contrast, 'quantum' dice do not have a predetermined value. In a way, they continue spinning until they are observed. The circumstances under which they are observed — the context of the measurement process — affect the outcome of the measurement. Kirchmair and colleagues[1] use a pair of trapped ions as their quantum dice to demonstrate the contextual nature of quantum mechanics.

In their experiment, Kirchmair and colleagues[1] used a pair of trapped ions (their