OCEANOGRAPHIC MODELLING

Balancing the books: dinoflagellate persistence in the oceanic environment

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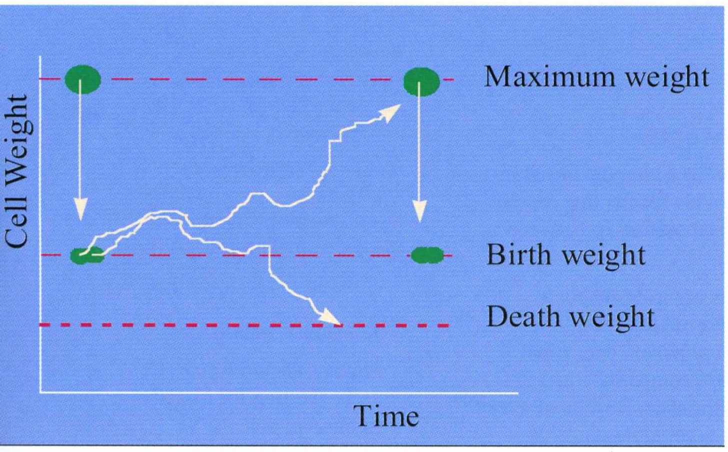
Although dinoflagellate algae are notorious for forming toxic blooms in coastal waters, the group as a whole has a tough time surviving in the ocean. Modelling has shown that if they couldn't swim, dinoflagellates probably wouldn't survive.

THE WORLD'S OCEANS are teeming with a diverse community of planktonic single-celled algae. The smallest are closely related to bacteria and are of a similar size (<2 μm). The largest are species of diatoms and dinoflagellates, which can be up to 1 mm long.

Regardless of size, all algae have the same basic requirements for life: an adequate supply of light energy for photosynthesis, suitable water temperatures and sufficient nutrients. Despite this, some species do much better than others when nutrient concentrations and/or light levels are low.

Generally, the smallest algae are best able to survive at the lowest nutrient concentrations, and are amongst the fastest growing when the environment is favourable. Of the larger algae, diatoms can also exhibit high growth rates and can grow at very low light intensities. They are also able to subsist on very low concentrations of the major nutrients (nitrogen, phosphorus). However, unlike other algae, they do require a supply of silicate. In contrast, dinoflagellates are slow growing, and require comparatively high light intensities. There is also evidence that they do not grow as well as diatoms when nutrient concentrations are low. Furthermore, it appears that (non-toxic) dinoflagellates may be the preferred prey of many zooplankton. These observations beg the question: "Why are dinoflagellates not driven to extinction by other, seemingly superior algae"?



Cellular growth rules. If a cell is lucky enough to find itself in a favourable environment (plenty of nutrients and light) it will put on weight. The cell divides into two equal "daughter" cells when the cellular weight reaches an upper threshold value. If conditions are unfavourable the cell will lose weight, and it will die should its weight fall to a lower threshold.

The good news for dinoflagellates

Dinoflagellates have three characteristics that might contribute to their success.

1. In common with many other algae, they can form resistant spores, but these are usually negatively buoyant, i.e., they gradually sink down through the water. Although shallow-water species may be able to pass through unfavourable periods as resting spores on the sea floor, the spores cannot fulfill this role in the deep ocean, where dinoflagellates are known to be abundant.
2. An increasing number of dinoflagellate species are being shown to get energy both from photosynthesis and from consuming other organisms. In other words, they show characteristics of both plants and animals! This mixed nutritional mode is termed mixotrophy (see Hall, 1998). Mixotrophy may permit continued growth even when photosynthetic activity is restricted.
3. Finally, unlike most other algae, many dinoflagellates are motile, being able to "swim" at speeds of up to 30 m per day using their whip-like "tails". This ability to move around may enable them to better regulate their environment. Dinoflagellates usually grow best near the water surface where light levels (for photosynthesis) are greatest. However, when the nutrient concentration in the surface waters becomes too low to support growth – as often happens during the summer – motile dinoflagellates can swim down to nutrient-rich, deeper waters, replenish their nutrient stores and then return to the surface waters once more.

We have investigated whether the last of these three characteristics – the ability to swim – might allow dinoflagellates to coexist with other algae, particularly diatoms, that appear to be competitively superior.

A model to predict phytoplankton survival

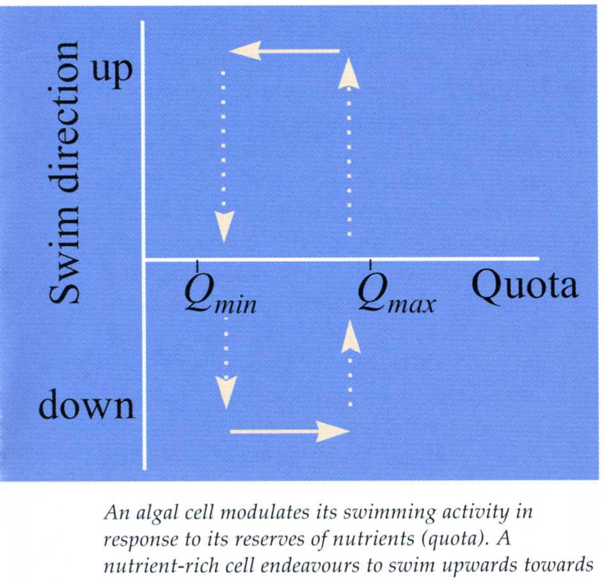
We have constructed a two-"species" (diatom and dinoflagellate) model of oceanic phytoplankton dynamics. Both groups are assumed to be strictly autotrophic (i.e., they gain their energy solely through photosynthesis), but the diatoms are able to photosynthesize much more rapidly whilst being much less mobile than the dinoflagellates. The figures on the right summarise part of the model, an example of an *individual-based population model* (IBPM). The great advantage of IBPMs is that they can take account of individual variability, rather than regarding the entire population as an undifferentiated group. This model represents the detailed physiological state of numerous individual algal "cells", each following a unique trajectory through the ocean (see Woods and Onken 1982). A key feature is the relationship between a cell's chosen swimming direction and its physiological state (see figure). Clearly, in reality, each cell would regulate its behaviour in response to its *own* state rather than to the population average state. This situation cannot be simulated using traditional (non-IBPM) techniques.

The model keeps track of the depth and the physiological state of "sample" cells. It also maintains a record of the number of algal cells that each "sample" cell might represent in reality. At any time, a cell's velocity is given by the sum of a term representing motion due to water turbulence and a term representing the current swimming characteristics of the cell.

The model shows that even negatively buoyant diatoms are easily able to persist in the ocean. Their high maximum photosynthetic potential and low respiratory costs allow them to grow at very low light levels and to survive for prolonged periods even in total darkness.

In contrast, the model suggests that, even with no competition from diatoms and with mortality only from starvation, non-motile dinoflagellates can survive only if they suffer no "background" mortality (such as grazing by copepods and deaths from viral infection). Even those dinoflagellates with higher swimming speeds can withstand only comparatively low rates of "background" mortality.

Life becomes still more difficult for dinoflagellates when diatoms are added into the system. Not only do the diatoms absorb some of the light, which would otherwise fuel dinoflagellate growth, but they also deplete the surface waters of nutrients during the summer. This puts the dinoflagellates on the horns of a dilemma. Either they must endeavour to stay near the surface, where light for photosynthesis is plentiful but there are insufficient nutrients for further growth, or they must descend to depths where there is little light but a plentiful nutrient supply to enable them to replenish their internal nutrient stores.



An algal cell modulates its swimming activity in response to its reserves of nutrients (quota). A nutrient-rich cell endeavours to swim upwards towards the light. Should the internal cell quota fall too far (because there is little nutrient in the water), the cell will switch to swimming downwards (because nutrients are almost always plentiful deeper in the water). Once it has replenished its stores, the cell reverts to swimming upwards.

Only the most motile of dinoflagellates are able to bear the competition from diatoms. They do so by making periodic migrations to depth in order to take up the nutrients which will fuel further growth when they return to the light-rich surface waters (see figure, right). These graphs also show that the diatoms – which cannot swim – are more evenly distributed though the water column than the dinoflagellates.

And the bad news for dinoflagellates...

This modelling exercise suggests that purely photosynthetic dinoflagellates have great difficulty "balancing the books". It suggests that motility is *essential* to dinoflagellate survival, even in the absence of competition from other algae. Motility, combined with the ability to build up an internal store of nutrients for later use *may* be sufficient to enable dinoflagellates to coexist with other algae, but only when the background mortality suffered by the dinoflagellates is low. The model suggests that it is difficult for dinoflagellates to make a living by photosynthesis alone, perhaps helping to explain the widespread occurrence of mixotrophy in this group of algae.

In the future, we intend to use this one-dimensional (vertically resolved) phytoplankton model as the basis from which to develop a three-dimensional one describing the fate of oceanic algae which are transported onto the coastal shelf. Some of these oceanic algae are toxic and, in the longer term, it is hoped that this modelling will improve our ability to forecast the development of toxic algal blooms. ■

Niall Broekhuizen is based at NIWA in Hamilton.

Acknowledgements

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Further reading

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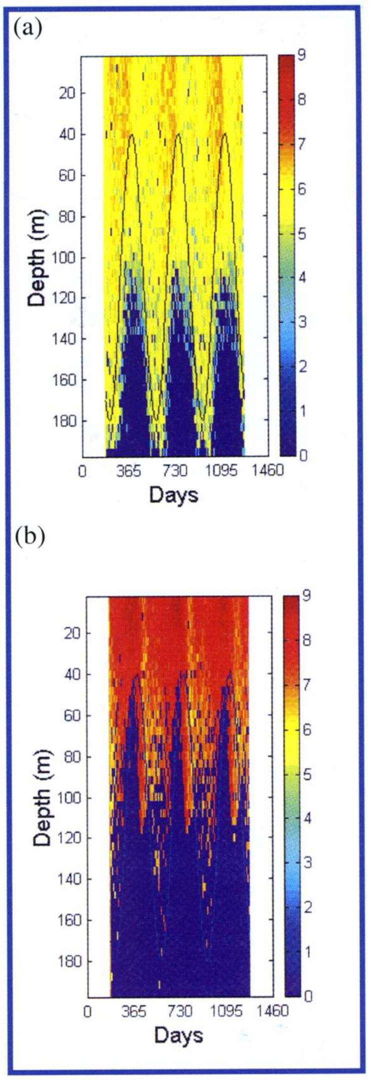

Simulated densities of (a) diatoms and (b) dinoflagellates. On the time axes days are counted starting from 1 January. The colour scale represents the logarithm (base 10) of the number of cells per cubic metre, whilst the black curve denotes the depth of the "turbocline". (Wind- and heat-driven mixing is rapid above this depth, mixing is very much weaker below this depth.) In this simulation the dinoflagellates were able to swim at 30 m per day whilst the diatoms were neutrally buoyant. Note that the dinoflagellates are much better able to maintain their position within the surface layer. It is only in mid- and late summer that substantial numbers of dinoflagellates are found below the turbocline. During this period the mixed layer nutrients are depleted and the dinoflagellates perform periodic vertical migrations in order to exploit the deep-water nutrient pool.