

of the industry was apparently about £1.6 billion, roughly one-third each from fishing, aquaculture and fish processing, but altogether representing only about 0.1% of total UK GDP. Who would have thought that aquaculture, basically salmon farming that only started seriously in the 1980s, would become so important so quickly, with economic output per employee greatly exceeding both of the other sectors? Clearly it is worth looking more closely at the figures involved. But here things rapidly get a bit flaky.

According to a table on p.7 of the document the total landings of the UK fishing fleet in 2017 was some 671 thousand tonnes, of which 448 thousand tonnes were landed by Scottish vessels. So far so good. But

immediately beneath the table, the next paragraph states that *'the aquaculture industry in the UK produced 194 million tonnes of fish and shellfish in 2016'*. Clearly, this is just a slip of a decimal point or two. Well, actually three, since it should say '194 thousand tonnes' (as in the cited source), so it is wrong by a factor of a thousand. If it wasn't, then the value of the production given as €995 million suggests pretty cheap fish at about €5 per tonne! But things get worse. The document goes on to say that *'The UK's aquaculture industry was the second largest in the EU in 2015 by tonnage – behind Spain which produced 294 million tonnes.'* But that's not all: *'For context,'* says the document (p.8), *'in 2015, Norway produced 1.4 billion (my underlining) tonnes of fish from aquaculture'*. So

that pesky moveable point has moved again, so that this number is *also* out by a factor of a thousand!

In the overall scheme of things, of course, none of this is very important; the errors are so blatant that no-one is going to be misled by them. But you would have thought, wouldn't you, that in the six months since the document was published, the odd MP that read it might have popped into the library and suggested a correction? But no-one has, which leads me to the sad conclusion that none of them are likely to read the excellent Shepherd and Horton article. What a shame!

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# 'The control of diatom populations by grazing'

## Richard Fleming and the first marine ecosystem model

Tom Anderson and Wendy Gentleman

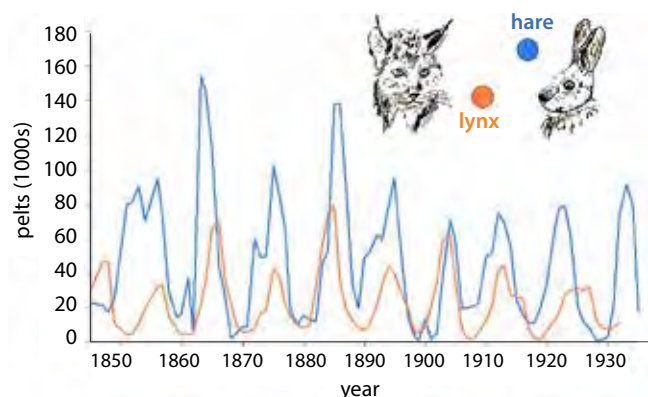
Marine ecosystem models play a central role in the progress of oceanography, and modelling is usually included as a major component in large scientific programmes to complement experimental and observational work. Today's models often exhibit great complexity in terms of the numbers of variables and processes that are represented, and are frequently embedded in large 3D circulation models. It all seems a far cry from the early beginnings, notably the development of the first ever marine ecosystem model by Richard H. Fleming just over eighty years ago, in 1939. Fleming (1909–1989; Figure 1) was a chemical oceanographer who, at the time, was working at the Scripps Institution of Oceanography at La Jolla in California. Here, we tell the story of Fleming's achievement and highlight how it demonstrated the importance of grazing for the dynamics of marine ecosystems and associated biogeochemical cycles.

### The 'grazing hypothesis'

In the early 20th century, marine ecologists were focussing their attention on the 'agricultural hypothesis' which says that primary production (the growth of phytoplankton), and more specifically the timing and magnitude of the spring bloom seen in high-latitude waters, is driven by availability of nutrients and light and that these factors control plankton biomass 'bottom up'. Results were, however, equivocal in that the data showed no straightforward conversion of nutrients to algal biomass. Hildebrand Harvey, working in the 1930s, studied the spring bloom in the English Channel and noticed that most of the diatom crop disappears, without evidence of dead cells in the water. He therefore broke away from the established dogma and proposed the 'grazing hypothesis', whereby the magnitude and timing of the spring outburst of diatoms is controlled by herbivorous zooplankton, i.e. 'top down'.



**Figure 1** Richard Fleming, drawn by John Zane in 1945 (By courtesy of the University of Washington)



**Figure 2** Oscillation in populations of snowshoe hare and Canadian lynx, based on data from the trapping industry.

The interplay of bottom-up and top-down factors in food webs had already been subject to theoretical investigation by Alfred Lotka and Vito Volterra in the early 20th century. They built a model of predator-prey interactions that can, for example, be used to explain the iconic oscillations seen in the populations of snowshoe hare and Canadian lynx (Figure 2). The hare population grows quickly (bottom up) when lynx numbers are low. The lynx population then expands as the hares become plentiful as food, leading to a decline in the hare population (top down). In turn, the lynx population is decimated and the cycle repeats itself.

With the grazing hypothesis in mind, Richard Fleming took up the challenge of constructing a mathematical model to study plankton blooms in the ocean. He decided to use Harvey's data and to focus on the diatom bloom that occurred in the English Channel during the spring of 1934.

### Fleming's 1939 model

Fleming's model used a single differential equation to describe the rate of change of the phytoplankton population with time:

$$\frac{dP}{dt} = (\mu - m_1 - m_2 t) P \quad (1)$$

where  $P$  is phytoplankton biomass in plant pigment units,  $\mu$  is the constant phytoplankton specific growth rate ( $\text{day}^{-1}$ ),  $m_1$  is a constant baseline mortality loss due to grazing, and coefficient  $m_2$  accounts for the increase in grazing pressure that was assumed to occur (linearly) over time,  $t$ , during the progression of the bloom. Note that here we have recast Fleming's equation using modern notation, mathematically equivalent to the original. In the 1930s, there were no computers to generate  $P(t)$  from equation (1). The equation is, however, relatively straightforward to solve analytically, although use of this solution would have still required Fleming to calculate exponentials by looking up values in tables.

We recreated Fleming's simulation using his parameter values of  $\mu - m_1 = 0.1123 \text{ day}^{-1}$  and  $m_2 = 0.003038 \text{ day}^{-2}$ , which were derived in order to reproduce Harvey's observed initial and peak diatom

biomass, as well as the duration of the bloom. The fit to the data is by no means perfect (Figure 3(a)), but the model does nevertheless capture the boom and bust of the bloom. Fleming also derived a formula for total production, from which he was able to reproduce the observed trend in phosphate consumed over time by assuming that 1 unit of pigment corresponds to  $1/9000 \text{ mmol phos m}^{-3}$  (Figure 3(b)). He was thereby able to demonstrate that there is no simple correlation between the population size of phytoplankton and change in nutrient concentration. Fleming also showed that, assuming a constant zooplankton 'filtration volume' (modern-day clearance rate), the efficiency of feeding decreases as the number of grazers increases, such that grazing pressure does not vary directly with zooplankton abundance. Overall, Fleming's main achievement was to demonstrate, for the first time, the quantitative importance of grazing in controlling the peak and decline of phytoplankton biomass: 'It is obvious that any large increase in the grazing associated with an increase in the number of grazers will reduce the diatom population very rapidly.'

Fleming's model is an excellent example of how to develop mathematical representations based on conceptual understanding of processes of interest. He used clear definitions of assumptions and terminology, along with carefully derived metrics to help consider the relative importance of growth versus grazing. The model is undoubtedly simple. Zooplankton numbers, and associated grazing pressure, will not in reality keep on increasing indefinitely with time. Phytoplankton growth rate is not constant but varies with changing light and nutrients, while phytoplankton density is influenced by physical losses due to sinking or vertical mixing. Take-up by the scientific community was limited. Notably, the model was not referenced in the first oceanography textbook, *The Oceans* (published in 1942), which was co-authored by Fleming himself. Gordon Riley, the great marine ecosystem modeller who was to follow on from Fleming, initially thought of the work as 'a burr under my saddle' and that 'it was quite contrary to my point of view about ecological matters'. New ideas are often slow to be accepted in science and, reflecting some time later, Riley acknowledged the importance of Fleming's work: 'I was probably influenced considerably by the paper. I don't know if I would have gone the way I did without it.' Riley went on to great achievements as a marine ecosystem

modeller, in the first instance developing a new model, published in 1946, in which Fleming's phytoplankton equation was elaborated to include explicit terms for the influence of light, nutrients and vertical turbulence on photosynthesis, as well as respiration.

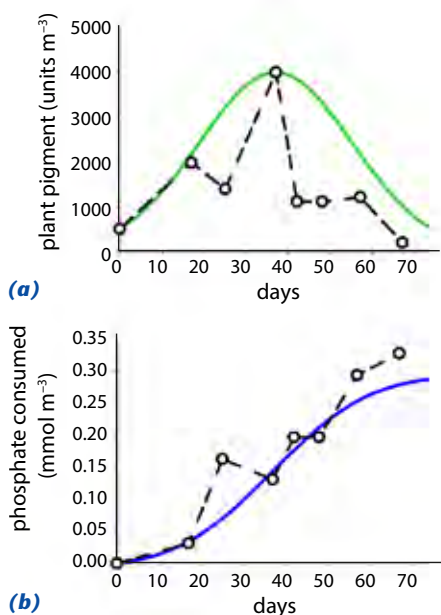
### Modern perspective

The top-down control of plankton dynamics remains incompletely understood today, and is by no means straightforward to reliably parameterise in biogeochemical models, including those at the global scale. Perhaps nobody has done more to promote the importance of top-down controls in marine ecosystems than Karl Banse, of the University of Washington. His contention is that 'grazing rather than cell division rate regulates the abundance and size composition of phytoplankton'. A good example is the low phytoplankton biomass seen in high-nutrient-low-chlorophyll (HNLC) systems that occur in areas such as the Southern Ocean, and the equatorial and sub-Arctic Pacific. It is well known that shortage of iron restricts phytoplankton growth in these regions and yet many modelling studies, notably those of John Steele and Bruce Frost, have demonstrated the essential role of grazers for suppressing blooms in these systems.

Modelling zooplankton, and thereby top-down controls in the ocean via grazing, is a considerable challenge for two main reasons. First, zooplankton are an immensely diverse group in terms of size, feeding behaviours and rates, life histories, etc. Contemporary marine ecosystem models often separate zooplankton into two groups, microzooplankton (typically 20–200  $\mu\text{m}$  in size) and mesozooplankton (>200  $\mu\text{m}$ ), given that the smaller organisms may dominate grazing while larger zooplankton, such as copepods, contribute most to export flux via faecal pellets and vertical migrations, as well as transfer to higher trophic levels. Yet there is great diversity within each of these groups, e.g. microzooplankton include flagellates, dinoflagellates, ciliates, rotifers and foraminiferans. Matters are further complicated by the fact that many microzooplankton are mixotrophs, i.e. combine elements of both phytoplankton and zooplankton by using light for photosynthesis while also ingesting prey.

The second challenge facing zooplankton modellers is the sensitivity of predictions to the precise form of the equations, as well as the parameter values chosen to represent zooplankton processes. Bottom-up controls on plankton growth

**Figure 3** Fleming's simulation for the English Channel (coloured lines) compared with data for (a) phytoplankton and (b) cumulative phosphate consumed.

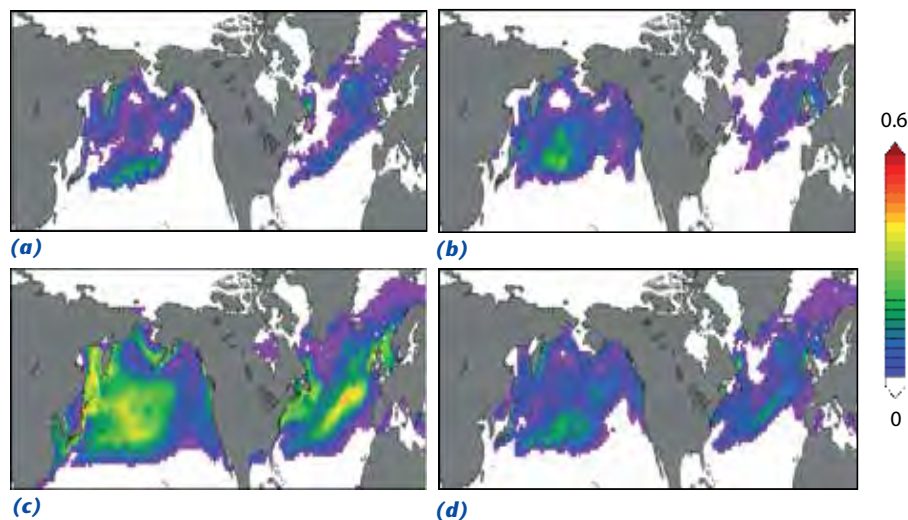


are, at least to some degree, constrained by the availability of nutrients and light, whereas this is not so for zooplankton grazing on phytoplankton. In support of this claim, we show results from our work in 2010 where we compared the impact of four subtly different grazing functions on predicted phytoplankton distributions in a complex global ocean biogeochemical model that included multiple plankton groups and nutrients, all coupled to 3D physics (Figure 4). The four grazing functions differed in terms of their shapes, but were otherwise set up to be as close as possible to each other in terms of parameter values. As can be seen in the Figure, the small differences among grazing functions, and thereby the top-down impact of zooplankton, become amplified to generate large differences in predicted distributions of diatoms. The predictions of marine ecosystem models are likewise highly sensitive to the parameterisation of zooplankton mortality, which is difficult to measure and is usually poorly constrained by data.

### Postscript

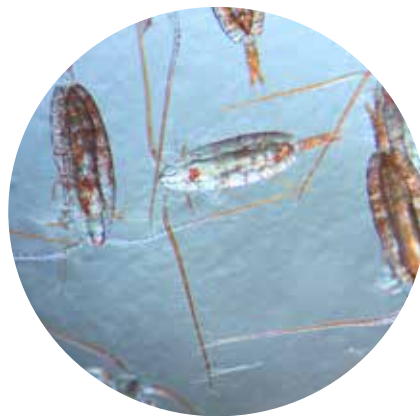
Zooplankton constitute a fascinating and beautiful group of organisms, such as copepods of the genus *Calanus* (Figure 5) which dominate the zooplankton biomass throughout the North Atlantic and Arctic oceans, where they provide a crucial link between phytoplankton and fish. Zooplankton research continues apace today on a range of topics including vertical migration, export flux, the lipid pump, environmental control of spatial patterns and potential impact of climate change, with models playing a central role. Fleming emphasised the need for synergy between observational and theoretical work: 'The future of oceanography lies in carefully coordinated programs involving work at sea, laboratory studies, and theoretical investigations. The observational program must guide the theorist in his work, and the latter must assist by indicating the kinds of observations and equipment that will lead to the most valuable results.'

World War II intervened shortly after Fleming had published his model and he was recruited to work on under-sea warfare by the Division for Water Research of the University of California, between 1941 and 1946. He never returned to ecological modelling, leaving Gordon Riley and others to pick up the mantle. Fleming nevertheless pursued a successful career in oceanography with many interests including chemical and biological oceanography, ocean currents and sedimen-



**Figure 4** Predicted diatom concentrations ( $\text{mg chl m}^{-3}$ ), March–May, in four runs of a global biogeochemical model, each run representing a different grazing function: (a) Michaelis-Menten; (b) Blackman; (c) Sigmoidal; (d) Ivlev. (Anderson et al., 2010; © 2010 Elsevier BV)

tation, as well as naval applications in oceanography. He returned to Scripps as Assistant Director from 1946 to 1950, after which he became the founding Director of the University of Washington's School of Oceanography in 1951, serving until 1967 and thereafter continuing his work as Professor of Oceanography. Fleming was instrumental in the development of curricula, in particular establishing the undergraduate programme in Oceanography, which was the first in the world. He is also well known for progressing the careers of the many oceanographers who came through his educational programmes. When it comes to his 1939 model, however, Fleming is largely an unsung hero of zooplankton modelling. Let us remember that it was he who first quantitatively demonstrated the importance of grazing in the control of phytoplankton blooms, and who acted as the forerunner of the ecosystem modellers that followed.



**Figure 5** The marine copepod *Calanus finmarchicus* (main body length 3 mm). (© Daniel Mayor)

### Further reading

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