



A chronology of plankton dynamics *in silico*: how computer models have been used to study marine ecosystems

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Abstract

Research on plankton ecology in the oceans has traditionally been conducted via two scientific approaches: *in situ* (in the field) and *in vitro* (in the laboratory). There is, however, a third approach: exploring plankton dynamics *in silico*, or using computer models as tools to study marine ecosystems. Models have been used for this purpose for over 60 years, and the innovations and implementations of historical studies provide a context for how future model applications can continue to advance our understanding. To that end, this paper presents a chronology of the *in silico* approach to plankton dynamics, beginning with modeling pioneers who worked in the days before computers. During the first 30 years of automated computation, plankton modeling focused on formulations for biological processes and investigations of community structure. The changing technological context and conceptual paradigms of the late-1970s and 1980s resulted in simulations becoming more widespread research tools for biological oceanographers. This period saw rising use of models as hypothesis-testing tools, and means of exploring the effects of circulation on spatial distributions of organisms. Continued computer advances and increased availability of data in the 1990s allowed old approaches to be applied to old and new problems, and led to developments of new approaches. Much of the modeling in the new millennium so far has incorporated these sophistications, and many cutting-edge applications have come from a new generation of plankton scientists who were trained by modeling gurus of previous eras. The future directions for modeling plankton dynamics are rooted in the historical studies.

Introduction

Research on plankton ecology in the oceans has traditionally been conducted via two scientific approaches: *in situ* (in the field) and *in vitro* (in the laboratory). There is, however, a third approach: exploring plankton dynamics *in silico*, or using computer models to study marine ecosystems. In today's information age, such simulations are recognized as important components of government-funded projects and university courses are training young scientists how to build and apply these quantitative tools. But this is not a new movement – plankton models have aided scientific inquiry for over 60 years. While their first applications occurred before computers existed, technological advances over the decades facilitated analyses and allowed new kinds of models to be developed. The innovations and implementations of these historical studies provide a context for how future model applic-

ations can continue to advance our understanding. To that end, this paper presents a chronology of the *in silico* approach, from its origins to modern times.

Modeling pioneers who worked in the days before computers

Population modeling began over 800 years ago when the Italian mathematician Leonardo of Pisa, also known as Fibonacci, developed his now-famous sequence of numbers (1, 1, 2, 3, 5, 8, 13, 21...) to quantify hypothetical pairs of reproducing rabbits (Boyer & Merzbach, 1991). The first time a model was used to study the dynamics of actual populations, however, was not until the mid-1600s, when John Graunt of England estimated human population density using mortality data (Graunt, 1662), which for that era included death from the plague, boils, and an ail-

ment called the king's evil. Over a hundred years later, Thomas Malthus observed that biological populations grew at rates proportional to the size of the population, e.g.

Rate of Change = Growth

$$\frac{dP}{dt} = aP, \text{ where } a \text{ is a constant} \quad (1)$$

and that left unchecked, such exponential growth would ultimately outstrip resource availability resulting in dire consequences (Malthus, 1798). Malthus' ideas did not account for the tendency of growth rates to decrease as population size increased, and the first model to incorporate such density-dependence was developed by Pierre-Francois Verhulst (Verhulst, 1845). He assumed that limiting factors increased with the square of the population size (Equation (2)):

Rate of Change = Growth – Limiting Factors = Net Growth

$$\frac{dP}{dt} = aP - \frac{a}{K}P^2 = \left(1 - \frac{P}{K}\right)aP \quad (2)$$

and introduced the concept of a carrying capacity, K , or maximal population size sustainable by the environment. Verhulst's work went largely unnoticed until the mid-1920s, when the equation was rediscovered by Raymond Pearl and Lowell Reed, who touted this logistic growth model as a "Law of Nature" (Kot, 2001). At roughly the same time, Lotka and Volterra developed their famous predator-prey model (Equation (3)):

Rate of Change of Prey = Growth – Predation

$$\frac{dP}{dt} = (a - cZ)P$$

Rate of Change of Predator = Birth – Death

$$\frac{dZ}{dt} = (bP - d)Z \quad (3)$$

where P is the prey density, Z is the predator density, and a , b , c , d are constants, which they used to explain observed cycles of fish populations (Lotka, 1925; Volterra, 1926).

The first dynamical model of plankton populations was introduced in 1939, when Richard Fleming, a chemical oceanographer at Scripps Institution of Oceanography, used a differential equation to study how grazing by zooplankton affected the temporal variability of phytoplankton (Fleming, 1939). In developing his model, Fleming assumed that other loss processes, such as sinking and cell death, were negligible compared to grazing. He also assumed advective

effects were negligible, as would be the case for plankton in a specific water mass, or those in regions with insignificant gradients along streamlines. He therefore described the rate of change of phytoplankton density as resulting from the difference between growth and grazing (Equation (4)).

Rate of Change = Growth – Grazing

$$\frac{dP}{dt} = (\mu - g)P \quad (4)$$

Fleming further limited his model to a time of year when environmental conditions were such that the phytoplankton specific growth rate (μ) could be treated as a constant cell division rate (e.g. no variations from light or nutrient limitation). He described the per capita phytoplankton mortality due to grazing (g) as though zooplankton had constant clearance rates (i.e. $g=cZ$, where c is a constant), meaning his model was analogous to Lotka-Volterra's prey equation. But, instead of using an analogous predator equation to model the zooplankton, he assumed their population size increased linearly in time, such that g increased linearly in time (i.e. $g=g_1+g_2t$).

Because of his simplifying assumptions, Fleming was able to integrate Equation (4) analytically, yielding a mathematical expression for the size of the phytoplankton population at any time t .

$$P(t) = P(t_0)e^{[\mu - (g_1 + g_2t/2)]t} \quad (5)$$

Despite the simplifications, he obtained reasonable agreement between his model and data for the spring bloom in the English Channel, allowing him to use the model to draw conclusions about controlling processes. He demonstrated how the model bloom was shaped by the relative rates of phytoplankton growth and grazing, and emphasized that a good understanding of zooplankton ingestion and growth was required to understand the temporal dynamics of phytoplankton. He showed how the model could be used to estimate grazing rates in the field when phytoplankton density and growth rates were known, and he further explained how experimentalists could use the model to estimate zooplankton clearance rates. Fleming also discussed how modeled dynamics could be made more realistic by including time-varying growth rates to account for changing physical and chemical factors, and by improving quantification of how zooplankton feeding mechanisms and filtration capacity vary with environmental conditions.

Although he had demonstrated a variety of ways in which models of plankton dynamics could aid re-

search, Fleming's approach was not readily embraced by the oceanographic community. In fact, the first integrated text on oceanography (Sverdrup et al., 1942), which Fleming co-authored, only gave a cursory reference to his model as an illustration of how small changes in herbivore populations could have big impacts on phytoplankton. Part of the reason for the slow acceptance of this novel approach was that the community felt it too simple to be biologically useful. That was certainly the first impression of Gordon Riley (Mills, 1989), a biological oceanographer at the Woods Hole Oceanographic Institution.

When he first encountered Fleming's model, Riley was participating in an extensive survey of the plankton on Georges Bank that took place between 1939 and 1941, or what some today call "The *first* Northwest Atlantic GLOBEC program". Riley had been employing statistical techniques to quantitatively study plankton production, but he was frustrated by the limited ability of statistics to provide causal explanations for his observations (Riley, 1946). Eventually, he became intrigued with the idea of taking the opposite approach, or "developing the mathematical relationships on theoretical grounds and then testing them statistically by applying them to observed cases of growth in the natural environment" (Riley, 1946). He called this the synthetic approach (Riley, 1946).

Four of Riley's early models each constituted landmark advances. Riley & Bumpus (1946) incorporated a linearly increasing growth rate into Fleming's equation (i.e. $\mu = \mu_1 + \mu_2 t$), as such a temporal change was indicated by their observations, and used the model to estimate *in situ* grazing rates for Georges Bank. They noted that these estimates were upper bounds, as model results were sensitive to the assumption that no other processes caused phytoplankton losses. Given the regional hydrography, they realized that turbulence likely affected the biology, and so modified their equation to include dilution of the population from mixing:

$$P(t) = P(t_0)e^{[\mu_1 + \mu_2 t/2 - (g_1 + g_2 t/2)]t[1 - t(d_1 + d_2 t)]} \quad (6)$$

where $d = d_1 + d_2 t$, is a linearly increasing dilution rate. Primitive though the formulation was, inclusion of mixing meant Riley & Bumpus (1946) devised the first coupled physical-biological plankton model. They used this model to estimate the dilution rate for phytoplankton, which they found was comparable to estimated grazing rates, but more than 20 times estimated turbulent losses for zooplankton. Through further

model modifications, they were to able test and reject the hypothesis that the discrepancy between phytoplankton and zooplankton dilution rates was due to additional phytoplankton losses from natural death. This led Riley & Bumpus to develop a new hypothesis: turbulence differentially affected plants and animals owing to vertical migration of the zooplankton.

Motivated by his statistical analyses of Georges Bank data, which indicated most phytoplankton variability could be explained by five factors (phosphate, nitrate, temperature, water depth and zooplankton abundance) with the dominant factor changing seasonally, Riley developed a second model to identify the controlling processes (Riley, 1946). In this model, he represented temporal changes in phytoplankton as resulting from the difference between net growth and grazing, like Fleming. But Riley's innovation was that physiological rates changed non-linearly in time, according to their dependence on seven environmental variables:

$$\begin{aligned} \text{Rate of Change} &= \text{Net Growth} && - \text{Grazing} \\ &= (\text{Growth} && - \text{Respiration}) - \text{Grazing} \\ \frac{dP}{dt} &= (p_h(l, k, h, N, m) - r_p(T) - g(Z)) P \end{aligned} \quad (7)$$

He modeled the gross growth rate (or photosynthetic rate p_h) as a function of light intensity (l), water transparency (k), and euphotic zone depth (h), and included reductions in the growth rate due to both nutrient-limitation (N) and vertical turbulence (i.e. when the mixed-layer, m , became deeper than h). The net growth rate, $\mu = p_h - r_p$, accounted for respiratory losses (r_p), which in turn varied with temperature (T). Specific grazing rates were determined using sampled zooplankton densities (Z) and estimated constant clearance rates. Thus, Riley's 1946 model represented the first coupled biological-chemical-physical model of plankton dynamics. With it, he was able to reasonably match observed seasonal cycles and quantify temporal changes in controlling factors for Georges Bank (Riley, 1946), and later for other areas (Riley, 1947a; Riley & Von Arx, 1949).

Riley subsequently developed the first model of zooplankton dynamics (Equation (8)), which he used to determine the seasonal variation in processes controlling their populations on Georges Bank (Riley, 1947b). This model was essentially the zooplankton

analog to Equation (7):

$$\begin{aligned} \text{Rate of Change} &= \text{Net Growth} && - \text{Biological Losses} \\ &= (\text{Assimilation} - \text{Respiration}) && - (\text{Predation} + \text{Death}) \\ \frac{dZ}{dt} &= (a(P) && - r_z(T) && - f(C) - d)Z \quad (8) \end{aligned}$$

describing the temporal changes in the zooplankton population size as resulting from the difference between net growth (i.e. rate of assimilation of organic matter, a , minus respiration, r_z) and predation by carnivores (f). The equation additionally included losses from natural death (d). Temporal variations in biological rates were defined by their coupling to observed environmental variables, including phytoplankton density (P), temperature (T), and observed abundance of the chaetognath *Sagitta elegans* (C), which was considered the dominant carnivore in the region.

The model developed by Riley et al. (1949) marked an important change in approach. Instead of forcing individual equations with observed population densities and chemical concentrations, they dynamically linked the biota and chemical elements in a nutrient–phytoplankton–zooplankton–carnivore food chain, and additionally considered how turbulence and gravity affected vertical distributions. As in Riley’s earlier models, physiological rates depended on environmental variables such as light, water transparency and temperature, and as in Sverdrup et al. (1942), nutrient densities were altered by both phytoplankton consumption and respiration. The food chain interactions were considered at different depths above an abiotic deep layer, which had a constant nutrient concentration, and vertical biochemical fluxes were caused by sinking of phytoplankton (s) and turbulent diffusion (D) of both phytoplankton and nutrients. Thus, the rate of change of nutrient and phytoplankton densities at a given depth were described by the coupled equations:

$$\begin{aligned} \text{Rate of Change} &= \text{Bio sources} && - \text{Bio Losses} && + \text{Physical Effects} \\ \frac{dN}{dt} &= \text{Respiration} && - \text{Consumption} && + \text{Mixing} \\ &= (r_p P + r_z Z + r_c C) - p_h P && + \frac{\partial}{\partial z} D \frac{\partial N}{\partial z} \quad (9) \\ \frac{dP}{dt} &= \text{Net Growth} && - \text{Grazing} && + \text{Mixing} && - \text{Sinking} \\ &= (p_h - r_p) P && - g Z && + \frac{\partial}{\partial z} D \frac{\partial N}{\partial z} - s \frac{\partial P}{\partial z} \end{aligned}$$

Vertical migration of zooplankton was assumed to dominate physical transport processes such that mixing could be neglected. Animals were assumed to

spend an equal amount of time at each depth, resulting in vertically homogenous zooplankton distributions. This meant herbivore population densities changed according to the difference between net growth and predation by carnivores, as in Equation (8), although natural death was neglected. Limiting its application to late-spring/early-summer, a time of year when environmental conditions and population densities were relatively stable (i.e. when $d/dt \approx 0$), Riley et al. (1949) used their model to examine planktonic ecosystems in a wide range of North Atlantic environments, including shallow temperate coastal waters, temperate oceanic regions off the continental shelf, a segment of the Gulf Stream, and the oceanic subtropics. Model results were reasonably consistent with observations, allowing them to assess the controlling processes for each region.

Plankton modeling in the 1950s, 1960s and 1970s: the Steele Age

Solution of Riley’s more realistic models (Equations (7–9)) required numerical methods, as the non-linear formulations were too complicated to be integrated analytically. Generating these model results was laborious (Riley, 1952), at times taking 25–30 hours to solve a single pair of equations (Mills, 1989). It took so long because they had to perform the calculations manually – computers, as we know them, did not exist. The first electronic computer was unveiled to the world in 1946 at the same time as Riley’s first model, and could perform only 5000 calculations per second. The ENIAC (electronic numerical integrator and computer), as it was called, was a monster of machine, weighing 30-tons, taking up 1800 square feet of floor space and requiring 6000 switches be set by hand to program it (Kidwell & Ceruzzi, 1994). Over the next three decades, the nature of automated computation changed dramatically, culminating with the release of the Apple II personal computer in 1977. The Apple II could perform 100 000 calculations per second and was the first small machine to come with a keyboard, monitor and price tag to make it attractive and practical for individual scientists (Campbell-Kelly & Aspray, 1996).

While Riley and others continued to use and promote models as tools for studying marine ecosystems (e.g. Riley, 1952, 1963; Cushing, 1958, 1959; Dugdale, 1967; Walsh & Dugdale, 1972), modeling advances made during the 30-year period when com-

puters evolved from room-sized machines to desktop devices are virtually synonymous with the name John Steele, a mathematical biologist from Scotland. Steele's models elaborated on the food chain of Riley et al. (1949), by removing the steady-state constraint and solving for temporal dynamics using numerical methods. Initially, in order to keep the problem tractable, he had to simplify both environmental rate dependencies and dimensionality (e.g. Steele, 1956, 1958). This led Steele to develop a nutrient–phytoplankton–zooplankton, or NPZ, food chain model in a two-layer sea (Steele, 1958), wherein nutrients and biota were uniformly distributed throughout a surface mixed-layer, which received nutrient influxes and lost biomass through turbulent mixing with a deep abiotic layer. The biochemical components of NPZ models are virtually identical to Equations (8–9), but the physical terms for the two-layer sea reduce to:

$$\begin{aligned} \text{Mixing of Nutrients} &= -D(N - N^*)/m \\ \text{Mixing of Phytoplankton} &= -DP/m \\ \text{Sinking of Phytoplankton} &= sP/m \end{aligned} \quad (10)$$

where m , is the depth of the surface mixed-layer, and N^* is the deep water nutrient density. By 1974, when he published the seminal work *The Structure of Marine Ecosystems*, Steele was able to use computers to perform the calculations, and thus could incorporate additional biological complexity into his models, using the non-linear rate relationships emerging at this time. For example, the Michaelis-Menten chemical kinetic equation (Michaelis & Menten, 1913) was used to describe nutrient uptake by phytoplankton (Dugdale, 1967; Eppley et al., 1969), and various formulations were developed to characterize the density-dependence of prey consumption (e.g. Ivlev, 1955; Holling 1959, 1965), as well as variation of both ingestion and growth with environmental factors such as temperature and food (e.g. Mullin & Brooks, 1970a,b).

Like the other modeling pioneers, Steele used his early simulations to estimate primary production, physical and biological rates (e.g. Steele, 1956, 1958, 1959). But, he also used models in new ways. Increases in computational power meant Steele could more readily perform sensitivity studies, comparing results for different process formulations and parameter values. Through these investigations, he demonstrated how different biological responses affected ecosystem dynamics, and observed that often there was insufficient knowledge or evidence on which to

base mathematical descriptions (e.g. Steele, 1959, 1961, 1974). Steele saw the value of developing models of biological processes was that “By forcing one to produce formulas to define each process and put numbers to the coefficients, [a simulation of a natural ecosystem] reveals the lacunae in one’s knowledge...the main aim is to determine where the model breaks down and use it to suggest further field or experimental work” (Steele, 1974: p. 58).

Steele recognized that one of the most critical model aspects needing refinement was the characterization of zooplankton. Thus far, almost all applications treated the zooplankton assemblage as a single biomass variable, Z , which only changed through ingestion and predation. Formulations for these processes typically included a threshold response, although Steele questioned the mechanisms leading to thresholds in natural populations, and showed how switching between different prey types – by both zooplankton and their predators – greatly affected modeled dynamics (Steele, 1974). Steele also demonstrated that different assumptions about zooplankton migration resulted in large differences in modeled phytoplankton distributions (Steele & Mullin, 1977). He concluded that improved understanding of both the animals and their effect on primary production would require models (i) incorporate more mechanistic representations of grazing and predation, and (ii) expanded descriptions of zooplankton community structure, to distinguish between different species, sizes and/or stages (Steele & Mullin, 1977).

Bruce Frost, a biological oceanographer at the University of Washington, was just the scientist with whom Steele needed to collaborate to develop such models. Frost, who was well-versed in traditional *in situ* and *in vitro* approaches to zooplankton ecology, also recognized the importance of grazing in shaping planktonic ecosystems. In the early-1970s, he had performed extensive feeding experiments on copepods, assessing ingestion rates of different species and life stages on different prey types and describing the relationships mathematically (Frost, 1972, 1975). Frost had not yet done any modeling in 1974, when he took a trip to La Jolla, CA with his wife and children. He brought with him a hot-off-the-presses copy of Steele's book and started reading it just as the family left Seattle, WA. He was so intrigued by the potential he saw in the modeling approach that he could not put the text down before he had read it cover to cover, and his poor wife was left to drive the whole way to California. Frost's fascination persisted, mo-

tivating him to go to Scotland and work with Steele during his sabbatical in 1975–76. Out of that interaction came Steele and Frost's *The structure of plankton communities* (1977).

Steele and Frost expanded the NPZ model to consider the structure of the planktonic community by dividing the *P* and *Z* compartments into different size classes. The dynamics of each size class were governed by the same processes considered in Equations (8–9), but zooplankton growth resulted in recruitment from one class to the next, such that the rate of change of the zooplankton density in size class *i* was described by the equation:

$$\frac{dZ_i}{dt} = \text{Recruitment from } Z_{i-1} - \text{Recruitment to } Z_{i+1} - \text{Predation on } Z_i. \quad (11)$$

They specifically looked at the effect of passive size-selection by two differently sized copepods, *Calanus* and *Pseudocalanus*. They found that grazing influenced both size structure and total biomass of the phytoplankton, by differentially affecting the concentration of different cell sizes over time. They also found that the size structure of the phytoplankton assemblage could affect the copepod population structure, by differentially affecting recruitment rates, and altering the percentage of the population in each life stage for the two zooplankton species.

Plankton modeling in the late-1970s and 1980s

Computer simulations became more widespread research tools for biological oceanographers in the late-1970s and throughout the 1980s. The literature discussed specific techniques for developing mathematical formulations and implementing computer solutions (e.g. Wroblewski, 1983), and some publications even provided opportunities to purchase diskettes containing modeling software (e.g. Wulff et al., 1989). The rising popularity of plankton models was due in part to the changing computational context. While models of the early-1970s were still limited by computational constraints (Walsh & Dugdale, 1972), technological advances of this period allowed simulations to extend ecological structure, spatial resolution and temporal duration. The accessibility and skyrocketing performance of smaller machines increased their use in labs and on ships, and the availability of commercial software combined with improvements in graphics and user-interfaces made it much easier to develop

and de-bug code, and post-process and analyze model results.

The growing recognition of the utility of models was also due to there being more information available about the dependence of physiological rates on environmental factors (e.g. Anderson et al., 1978; Vidal, 1980a,b; Martin & Fitzwater, 1988; McClaren, 1989), which could be used to improve earlier models and inspired new model applications. New model applications also arose from marked changes in our conceptual understanding of planktonic ecosystem structure and function that occurred during this time period, including: (i) emerging paradigms of new, regenerated and export production (Dugdale & Goering, 1967; Eppley & Peterson, 1979; Walsh et al., 1981), (ii) discovery of significant bacterial biomass and productivity, indicating the importance of the microbial loop for nutrient cycling (Pomeroy, 1974; Azam et al., 1983), and (iii) strengthened correlation of production and circulation patterns coming from satellite views of the ocean (e.g. Gordon et al., 1980; Campbell & O'Reilly, 1988).

More modeling of process, structure and control

Many model studies of this period were extensions of the kind of process, structure and ecosystem control investigations done earlier. There were more examinations of how modeled dynamics were affected by different formulations and parameterizations of physiological processes. Several of these works focused on phytoplankton growth, examining limitation by light and nutrients (e.g. Jassby & Platt, 1976), and a number continued to emphasize the sensitivity of the ecosystem dynamics to the nature of both grazing and predation by higher trophic levels (e.g. Steele & Henderson, 1981; Franks et al., 1986b; Bollens, 1988). Process studies of microbial interactions indicated dynamics were also sensitive to bacterial responses (e.g. Thingstad & Perengrud, 1985; Thingstad, 1987), including whether nutrients were taken into cells in constant ratios according to Monod kinetics (Monod, 1942), or whether uptake occurred in variable ratios according to more realistic Droop formulations (Droop, 1968). There were also more structured models developed that differentiated between sizes, ages and/or stages in order to describe population demographics, and/or explicitly included biomass compartments for bacteria, protozoa, microzooplankton and detritus, as means of quantifying nutrient fluxes through the microbial loop and to the deep ocean (e.g. Pace et al., 1984; Molo-

ney et al., 1986; Hofmann & Ambler, 1988; Vezina & Platt, 1988; Ducklow et al., 1989; Batchelder & Miller, 1989; Carlotti & Sciandra, 1989).

There were more simulations made to determine the factors controlling the dynamics of particular systems. Some studies made this assessment by examining the sensitivity of modeled dynamics to different parameter values and mathematical formulations (e.g. Hofmann & Ambler, 1988). Some deduced controls through so-called network analysis, based on estimated nutrient flows between ecological compartments (e.g. Vezina & Platt, 1988; Ducklow et al., 1989). Others took a slightly different tack, which was "...to thoroughly explore, by means of a mathematical model, the plausibility of [a hypothesis] as an explanation of [the observations]The objective is to put sensible constraints on the possible mechanisms of control based on current knowledge" (Frost, 1987). Hence, in a manner reminiscent of Fleming and Riley, these models coupled only the specific processes the authors felt were important, and hypotheses were corroborated or revised based on whether or not simulated dynamics were consistent with observations.

For example, Geoff Evans and John Parslow used a two-layer sea NPZ model, with detailed environmental dependence for the phytoplankton growth rate, to explore the hypothesis that the spring bloom was caused by the rapid shallowing of the mixed-layer (Evans & Parslow, 1985). They found blooms could occur without any sudden change in phytoplankton growth rates, and could occur in deep mixed-layers. They also found blooms could be suppressed in areas where mixed-layers were shallow. Their modeling suggested the fundamental explanation for the difference between the classic spring bloom dynamics observed in the North Atlantic, versus the High-Nitrate-Low-Chlorophyll (HNLC) dynamics observed in the Subarctic Pacific, was the difference in mixed-layer depth between these regions.

Evans and Parslow's argument depended on the presence of zooplankton populations that reproduced continually year round, and were able to graze down the phytoplankton. Bruce Frost developed a model to specifically explore whether mesozooplankton, including the copepods *Neocalanus* spp., were the dominant consumers of phytoplankton in the Subarctic Pacific (Frost, 1987). Using an NPZ-type model, he showed that observed dynamics could not be captured when phytoplankton were eaten only by copepods or only by microzooplankton. However, he was able to reproduce observations using an expanded food web

model in which phytoplankton were principally grazed by microzooplankton, and both were consumed by omnivorous mesozooplankton. Frosts' results pointed to the critical role of smaller heterotrophs, and the need to survey their abundance and production.

New kinds of models: 2D circulation and the plankton

Thus far, most models had included vertical fluxes as oceanographers recognized that vertical mixing affected local plankton production and distribution through transport of phytoplankton and alteration of local environmental conditions (e.g. Steele & Mullin, 1977). However, correlations of plankton patterns with major circulation features suggested lateral advection and lateral eddy diffusion were also important processes. Theoretical studies of the interaction of zooplankton vertical migrations with sheared currents, tidal and residual flows indicated that factors affecting zooplankton swimming could also be significant for their large-scale patterns (e.g. Riley, 1976; Evans, 1978). But, prior to the late-1970s, models were only able to include rough approximations of horizontal circulation (e.g. Riley, 1951; Walsh & Dugdale, 1972). This changed with the increased accessibility of computational power in the late-1970s and 1980s, and researchers developed new models that coupled plankton dynamics to two-dimensional circulation fields along both horizontal and vertical planes.

Jay Wroblewski conducted one of the earliest such studies to explore the effects of wind forcing and upwelling on primary production along the Northeastern Pacific coast (Wroblewski, 1977). He used an expanded NPZ ecosystem model, including detritus and different forms of dissolved inorganic nitrogen, and considered that all ecological variables were transported by local currents and turbulence. He demonstrated that advection and wind variability were critical, controlling both spatial distributions and temporal trends in primary production. His results also suggested advection was important for zooplankton, but he was unable to draw further conclusions because of the insufficient realism included in the model – carnivore predation, zooplankton migration, and inshore population sources had been neglected.

To better understand how circulation affected zooplankton, Wroblewski subsequently coupled his flow fields to models of stage-structured zooplankton population dynamics. He showed how prolonged winds resulted in significant offshore transport of *Acartia clausi* in coastal upwelling regions (Wroblewski, 1980), and

hypothesized that this result explained why different copepod distributions are observed off the coast of Northwest Africa and in the Eastern Pacific. Wroblewski also explored how distributions of *Calanus marshallae* were affected by the interaction of tidal flows with diel migrations of late-stage copepodites (Wroblewski, 1982). His results suggested copepods might use such a mechanism to maintain themselves inshore while laying eggs, and expedite their transport offshore when they went into diapause.

Another 2D model was developed by Cabell Davis to test the hypothesis that observed seasonal and spatial variations in the population structure of *Pseudocalanus* on Georges Bank resulted from the interaction of their population dynamics with the bank gyre (Davis, 1984). While his circulation field was idealized, his biological component took models of zooplankton dynamics to new levels. He expanded the population structure to include age-within-stage, and represented recruitment from one stage to the next as probabilistic, depending on an individual's age. He also varied development and egg production rates with seasonal changes in temperature. Davis was able to reasonably match observations with simulations wherein adult females from the Gulf of Maine began reproducing once they were advected onto the Bank, and the maturing population was transported around the Bank. His results, therefore, supported the original hypothesis, and emphasized that understanding the dynamics of copepod distributions required knowledge of both their life history characteristics and the regional circulation.

Peter Franks and co-authors used an NPZ model coupled to a 2D flow field (radial distance from center and vertical) for a Gulf Stream ring, in order to investigate mechanisms causing enhanced productivity in the center of such warm-core mesoscale eddies (Franks et al., 1986a). Through a series of experiments in which they varied parameter values (e.g. upwelling velocities, vertical diffusion and light), they were able to support the hypothesis that production was driven by an upward flux of new nutrients occurring at the eddy core. Production in a Gulf Stream eddy was compared to production due to nutrient input from bottom intrusions along the southeastern U.S. continental shelf in a subsequent model investigation by Eileen Hofmann (Hofmann, 1988). Her ecosystem model included a size-structured phytoplankton assemblage and a stage-structured copepod population, with vital rates affected by both temperature dependencies and food limitation. Model results revealed funda-

mental differences in the biological response to the different frequency and duration of nutrient input from these two upwelling mechanisms (Hofmann, 1988). Primary production in eddies was generally transported offshore and was only able to support low copepod densities. In contrast, much of the primary production associated with bottom intrusions was transferred to the zooplankton biomass, and both primary and secondary production were transported across the shelf to inshore areas.

Diagnosis of controlling mechanisms in the Hofmann (1988) study was greatly aided by independent analysis of biochemical (Hofmann & Ambler, 1988) and advective (Ishizaka & Hofmann, 1988) model components. The influence of advection was explored with a technique called Lagrangian particle tracking, which calculates the distance and direction a particle moves over a period of time based on local currents and eddy diffusion, and any particle motions relative to the water mass (e.g. vertical migrations, sinking, floating). Neglecting stochastic effects from turbulence and behavior, they found that the length of time plankton were retained in an area, and the trajectories taken as they were transported to different areas, were determined by proximity to the Gulf Stream and nature of the wind forcing (Ishizaka & Hofmann, 1988).

Plankton modeling developments of the 1990s

In the 1990s, increased scope and resolution of observations and increased experimental information became available. Many of these data were products of interdisciplinary research initiatives such as the Joint Global Ocean Flux Study (JGOFS), and the Global Ocean Ecosystem Dynamics (GLOBEC) program, which were born out of a growing interest in understanding the effect of climate variability on ocean production. These programs encouraged the use of models for synthesis or prediction, and such large-scale/long-term applications were possible because of the technological advances occurring during this decade: (i) computer performance increased at such a pace that machines were virtually obsolete once removed from their packaging; (ii) the cost of computers plummeted, making modeling much more inexpensive than other research venues; (iii) an explosion in the use of the internet enabled sharing of data and computer resources with scientists around the world, and (iv) new versions of analytical and graphical software made it easier to generate, process and visualize

results. These changes enabled simulations to include unprecedented levels of physical and biological complexity, and to investigate new kinds of scientific hypotheses and questions. A wealth of plankton modeling publications ensued, and many reviews were written to help keep the community apprised of developments and recommend specific approaches (e.g. Evans & Fasham, 1993; Ducklow, 1994; Franks, 1995; Davidson, 1996; Hofmann & Lascara, 1998; Baird & Elmsley, 1999; Frost & Kishi, 1999).

Old approaches for old and new problems

Many *in silico* investigations in the 1990s were explorations of process, structure and control that used similar kinds of physical and biological couplings as the earlier models. The density-dependence of higher predation remained an unresolved problem, and numerous studies were performed to demonstrate the effect of different closure schemes on ecosystem dynamics (e.g. Hastings & Powell, 1991; Steele & Henderson, 1992; Caswell & Neubert, 1998). Variability in predation response alone was shown to be able to account for the different phytoplankton cycles in the North Atlantic and Subarctic Pacific (Steele & Henderson, 1992), indicating that appropriate representation of predation was required for accurate estimation of production. Simulations of a wide variety of species and systems continued to reveal that observed dynamics were explained by omnivory (e.g. Armstrong, 1994; Carlotti & Raddach, 1996), and suggested they could also be affected by food quality (e.g. Anderson, 1992), underscoring the need for models to incorporate additional structure to capture controlling mechanisms. Several process studies examined the extent to which interactions of biology with 1D and 2D theoretical circulation fields affected plankton distributions. These reinforced the idea that vertical motions of plankton (e.g. sinking, floating, swimming) could enhance population densities where there were gradients in the flow field, and could serve as a dispersal mechanisms, transporting populations to different regions even in the absence of residual currents (e.g. Hill 1991a,b; Franks, 1992, 1997a). They also emphasized the sensitivity of plankton patchiness to variability in wind forcing and frontal characteristics (e.g. Franks & Walstad, 1997).

Ecosystem models continued to be used to estimate and predict rates of primary production and biochemical fluxes for specific areas (e.g. Moloney & Field, 1991a,b). Perhaps the best known application was the

study by Mike Fasham and co-authors (Fasham et al., 1990), due in part to the authors' having freely distributed their model code among the community. As in earlier models, they accounted for community structure through inclusion of bacteria and detritus in addition to phytoplankton and zooplankton. They also included different forms of dissolved nitrogen, and used modeled uptake rates of these nutrients to account for new versus regenerated production and estimate *f*-ratios (*sensu* Eppley & Peterson, 1979). Sensitivity studies, conducted by varying parameter values, were used to test hypotheses about mechanisms controlling dynamics in HNLC regions (Fasham, 1995). Sensitivity analysis was also used to assess the kinds of data that were needed to narrow the uncertainty of predictions for new production (Evans, 1999), as this was important for climate-change applications.

Other models were developed by Bruce Frost to test hypotheses about ecosystem control in HNLC areas, including one examining the relative importance of grazing control versus iron limitation for the Equatorial Pacific (Frost & Franzen, 1992). This model simulated the upwelling supply of iron and lateral advection of biota using a chemostat analogy, which resulted in the same mathematical form of the equations as Steele's two-layer sea (Equation 10), with mixing rates replaced by dilution. They found that modeled phytoplankton and microzooplankton dynamics were tightly coupled, and quite sensitive to the structure of the whole zooplankton community, leading them to conclude that grazing was an essential aspect of the HNLC condition. Frost also extended his earlier model investigations of the Subarctic Pacific to differentiate nitrogen sources between nitrate and ammonium, and to explore vertical distributions of nutrient utilization and primary production in light of new observations for the region (Frost, 1993). His results suggested that grazing and preferential uptake of regenerated forms of nitrogen could explain the observations. However, a later model, which had more realistic representations of turbulence, suggested ammonium inhibition of nitrate uptake was not as important as mixing, and pointed to the need to account for nitrification in order to properly quantify new production (Kawamiya et al., 1995).

Individual-based models, the new name for structure

Theoretical ecologists were growing increasingly aware of problems with classical ecological models such as the logistic and Lotka-Volterra equations.

They realized that since these models represented populations using a single state variable, they were effectively treating populations by their average properties and ignoring variability in individual behavior or genetics. Thus, beginning in the late-1980s, modelers began to increase their demographic resolution, representing populations either by their size, stage, and/or age structure (e.g. Caswell, 1989), or as collections of large numbers of unique individuals (e.g. Hutson, 1988). Both of these approaches are termed Individual-Based Models, or IBMs, and their usage increased throughout the 1990s (e.g. DeAngelis & Gross, 1992), as computer processor speed, memory and storage required to run such models also increased.

While models formulated with size and stage specific responses (e.g. migrations, feeding and behavior) had been commonly used to study plankton dynamics since Steele & Frost (1977), before the 1990s only a handful of plankton models had accounted for stochasticity from individual variability or variability between cohorts (e.g. Davis, 1984; Batchelder & Miller, 1989; Carlotti & Sciandra, 1989). During the 1990s, more IBMs were used for plankton modeling, as biological oceanographers began to recognize the effectiveness of these structures for addressing many of their research questions. For example, they are useful for the exploration of food-limitation, because they can account for an individual's feeding history, physiological condition and mortality risk. Thus, IBMs can distinguish between scenarios where food effects are truly unimportant for the population, versus ones where they only appear unimportant because starving animals suffer higher mortality and surviving animals (i.e. those in the population) are those that were not limited (Kleppel et al., 1996). Many IBMs were developed to assess ontogenic changes in zooplankton demography (e.g. Carlotti & Nival, 1992; Miller & Tande, 1993; Aksnes & Ohman, 1996; Carlotti & Hirche, 1997), and explore how spatial patterns in populations arise from responses of individual copepods or ichthyoplankters to heterogeneous environmental conditions (e.g. Davis et al., 1991; Werner et al., 1993, 1996; Carlotti & Raddach, 1996; Hinkley et al., 1996; Grunbaum, 1998, 1999; Carlotti & Wolf, 1998; Flierl et al., 1999).

New models with sophisticated mathematics formalize old modeling approaches

In the late-1980s and throughout the 1990s, new plankton models were developed using sophisticated mathematical approaches that formalized the trial-and-error ways model investigations had been conducted before. For example, earlier studies typically projected a particular model structure and set of parameter values forward in time from some initial state, examined how well results could match data, and 'tweaked' models repeatedly until simulations were consistent with observations. But, in the late-1980s, biologists began using a new mathematical technique that solved the inverse problem (e.g. Vezina & Platt, 1988; Ducklow et al., 1989). That is, given some pre-defined model structure and set of observations, the inverse model produces a set parameters or rates that result in the best fit between model and data. 'Best fit' is measured in terms of minimized quantities such as differences between measured and modeled biomass or fluxes between ecological components. In this way, inverse modeling is conceptually similar to statistical regression, but is created for situations with fewer observations, and requires more intensive computation.

During the 1990s, inverse models, which are the basis of data assimilation, were applied to a variety of problems to estimate biological rates and associated fluxes (e.g. Huntley et al., 1994; McGillicuddy et al., 1995a,b; Lawson et al., 1996; Aksnes & Ohman, 1996; Ohman & Wood, 1996; Aksnes et al., 1997). Other kinds of new plankton models were constructed by combining mechanistic formulations and novel statistical techniques to infer dynamical processes underlying time-series observations (Carpenter et al., 1993; Kendall et al., 1999). Identification of key processes was also assessed using algebraic methods, such as analysis of orthogonal eigenfunctions (Flierl & Davis, 1993), designed to determine factors contributing to the dominant modes of variability. Stability analysis, an algebraic method that examines relative rates of change of biological processes for small perturbations in state variables, was used to predict how systems would respond to changes in ecological conditions (Armstrong, 1999; Pitchford & Brindley, 1999).

Modeling realistic circulation and plankton dynamics

Owing to increased computational power and higher resolution physical data, circulation models in the 1990s were able to produce realistic time-varying regional and basin-scale flows in three dimensions. These models often incorporated advanced descriptions of turbulence (e.g. Mellor & Yamada, 1982), thereby greatly improving modeled mixed-layer physics. Availability of these flow fields allowed for more accurate quantification of physical–biological interactions (Franks, 1997b), and provided new opportunities for oceanographers to study the effects of advection and mixing on plankton dynamics.

There was continued use of Lagrangian techniques to explore spatial and temporal patterns resulting from interaction of plankton behavior with the circulation. Models incorporated various kinds of plankton motility, from treating them as passive particles, to assuming they could maintain themselves at a particular depth, to cueing their behavior to specific environmental factors (e.g. light, temperature, prey density). These studies were able to estimate time-scales over which plankton were retained in an area, suggest mechanisms of dispersal, and quantify transit times between different regions (e.g. Hannah et al., 1998; Bryant et al., 1998). Some investigations were even able to identify circulation features, such as convergence and recirculation zones, which were previously unrecognized, but which greatly affected spatial distributions of organisms (e.g. Hood et al., 1999). As these Lagrangian studies follow an ‘individual’ particle, they naturally lend themselves to coupling with IBMs. One such coupling explored the demographic patterns of *Calanus finmarchicus* in the Gulf of Maine (Miller et al., 1998). Since *C. finmarchicus* egg production creates new individuals at a rate of roughly 50 per day, following every individual was still a computationally overwhelming problem for machines of the 1990s. These authors kept the problem tractable by starting with a small number of overwintering animals, and sub-sampling the modeled population as their offspring matured.

Most models coupling realistic circulation fields to plankton dynamics did so in an Eulerian manner, producing spatial patterns of population densities and estimates of production and biochemical fluxes (e.g. Sarmiento, 1993; Lewis et al., 1994; Franks & Chen, 1996; Kawamiya et al., 1996; Slagstad & Tande, 1996). Several of these simulations were designed to dynamically interpolate between observed

data at different points in time to diagnose the factors controlling observed changes. For example, models initialized with early-winter spatial data for *Calanus finmarchicus* and *Pseudocalanus* spp. in the Gulf of Maine/Georges Bank region, and attempting to reproduce observations for spring, strongly indicated that extreme food limitation occurred in the Gulf (Lynch et al., 1998; McGillicuddy et al., 1998). Sensitivity studies with these models highlighted other important features of the system, such as high mortality rates of early life-stages, reproductive status of females and vertical distributions of animals over deeper water. As these features were unobserved in historical surveys, the model investigations were able to indicate quantities needing sampling in future field surveys.

Modeling in the new millennium so far

The year 1999 marked 60 years since Fleming wrote the first mathematical model to describe plankton dynamics. During those six decades, models were used as frameworks for synthesis, as ways to identify gaps in our knowledge, as guides for future research, and as hypothesis-testing tools. They were also used to estimate unmeasured quantities, to aid interpretation of data, and to predict responses to environmental changes. *In silico* research in the new millennium so far has continued to use models for such applications. Many cutting-edge studies have come from a new generation of scientists, who grew up in the information age, accept the *in silico* approach as a valuable research tool, and who were trained by modeling gurus of previous eras.

Several process studies conducted by these young researchers employed the new modeling approaches that emerged in the 1990s. Thorough stability analyses were used to revisit the issue of higher predation, and assess dynamical effects of processes such as omnivory, vertical mixing and detrital remineralization (e.g. Edwards & Yool, 2000; Edwards et al., 2000; Edwards & Bees, 2001; Edwards in press). IBMs were used to explore how foraging strategies and development of individuals in patchy food environments affected population demographics and spatial distributions (e.g. Leising & Franks, 2000; Crain & Miller, 2001). One of the most intriguing new works was an investigation of evolutionarily stable phenology for copepods, regarding the timing of their initiation and emergence from diapause (Fiksen, 2000), which used

a mathematical optimization method based on natural selection, called a genetic algorithm.

Budding scientists developed other models to simulate plankton dynamics and investigate controlling processes for specific regions. Ecosystem models coupled to different frequencies of physical forcing for the central Equatorial Pacific indicated internal waves had large influences on production, and suggested how data assimilation techniques could guide future model developments (Friedrichs & Hofmann, 2001; Friedrichs, in press). Three-dimensional ocean circulation models with realistic mixed-layer physics were coupled to ecosystem models having several forms of dissolved nitrogen to investigate mechanisms driving phytoplankton cycles in different regions of the Pacific (Kawamiya, 2000a,b). Eulerian studies of structured population dynamics and plankton transport in 3D regional flow fields investigated factors controlling seasonal trends of *Calanus finmarchicus* for different subregions of the Gulf of Maine, and suggested wind variability and food limitation were important sources of variability in secondary production (Gentleman, 2000; Lewis et al., 2001). Lagrangian particle tracking for the same region, demonstrated how wind variability could induce both temporal and spatial variability in plankton dispersal (e.g. Shore et al., 2000).

The future of *in silico* plankton dynamics

Looking back over the findings of historical models, we can see future directions for plankton dynamics research. *In silico* investigations have demonstrated time and again that plankton dynamics are extremely sensitive to the nature of growth, grazing and predation responses. Modeling publications have continually pushed for a better mechanistic understanding of these biological processes, including how they change with changes in environmental conditions. We have learned of the importance of omnivory, size-class and ontogeny for understanding variations in community production, and there is a continued need to determine the fundamental structure of different systems. We have seen that regional circulation affects primary production through changing the physical and chemical environment, and affects the distribution of zooplankton populations through physical transport coupled with behavioral response. We have also discovered that details of vertical mixing are essential for estimating vertical fluxes, and variability in winds and water density contribute to variability in spatial distri-

butions. Hence, there is a continued need to improve our descriptions of the circulation, especially in critical areas, such as convergence and divergence zones and fronts, and to understand the scales of variability in the circulation arising from variability in physical forcing.

Plankton models in the future will essentially be unconstrained by computational capabilities as computational power in the 21st century has come a long way from the ENIAC – we are now seriously talking in terms of trillions of calculations per second. Although we will be able create models at levels of complexity that were previously inconceivable, we should recognize that a model's utility is maximized when it is employed in the same judicious manner advocated by Bruce Frost, who said "...the model has been kept as simple as possible to facilitate interpretation" (Frost, 1987), which is in keeping with Albert Einstein's sentiment that "Everything should be as simple as possible, but not simpler." The real challenge for future modelers – and other scientists – studying plankton dynamics is to determine what constitutes "as simple as possible".

The innovations and implementations of historical studies provide a context for making this determination. Past researchers developed ingenious ways of simplifying their models, recognizing, for example, when situations justified neglecting advection, or when circulation effects could be represented using two-layer sea or chemostat formulations. They forced models with time-varying environmental factors when these were known, and they solved for equilibrium conditions when this was acceptable. They adjusted parameters and removed (or added) processes and community structure as indicated. They determined where sensitivities lay, and whether results were robust or whether the model design had to be refined.

We can direct our increased computational ability to assess whether we have attained "as simple as possible". We can now make calculations so rapidly that it is possible to perform thorough sensitivity studies to assess which components and processes are critical to the dynamics and which are redundant. It is also possible to readily incorporate sophisticated mathematical approaches in these models, because the algebraic manipulations and statistical formulae forming the basis of such methods are standard components of most mathematical software packages today. These software packages also make it easier to visualize both model results and data, with color images, movies and easily manipulated graphical controls, which facili-

tates interpretation of results, and often reveals features of both actual and modeled systems that may not have been predicted *a priori*.

In silico studies of the future will continue to focus on how interactions of biological and physical processes lead to observed temporal and spatial patterns in plankton populations and production, and will strive to improve predictions of systems' responses to changes in environmental conditions. Through intelligent model development and careful assessment model assumptions, we will determine the minimal level of complexity necessary to explain observations. Models will continue to be improved as we gain more knowledge and data through field and lab investigations. By identifying where contradictory hypotheses cannot be resolved, or where predictions cannot be made with narrow estimates, modeling will provide direction for *in situ* and *in vitro* investigations. In this way, the *in silico* approach will continue to be an indispensable tool for researching plankton dynamics.

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