

The legacy of Gordon Arthur Riley (1911–1985) and the development of mathematical models in biological oceanography

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ABSTRACT

Gordon Arthur Riley (1911–1985) is remembered for his pioneering work in the development of marine ecosystem models during the mid-20th century. Using models that were necessarily simple because of the limited understanding of plankton physiology at the time, as well as the fact that calculations had to be done by hand, Riley studied the processes that control plankton stocks, production, and nutrient cycling, notably at Georges Bank. His great achievement lay not so much in the simulation of plankton dynamics *per se*, but rather in bringing to the fore the concept of using modeling as a means of explaining and interpreting the dynamics of marine ecosystems.

In this article, we examine Riley’s approach and philosophy to ecosystem modeling, which we discuss in context of modern day approaches. In particular, we focus on his landmark paper describing a model study of the dynamics of phytoplankton production on Georges Bank (Riley, 1946: *J. Mar. Res.*, 6, 54-73). After reconstructing the model, we show how Riley created new mathematical characterizations of the environmental dependencies of each process in the phytoplankton equation, and how these relate to modern day formulations. We then reproduce Riley’s results and conduct further analyses and sensitivity tests which serve to illustrate Riley’s conviction that mathematical models can provide clear, rational explanations for the observed temporal changes in ecosystems.

Riley’s methods and outlook are discussed in context of the ongoing debate about the merits of complex versus simple marine ecosystem models. Based on our analyses of Riley’s model, as well as his own critiques, we argue that although recent decades have seen a proliferation of complex ecosystem models that are intended to reflect our expanded understanding, the doctrines proposed by Riley are no less relevant today. In particular, Riley noted that while increasing model complexity is generally desirable, it can only be done within the confines afforded by observational data and knowledge of the physiology and ecology of key species and their interactions.

1. Introduction and historical background

Recent decades have seen a proliferation of marine ecosystem models, and in particular the development of complex models that include multiple plankton functional types, multiple nutrients, dissolved organic matter and the microbial loop, etc. This emphasis

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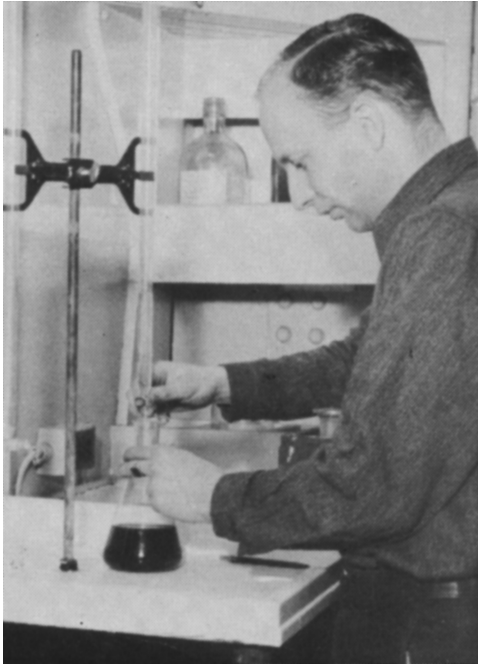


Figure 1. Gordon A. Riley (from Wroblewski, 1982).

on representing the many diverse organisms and processes that characterize marine food webs seems a far cry from the models produced during the pioneering era of the mid 20th century. The work of Gordon Riley is particularly relevant in this regard, an illustration of how simple models, with formulations chosen carefully on the basis of observation and experiment, can be used to provide new insight into the functioning of marine ecosystems. Riley's achievements were in turn to inspire the generations that followed including other legendary marine modelers such as John Steele and Mike Fasham (Gentleman, 2002). Riley was remarkably philosophical and self critical in his outlook and writing, displaying a discerning and shrewd rationality of thought in his approach to science. It is never a bad idea to go back to basics and, through an appreciation of the legacy that Riley has bestowed upon us, we would do well to revisit the methods of marine ecosystem modeling in use today.

Gordon Arthur Riley (1911–1985; Fig. 1) was educated at Drury College, Missouri, before progressing with a M.S. degree in experimental embryology from Washington University in 1934. Although he initially intended to pursue work in embryology, having moved to Yale in the autumn of that year, he was instead captivated by the lectures of George Evelyn Hutchinson and was awakened to the exciting world of limnology. Riley quickly switched disciplines, becoming Hutchinson's first graduate student as he embarked on a PhD focused on the copper cycle of lakes in Connecticut. He readily embraced Hutchinson's approach to

science, namely testing hypotheses and studying populations in terms of dynamic processes such as rates of production and consumption. Thus, casting aside the empirical tradition of fact gathering in ecology, Riley embarked on a journey of discovery based on a rigorous quantitative ideology. He was, however, no desk-top scientist immersed solely in numbers and equations, having developed a liking for going to sea following a cruise to the Gulf of Mexico in 1937. Hired by Albert Parr as a marine biologist at the Bingham Oceanographic Laboratory in the following year, he was to investigate the factors controlling primary production in Long Island Sound. Soon afterward he joined the research vessel *Atlantis* to undertake similar studies on a series of cruises to Georges Bank. Initially adopting statistical approaches to unravel the relationships between plankton and environment, Riley was to turn his attention to the use of differential equations for this purpose. The resulting mathematical modeling of plankton dynamics, underpinned by a sound knowledge of physical oceanography and plankton physiology, is surely Riley's greatest achievement (Mills, 1989).

The ecosystem models developed by Riley were necessarily simple because, as he acknowledged, "I didn't know how to escape from the simplistic constraints of the linear food chain," and that "further advance could not be made until we had a better knowledge of both physiological ecology and mixing processes in the surface layer of the ocean" (Riley, 1984). Nevertheless, he had the foresight to appreciate that, despite being "oversimplified," these models were sufficiently faithful to the real world to be useful. Our knowledge of marine ecology has advanced considerably since Riley's day. Model development has advanced in tandem, the impetus being to include advances accrued from observation and experiment in order to ensure that key processes and system feedbacks are adequately represented (Raick *et al.*, 2006). Contemporary models often incorporate dozens of state variables, require the specification of hundreds of parameters and, when run in 3D general circulation models, produce output files that are giga- or tera-bytes in size (e.g., Moore *et al.*, 2004; Le Quéré *et al.*, 2005). The modern perception appears to be that complexity is necessary, in which case the simple models of yesteryear can be easily castigated as being unrepresentative of the many processes essential to ecosystem structure and function (e.g., Le Quéré, 2006). One is left wondering what Riley would have made of all of this, and whether the modeling method as we know it today has diverged from the foundations that he laid down 70 years ago.

In this article, we examine Riley's approach and philosophy to ecosystem modeling, focusing in particular on his landmark paper describing a model study of the dynamics of phytoplankton production on Georges Bank (Riley, 1946). Of all his papers, he was most proud of this one. "I really cudgelled my head harder on that than on anything else I've ever done," Riley remarked, "... The '46 paper was the hardest one ... that kind of set the pace and everything else came along more smoothly" (Riley, 1980). We reconstructed this model and were thereby able to dissect Riley's approach as well as provide additional analysis which serves to further strengthen, beyond the material published by Riley himself, the case for the utility of simple models as tools for ecological research. We conclude by discussing Riley's

methods and outlook in context of contemporary oceanography, with a view to engaging the debate about the merits of complexity versus simplicity in models used to address issues such as the response of ocean biota to changing climate.

2. The dawn of biological oceanography as a quantitative science: Riley and the “synthetic method”

In the early 20th century, most ecologists were preoccupied with fact gathering in what was primarily a descriptive discipline. Quantitative reform was amazingly slow in forthcoming. One voice to buck the trend was that of Thomas Park, an American population ecologist, who berated ecologists for having “a great amount of careless observation and experiment, misdirected overenthusiasm and lack of intellectual focus” (Park, 1939). It was necessary, he argued, to formulate understanding in terms of concepts that had a theoretical basis, a change of emphasis that would require a “well planned program of refurbishing”. Riley and Hutchinson were suitably renegade to extol Park’s philosophy, “young Turks bringing quantitative reform to ecology in the United States” (Mills, 1995). Hutchinson’s approach to scientific investigation had been rigorously mathematical from the outset. He is well known, for example, for his quantitative analysis of phosphorus cycling in Connecticut lakes (Hutchinson, 1941). Riley enthusiastically joined Hutchinson’s revolution in approach. “This was the way we were going,” Riley remarked, “and damn it we were going to do it even if it wasn’t appreciated and we had a rather snooty attitude towards some of those old boys that were still content to publish species lists and call it ecology” (Riley, 1980).

The development of correlation methods within statistics had been pioneered by Sir Francis Galton toward the end of the 19th century and Riley enthusiastically embraced the new method of multiple regression. He took a statistics course given by Oscar Richards, a professor of international renown who published widely on biology and microscopy. Richards had, for example, an interest in the factors controlling the growth of yeast (e.g., Richards 1928a,b) and his mathematical approach to solving problems such as this was likely a further source of inspiration for Riley. Indeed, the two men became friends and were to write a paper together on the growth of amphibian larvae (Richards and Riley, 1937). Riley chose to apply quantitative techniques to investigate the interplay between biology, chemistry and geology in lakes. Starting his PhD in 1936, he used multiple regression to examine how copper in lakes in Connecticut related to alkalinity, precipitation and organic matter content. During the final year of his thesis, Riley was invited by Albert Parr, director of the Bingham Oceanographic Laboratory, on a cruise to study plankton dynamics off the mouth of the Mississippi. He worked on plant pigments and nutrient chemistry. Suitably impressed, Parr was subsequently to offer him a job in the Bingham Lab and, without further ado, Riley’s career as an oceanographer was underway. Field work initially focussed on Long Island Sound, Riley’s interest being to elucidate the roles of different environmental factors in phytoplankton growth and spring “flowerings”. The work soon shifted to focus on Georges

Bank following a major initiative led by the Woods Hole Oceanographic Institution and it was this program, from 1939 to 1941, that was to provide the main foundation for Riley's modeling work. In terms of field work, Riley continued with pigment and nutrient analyses, augmented with light and dark bottle incubation experiments to study photosynthesis.

For the analysis and synthesis of Georges Bank data, Riley again used multiple regression, as he had for his PhD and in the study of Long Island Sound. A series of papers followed (Riley, 1941b, 1942, 1943; Riley and Bumpus, 1946) with the first of these providing a lengthy account of how phytoplankton correlated with various environmental variables, namely water depth, temperature and dissolved nutrients. The problem, however, was that no single variable had ultimate control of phytoplankton stocks, rather different factors came into play at various times during the season. Throughout much of the year, for example, chlorophyll and nutrients on Georges Bank were negatively correlated, as one might expect, but not in summer indicating the importance of other factors in controlling plankton stocks at that time (Riley, 1941b). Further, Riley understood that plankton stocks were a balance of opposing forces – accumulation and degradation, consumption and regeneration (Riley, 1941a). Low standing stock of phytoplankton could, for example, be due to unfavorable growth conditions (e.g., in winter) or grazing (in summer). Observed changes in the stocks of phytoplankton and other variables thus involved shifts in the balance of two or more processes. Riley depicted the relationship between plankton and their environment in Figure 2 (redrawn from Riley, 1941c) commenting that “the diagram as presented is admittedly far from complete”. Correlation analysis was of limited value in untangling the mire of interactions. For sure, the method went beyond the generally qualitative work that had gone before and was useful in identifying which environmental variables were potentially important. But it provided little evidence as to how the variables operated. “The multiple correlation coefficient obtained,” Riley reflected, “...implies no causal significance” (Riley, 1939). Further, just as puddles under a sunny sky say nothing of the snowman that perished in the heat, Riley realized that statistics could not adequately account for the fact that the state of an ecosystem at any point in time is dynamic and depends on history. As he put it, “observations as they exist in successive moments do not tell us much about how populations got that way” (Riley, 1984).

The stage was set for Riley to adopt a new theoretical approach – the “synthetic method” as he called it – to plankton modeling. Hutchinson had always maintained that populations needed to be studied in terms of dynamic processes; i.e., the way in which production and consumption are affected by variable ecological factors. Thus, environmentally-dependent rates of change, expressed as differential equations, provided the main emphasis rather than the study of correlative relationships between variables. The idea was to “establish continuity between some purely descriptive studies that have been made and mathematical concepts based on what seem to be logical assumptions about plankton physiology” (Riley, 1946). The approach should be capable of “discriminating between cause and effect and helping to establish certain quantitative relationships that are not likely to be derived empirically” (Riley, 1946).

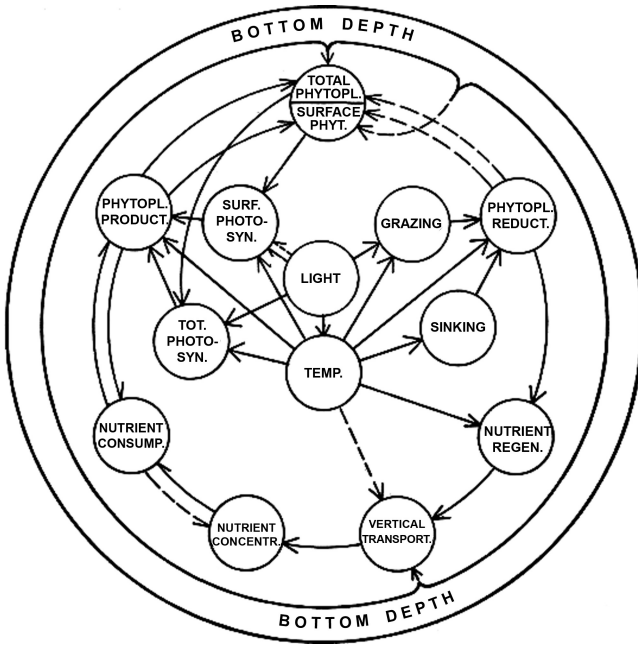


Figure 2. Relationships of plankton and environment (redrawn from Riley, 1941c).

Mathematical models had by now been used for some time in physical oceanography, the first steps having been taken by a Scandinavian meteorologist, Henrik Mohn and his colleague Cato Guldberg. Together they had developed equations to describe cyclonic systems in the atmosphere that took into consideration the effect of the Earth's rotation, centrifugal and tangential forces involved in air movement, and friction. Mohn realized the potential for applying the principles of mathematical meteorology to ocean currents and was able to extend his approach and calculate both surface and deep currents in the Norwegian Sea from wind velocities and the earth's rotation (Mohn, 1887), an outstanding achievement for the late 19th century. As was the case for Riley and biological oceanography, however, theoretical approaches to ocean circulation became accepted only slowly within a discipline that was entrenched in the notion that accumulation of data would in itself provide the desired insight into the nature and causes of ocean circulation (Mills, 2009). Nevertheless, notable contributions were made by, amongst others, Vilhelm Bjerknes (Bjerknes, 1898), O. Krümmel (Krümmel, 1907, 1911) and V.W. Ekman (Ekman, 1905) (e.g., see von Arx, 1962; Mills, 2009).

Riley took an interest in physical oceanography and was aware of the mathematical rigour being applied to that discipline. He was, for example, impressed by Sverdrup's chapters on physical oceanography in *The Oceans* (Sverdrup *et al.*, 1942). He also knew of the theoretical work that had been applied to the study of population growth. Pierre Verhulst,

and later Raymond Pearl, had introduced equations, based on the ideas of Thomas Malthus, that included the concepts of exponential growth and carrying capacity (Kingsland, 1985). In the early 20th century, Alfred Lotka and Vito Volterra were to extend the basic concept of population growth to their well-known equations for the dynamics of a predator-prey system (e.g., see Lotka, 1956), developments which Riley was well acquainted with. But it was a meeting with Richard Fleming, a chemical oceanographer based at Scripps Institution of Oceanography, that was to pave the way for Riley's transition to the theoretical approach. Fleming wanted to understand the factors controlling the spring phytoplankton bloom at high latitudes and developed a model that tracked changes in phytoplankton, P , using a single differential equation (Fleming, 1939):

$$\frac{dP}{dt} = [\mu - (b + ct)]P. \quad (1)$$

Here, Fleming assumed that phytoplankton have a constant growth rate, μ , representative of when there are abundant nutrients, sufficient light and suitable physical conditions for growth. The bracketed term $(b + ct)$ represents the fraction of phytoplankton removed by grazing, which was assumed to increase linearly over time. Fleming used the model to study the diatom bloom that occurred in the English Channel during the spring of 1934, adjusting parameters b and c to provide an exact fit between the initial cell number and the maximum observed after 37 days. The resulting simulation for the course of the bloom showed a close match with observations. "Computed production agrees excellently with estimates based on phosphate utilization," concluded Fleming. After publishing his seminal paper (Fleming, 1939), Fleming changed direction, applying his oceanographic skills instead to various other problems, including that of undersea warfare.

Fleming personally demonstrated his model to Riley. It was, however, an inauspicious start as Riley failed to be impressed with the work, commenting that it was "merely a slight adaptation of the Lotka-Volterra prey equation" and that the results appeared "self intuitive" (Riley, 1984). Further, the model was too simple for Riley's liking. The assumption of, for example, a constant phytoplankton growth rate seemed illogical given the multitude of environmental variables impinging on it. Nevertheless, Riley was complimentary of Fleming in his writing, describing his model as an "excellent theoretical treatment" of the subject (Riley, 1941a). He later remarked that Fleming's approach instilled a "pure kind of theory" (Riley, 1980), paving the way for his own advances in the field.

3. Riley's 1946 phytoplankton model

As Riley acknowledged, his development of the synthetic approach was rather slow in forthcoming, partly because of the war effort. "I really had no time at all to work on these things," he remarked (Riley, 1980). Nevertheless, develop it he did, the work coming to fruition in his study of the factors controlling the seasonal phytoplankton dynamics on Georges Bank (Riley, 1946). Riley's approach, like that of Fleming, involved just a single state variable, phytoplankton biomass (P), but incorporated an improved description of the

growth and loss terms, namely average photosynthesis in the euphotic zone (\bar{P}_h), respiration (R) and grazing (G):

$$\frac{dP}{dt} = (\bar{P}_h - R - G)P. \quad (2)$$

Riley recognized that these three terms varied seasonally but, unlike today where there are established formulations characterizing the relevant environmental dependencies, he had to develop most of the relationships himself. He therefore set about constructing a model that synthesized the existing literature on plankton physiology, as well as exploiting insights based on his own experiments and statistical correlations. "Insofar as possible," Riley remarked, "I was using both seagoing and lab experiments to derive the necessary physiological coefficients, but the data were so fragmentary that I had to introduce a lot of arbitrary assumptions." It was a challenge indeed as "by modern standards, the results may look primitive, but in the context of what was known at that time, it required more hard cogitation than anything else I have done" (Riley, 1984). It should be noted that what Riley called photosynthesis would today probably be referred to as gross growth because his \bar{P}_h term includes the influence of nutrient uptake, a process which is separate to carbon fixation. We keep with Riley's definition in order to keep the description provided herein as faithful as possible to the original, but it is necessary to be aware of the distinction because of the disparity with the contemporary literature.

Photosynthesis in the model was influenced by light, turbulence (via mixing depth) and nutrients. The first of these, light, was accorded primary status on the basis that numerous investigators, including Riley, had found that "photosynthetic rate in actively growing cultures is proportional to light intensity within wide limits" (Riley, 1946). Based on bottle experiments he had carried out on deck during the cruises to Georges Bank (inset to Fig. 15 in Riley, 1946), Riley assumed a linear relationship between photosynthetic rate, P_h , and incident solar radiation, i.e. $P_h(I) = pI$, where parameter p was a growth constant. Riley knew that light decreases exponentially with depth, z , and formulated this dependency, in the same way that many models do today, as $I_z = I_0 \exp(-kz)$ where I_z and I_0 are light at depth z and the ocean surface respectively and k is the extinction coefficient. He defined the depth of the euphotic zone, z_{euph} , as the depth at which light intensity has a fixed minimum value, I_{min} (z_{euph} is then equal to $\ln(I_0/I_{min})/k$), which approximated the light value at the maximum depth of photosynthesis based on measurements in the western North Atlantic by Clarke (1936). It is worth noting that Riley's use of a fixed light level to define the euphotic zone implies that the euphotic zone depth varies with both the rate of light extinction in the water column (Secchi disc reading) and surface light intensity (such that z_{euph} varies seasonally). Nowadays, the depth of the euphotic zone is usually expressed as a percentage of surface irradiance, i.e. depends only on Secchi depth. Average photosynthetic rate in the euphotic zone, in the absence of limiting factors other than light, was then calculated by integrating $P_h(I)$ with respect to z throughout the euphotic zone and dividing by the euphotic zone depth.

Next, Riley reduced the vertically-averaged light-dependent photosynthetic rate by two nondimensional limitation factors, L_V and L_N (Riley used “(1-V)” and “(1-N)” respectively; our nomenclature avoids possible confusion that may arise if turbulence and nutrients are denoted V and N) which quantify the effects of turbulence (more specifically, the fraction of time spent mixed below the euphotic zone) and nutrients, respectively. In the case of the former, photosynthesis was decreased whenever the depth of the mixed layer, z_{mix} , was deeper than the euphotic zone using a linear scaling, i.e., $L_V = z_{euph}/z_{mix}$ applied only for $z_{euph} < z_{mix}$ (here also, our nomenclature differs from Riley’s, in that he used z_1 and z_2 for z_{euph} and z_{mix} respectively). Regarding L_N , Riley assumed that photosynthesis was decreased when phosphate, $Phos$, was below a critical level, $Phos_{crit}$, citing experimental work with diatom cultures undertaken by Ketchum (1939). A rectilinear dependency analogous to L_V was used, i.e., $L_N = Phos/Phos_{crit}$, applied only for $Phos < Phos_{crit}$. Thus, the average photosynthesis in the euphotic zone was calculated as:

$$\bar{P}_h = \frac{pI_0}{kz_{euph}}(1 - e^{-kz_{euph}})L_N L_V. \quad (3)$$

Respiration by phytoplankton was relatively more straightforward to parameterize. Riley chose a formulation based on his own analyses of measured rates for the plankton community in Long Island Sound:

$$R = R_0 e^{rT}, \quad (4)$$

where T is temperature, R_0 the rate at 0°C , and constant r expresses the exponential rate of change with T .

Finally, there was the question of characterizing grazing. Fleming’s earlier model had used a formulation in which zooplankton were assumed to have a constant filtration capacity (constant clearance rates), which is equivalent to assuming they exhibit a Holling Type 1 functional response in modern terminology (Holling, 1959). Riley also assumed a constant clearance rate (parameter g , described by Riley as the “rate of reduction of phytoplankton by a unit quantity of animals”) such that grazing, G , was related linearly to the abundance of zooplankton, Z :

$$G = gZ. \quad (5)$$

Riley justified this assumption based on his knowing that the greater part of the zooplankton population at Georges Bank were filter-feeders (i.e., copepods) which process a relatively constant volume of water per unit time, irrespective of the quantity of food material present. While Riley acknowledged that grazing might be expected to correlate with temperature, his field data did not support a direct dependency and he therefore concluded that other (unknown) physiological factors must counteract any temperature effect. The major difference from Fleming’s model regarding grazing was that, whereas Fleming had no data and so assumed that the zooplankton population increased linearly over time during

the phytoplankton bloom, Riley was able to use an annual cycle for Z based on actual numbers measured on the Georges Bank cruises (Riley and Bumpus, 1946).

The model thus depended on just 6 parameters (p , I_{min} , $Phos_{crit}$, r , R_0 and g) and 6 environmental forcing variables (I_0 , k , $Phos$, z_{mix} , T and Z). In order to solve for the temporal evolution of phytoplankton, Riley had to assign a value to each parameter, describe the seasonal variation in the forcing variables and solve the differential equation. These same tasks are performed by modelers today, yet remain a significant challenge even with our present day body of knowledge and computational resources.

Assigning values to parameters is often a tricky business, yet Riley was unfailingly conscientious in this regard. Parameter p , the photosynthetic rate per unit irradiance, was assigned a value of $2.5 \text{ g C(g C)}^{-1} \text{ d}^{-1} (\text{g cal cm}^{-2} \text{ min}^{-1})^{-1}$ which converts to $0.036 \text{ g C(g Chl)}^{-1} \text{ hr}^{-1} (\text{W m}^{-2})^{-1}$ assuming that photosynthetically active radiation (PAR) is 41% of total irradiance (Riley's I was total shortwave; P-I curves today use PAR), daylight accounts for 50% of the day (Riley's p represented a photosynthetic rate over 24 hours whereas modern P-I curves usually represent instantaneous rates) and a C:Chl ratio of 50 by weight. This value of p is within the range of 0.014 to $0.149 \text{ g C(g Chl)}^{-1} \text{ hr}^{-1} (\text{W m}^{-2})^{-1}$ derived by Forget *et al.* (2007) from *in situ* production data for a variety of marine systems in the Atlantic Ocean and eastern Canadian seaboard. I_{min} , the threshold light intensity that determined the base of the euphotic zone, was $0.0015 \text{ g cal cm}^{-2} \text{ min}^{-1}$ (Clarke, 1936) which converts to 1.05 W m^{-2} . This was approximately 1% of irradiance arriving at the ocean surface and is thus consistent with more recent definitions of the euphotic zone based on this criterion (e.g., Ryther, 1956; Letelier *et al.*, 2004; Gattuso *et al.*, 2006). Riley assumed a Q_{10} of 2 for respiration by setting $r = 0.069 \text{ }^\circ\text{C}^{-1}$. Similar Q_{10} values for phytoplankton respiration have been employed in other studies (Soetaert *et al.*, 1994; Waku and Furuya, 1998; Rose *et al.*, 2007). The respiration rate of phytoplankton at 0°C , R_0 , was set at 0.0175 d^{-1} , the mean of two estimates from Long Island Sound (Riley, 1941a). Finally, the clearance rate of grazers, g , was set at $0.0075 \text{ d}^{-1} (\text{g C m}^{-2})^{-1}$. This value was tuned by Riley, but within ranges for daily food requirements of *Calanus finmarchicus* estimated by Marshall *et al.* (1935). The resulting specific ingestion rates in the model were between 0.02 and 0.25 d^{-1} . The zooplankton assemblage at Georges Bank is characterized by species such as *Calanus finmarchicus*, *Centropages* spp. and *Pseudocalanus* spp. (Kane, 2007) which typically have specific grazing rates of between 0.01 and 0.5 d^{-1} (Durbin *et al.*, 1995; Mayor *et al.*, 2006; Debes *et al.*, 2008; Saage *et al.*, 2009). Modeling studies of the Georges Bank ecosystem have used a maximum ingestion rate of 0.5 d^{-1} (Franks and Chen, 1996, 2001), which is also consistent with Riley's calculated ingestion rates. The initial value of P also needed to be specified in order to run the model. It was also tuned, giving a phytoplankton biomass of 3.377 g C m^{-2} occurring at 15 days (one model time step) before 1 January.

Parameter $Phos_{crit}$, the phosphate concentration that defines the onset of the linear nutrient limitation in the model, was set at 0.55 mmol m^{-3} . In modern terminology, the equivalent half saturation constant for phosphorus is $0.275 \text{ mmol m}^{-3}$. Experimental estimates of this

constant tend to be rather variable, but may be similar in magnitude to Riley's (e.g., Stross *et al.*, 1973; Carney, 1987), although the values used in modeling studies are often at least an order of magnitude lower (e.g., Six and Maier-Reimer, 1996; Aumont *et al.*, 2003; Coles and Hood, 2007). It is now thought that nitrate and silicate are the limiting nutrients for phytoplankton growth on Georges Bank (Townsend and Thomas, 2001), suggesting that nutrient limitation is more severe than that represented in Riley's model. Riley had both phosphate and nitrate data at his disposal from the Georges Bank cruises and chose to use the former because, unlike nitrogen, the phosphorus cycle was relatively well understood at that time (phosphate was also easier to measure than nitrate).

The seasonal variation of forcing variables I_0 , k , $Phos$, z_{mix} , T and Z were all prescribed from data. Light at the ocean surface in the model, I_0 , was obtained from calculations based on latitude and atmospheric transmission published by Kimball (1928). The remaining variables were characterized by curve fitting data from the 6 Georges Bank cruises that took place between 1939 and 1941. The mathematical techniques for undertaking this interpolation were not well developed in Riley's day and so he probably did it by eye. The depth of the mixed layer, z_{mix} , was calculated from profiles of density and was "arbitrarily defined as the maximum depth at which the density is no more than 0.02 of a σ_t unit greater than the surface value" (Riley, 1946). This value is, however, not dissimilar to a threshold density criterion used today to define mixed layer depth, e.g. a 0.0125 kg m^{-3} difference from surface density (e.g., Monterey and Levitus, 1997; Thomson and Fine, 2003). The annual cycle for parameter k , the attenuation of light in the euphotic zone, was based on Secchi disc measurements using the same conversion as is done today (i.e., $k = 1.7/\text{Secchi}$). Curiously, however, this parameter is partially redundant because it varies with the reciprocal of z_{euph} (see above); the only effect of k on the vertically-averaged P_h term (Eq. 3) is therefore through its influence on L_V . The exact phosphate concentrations used to calculate L_N , presumably those at the surface, were not provided by Riley in his paper (Riley, 1946), rather the values of L_N were tabulated directly.

It should be noted that the data presented by Riley in his model-data intercomparison were averaged for the various cruises. In each case (January, March, April, May, June, September), data were collected throughout Georges Bank, between $40^\circ 40' - 42^\circ 10' \text{N}$ and $66^\circ - 69^\circ \text{W}$ (e.g., see Riley, 1941b). The depth of the water column is variable, typically between 55 and 73 m in the south and east, but is shallower, often less than 37 m, in the northwest (Riley, 1941b). This has an impact on spring bloom development which occurs about a month earlier in the shallower parts of the Bank.

There were no computers or electronic calculators available to Riley and so the computations had to be done manually, an impressive feat in itself. Riley devised a method wherein he could solve the differential equation over a series of time steps by assuming that the rate of change was constant for a period of 15 days and deriving an analytic formula for the phytoplankton density at the end of that 15-day period. Even this simplified integration method would have been onerous, as evaluation of the exponential and logarithmic terms for each time step would have had to be interpolated from tabulated values. Integrations

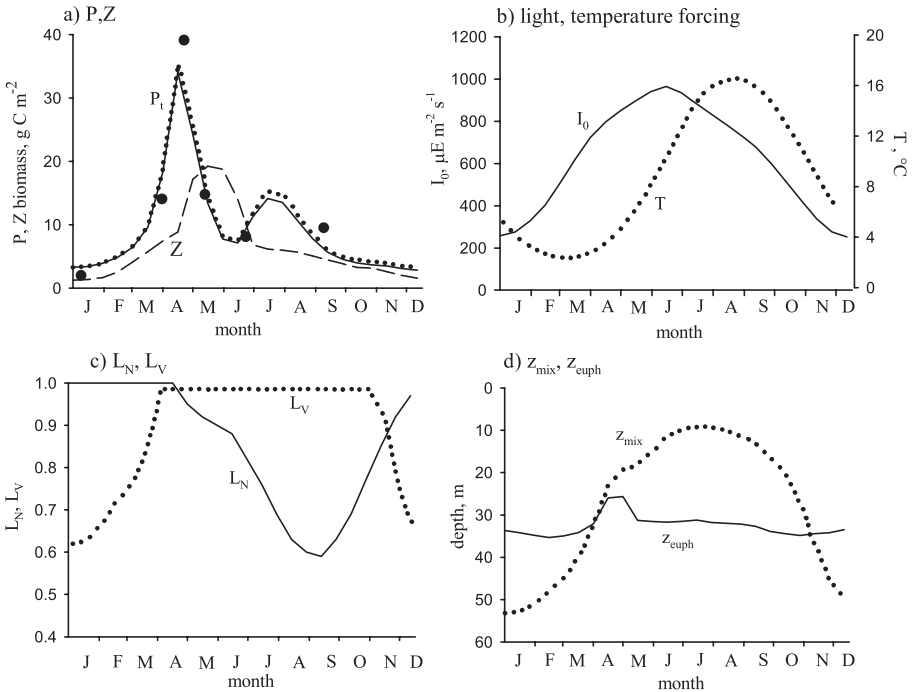


Figure 3. Riley's (1946) model of Georges Bank: (a) simulated seasonal cycle of phytoplankton biomass (solid line – our solution, dotted line – Riley's solution; large dots are cruise data for Georges Bank as shown in Riley, 1946) plus annual cycle of zooplankton (from data – used to force the model – dashed line); other variables used to force the differential equation for P were I_0 and T (Fig. 3b), L_N and L_V (Fig. 3c) and z_{euph} and z_{mix} (Fig. 3d).

likely took many hours, if not days, to complete. In the case of his later model of plankton dynamics in the western North Atlantic (Riley *et al.*, 1949), for example, in which steady state solutions were derived for simultaneous equations, calculations took as much as 25 to 30 hours of “arithmetic diddling” in order to complete (Riley, 1984).

Much to Riley's credit, all the information required to reconstruct the model, both equations and forcing, is provided in his 1946 paper. In order to fully appreciate Riley's achievement, and to explore the ramifications of the model in greater detail, we therefore set up the model ourselves. This was undertaken in Microsoft Excel – the resulting spreadsheet is available on request from the first author.

The annual cycle of phytoplankton as predicted by the model (both our version and Riley's) is shown in Figure 3a, along with the cruise data for Georges Bank (shown as Fig. 21 in Riley, 1946). The exact dates corresponding to the measurements of algal biomass were not tabulated by Riley. We estimated them as the midway point of sampling in each cruise (dates provided in Riley, 1941b). Phytoplankton data are provided in “Harvey units”

in Table 1 of Riley (1946), subsequently multiplied by 1.7×10^{-5} to convert to grams of carbon. Our solution is almost identical to Riley's, with the slight difference attributable to the limited precision that he was able to achieve when using tabulated values of exponentials and logarithms. Also shown in Figure 3a is the annual cycle of zooplankton, as interpolated by Riley from cruise data (Riley and Bumpus, 1946). The other forcing variables used in the model are shown in the remaining panels of Figure 3: I_0 and T (Fig. 3b), L_N and L_V (Fig. 3c) and z_{euph} and z_{mix} (Fig. 3d).

The agreement between model and phytoplankton data is remarkably good (Fig. 3a). It should be noted, however, that Riley tuned g and P_0 and so perhaps the fit is not surprising (we investigate this further by undertaking parameter sensitivity analysis: Section 4b below). The phytoplankton spring bloom is a well-known feature of Georges Bank, typically beginning in March or April and declining by late April or early May (Cura, 1987; Townsend and Thomas 2001, 2002; Thomas *et al.*, 2003). The model faithfully reproduces this bloom, with maximum phytoplankton concentrations occurring in the model in mid April. What is more curious, however, is Riley's prediction of a second, albeit smaller, phytoplankton bloom in late summer (July–August). Although there is evidence for a fall (Aug–Nov) bloom in the surrounding Gulf of Maine (Thomas *et al.*, 2003), there is no indication that blooms occur in the latter half of the year at Georges Bank. Riley's data were insufficient to resolve the summer phytoplankton values on Georges Bank and he made little comment on this feature. Indeed, rather surprisingly, Riley was unusually economical in his text supporting the closeness of the fit with data in Figure 3a, remarking merely that “the average error is 27%,” which was “the same order of accuracy as the statistical estimate” (Riley, 1946).

What Riley did instead was to let the results speak for themselves in graphical form by providing provocative diagrams showing how the rate of change of phytoplankton is affected by the balance of the three primary factors in the model, namely photosynthesis, respiration and grazing. We reproduced these diagrams from our version of the model, two of which are shown in Figure 4a (Riley's Fig. 18) and Figure 4b (Riley's Fig. 20). The first of these (Fig. 4a) illustrates how gross photosynthetic rate varies throughout the year due to seasonal variation in incident radiation, and then how the rate is diminished due to terms L_N (nutrient limitation during summer and fall) and L_V (as the depth of the mixed layer exceeds that of the euphotic zone). The second panel (Fig. 4b) shows what Riley calls “estimated rates of production and consumption of carbon,” namely the three terms in the phytoplankton equation, photosynthesis, respiration and grazing, expressed as specific rates ($1/P \, dP/dt$). The two loss terms (respiration and grazing) are stacked under \bar{P}_h so as to show when net growth is positive (the bottom edge of the grazing stack is greater than zero) or negative (less than zero). As a means of further characterizing the success and merits of Riley's approach, we reordinated these results to present them as they might more commonly be shown today. \bar{P}_h (gross primary production), net production ($\bar{P}_h - R$) and G are shown unstacked in Figure 4c, again as rates specific to phytoplankton biomass. These are then converted to fluxes of carbon per unit area in Figure 4d, thereby illustrating changes in carbon stock over time. Total (net) primary production (the area under the $P_h - R$ curve

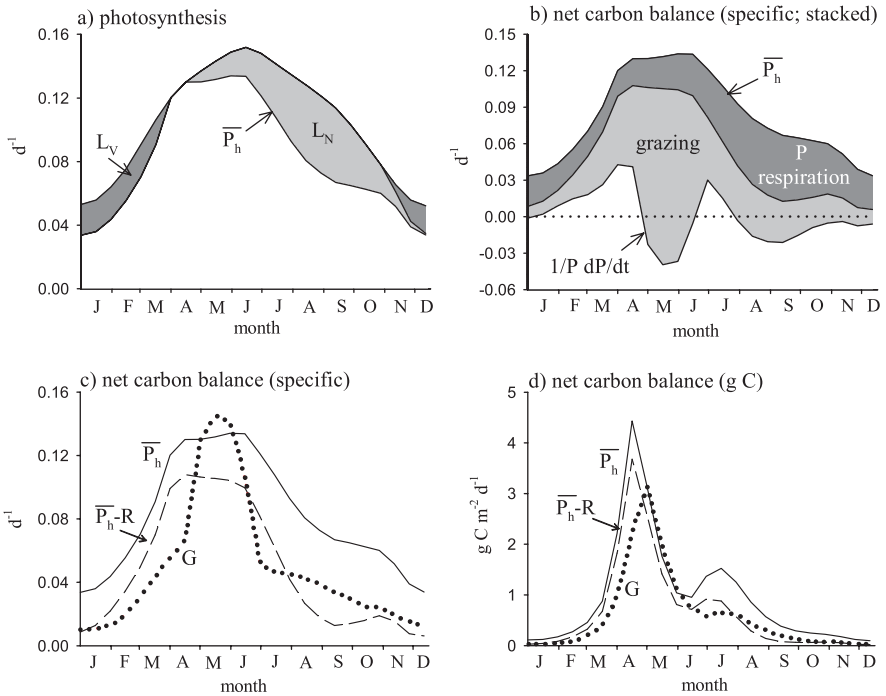


Figure 4. Carbon balance at Georges Bank from the model of Riley (1946): (a) photosynthesis, showing diminution of the maximum rate by L_N and L_V to give the realized gross rate, \bar{P}_h ; (b) production and loss terms for phytoplankton (biomass-specific, i.e. $1/P dP/dt$), upper bound is gross photosynthetic rate, lower bound net population growth rate, the difference between the two being accounted for by grazing and respiration; (c) biomass-specific rates as in panel (b), but re-ordinated illustrating the close coupling between production and grazing; (d) production and grazing rates expressed as C fluxes per unit area, $g C m^{-2} d^{-1}$. Equivalent versions of panels (a) and (b) appear in Riley (1946), as well as the cover of Wroblewski (1982). We derived panels (c) and (d), as well as (a) and (b), after reconstructing the model.

in Fig. 4d) is $233 g C m^{-2} yr^{-1}$ which, while on the low side, is not dissimilar to estimates of between 265 and $455 g C m^{-2} yr^{-1}$ for Georges Bank (O'Reilly and Evans-Zetlin, 1987).

These figures provide a quantitative demonstration of Riley's ideas about dynamic variation in controlling ecological processes, previously impossible without the synthetic approach. For example, the results clearly show that the specific rate of change of phytoplankton becomes strongly positive in spring as \bar{P}_h outstrips losses via respiration and grazing (Fig. 4b), and that net ideas photosynthesis ($P_h - R$) is in excess of grazing in spring (Fig. 4c,d). This supports Riley's previous statistical work, wherein he proposed that solar radiation and vertical turbulence limited production over winter with nutrients, temperature and grazing coming into play during the spring period (Riley, 1941b). Riley had noted that mean solar radiation doubled between January and March on Georges Bank and that, in

common with other areas including the English Channel (Atkins, 1928) and Long Island Sound (Riley, 1941a), the spring diatom bloom is correlated with this vernal increase in radiation (Riley, 1941b). Further, he grasped the importance of vertical turbulence in mixing phytoplankton below the “zone of active growth”. Indeed, Riley’s ideas on bloom initiation acted as a precursor to the principles later laid down by Sverdrup (1953) on the relationship between phytoplankton growth rate, light intensity and mixed layer depth.

By the end of April, grazing comes to the fore in the model, overtaking photosynthesis and sending the bloom into decline (Fig 4c,d), or as Riley put it, “the quick cessation of the flowering ... is a grazing effect” (Riley, 1947). Riley was undoubtedly aware that H.W. Harvey had concluded that “the sudden decrease in vegetation after the spring maximum [in the English Channel] was due to increased intensity of grazing” (Harvey, 1934). Fleming had also noted that “an increase in the number of grazers will reduce the diatom populations very rapidly” (Fleming, 1939). The role of grazing in controlling phytoplankton stocks is today undisputed (Banse, 2007) although other factors such as nutrient exhaustion and viruses may also be important in terminating phytoplankton blooms (Badoux *et al.*, 2006; Greenan *et al.*, 2008). The balance between production and grazing is a key feature of plankton dynamics, both at Georges Bank and in other systems (Banse, 1994) and so Riley chose well when selecting parameter g for tuning purposes.

Decreasing irradiance (at least after mid-June), as well as increasing limitation by phosphorus and temperature-dependent respiration beginning in late-April, nevertheless also play their part in terminating the spring bloom in Riley’s model (Fig. 4a). In reality, nutrient exhaustion often leads to sedimentation (Wassmann, 1994; Kjørboe *et al.*, 1996). This export flux may also serve as a significant loss term for phytoplankton during bloom periods and may be substantial at Georges Bank where much of this material settles on the bottom of the continental slope as shelf phytoplankton detritus (Walsh *et al.*, 1987). Curiously, Riley had noted that many diatoms on Georges Bank appeared senile, suggesting a loss via “natural death” rather than grazing (Riley and Bumpus, 1946), but nevertheless chose not to include a nongrazing mortality or explicit export flux term in his 1946 model. Other potentially important processes were also absent from Riley’s model. Although it took into account the fact that algal growth decreased when the depth of the mixed layer exceeded that of the euphotic zone (L_V), it did not consider the flipside of mixing on growth, namely that light levels within the mixed layer are relatively high, and growth enhanced, when the depth is less than that z_{euph} . Further, the model did not consider direct physical losses of plankton due to mixing or advection. Whereas Fleming had been explicit about what he included and neglected with his model, Riley was less diligent and we had to work carefully through his equations to determine what was included, ignored, or implicitly assumed.

4. Further analysis of Riley’s model

Riley’s model is a triumph, a milestone in the history of marine ecosystem modeling. Yet, other than the figures, Riley provided relatively little supporting analysis. It is peculiar that

he chose not to elaborate the text with a description and discussion of Figure 4b, as we have done above. Convention today requires that results be accompanied by such supporting text. Riley's omission probably did not help his cause in trying to gain widespread acceptance of his approach. Today, one also might expect to see sensitivity analysis of key parameters and assumptions. Whereas Riley also did not include this in his paper, he likely did perform sensitivity tests as part of his parameter tuning. Here, we undertake further analysis of Riley's model so as to illustrate the utility of such studies, and provide both historical background and additional information for the forthcoming discussion in context of modern methodologies.

a. Integration method

As with models today, Riley's approach involved using a differential equation that was too complicated to solve analytically, although an approximate solution could be found by numerically integrating over a series of discrete time steps. Typically, the solution would be obtained by integrating the equation for dP/dt (Eq. 2) directly, but Riley chose a different approach. Instead, he expressed this equation in terms of the specific rate of change, $f(t) = (\dot{P}_h - R - G)$:

$$\frac{dP}{dt} = f(t)P \quad (6)$$

and used the technique of separation of variables (giving $dP/P = f(t)dt$) to analytically integrate from the point in time τ to the point $\tau + \Delta t$:

$$\ln P_{\tau+\Delta t} - \ln P_{\tau} = f_{av}\Delta t \quad (7)$$

where f_{av} is the average value of $f(t)$ over the time interval:

$$f_{av} = \frac{1}{\Delta t} \int_{\tau}^{\tau+\Delta t} f(t)dt. \quad (8)$$

It is Eq. 7 that Riley provides for the reader (Riley 1946), although with a typographical error in that the Δt term is missing in the text (but not from his undertaking of the actual calculations). Using this approach, the model solution could be obtained by taking the exponent of the natural logarithm (i.e., $P_{\tau+\Delta t} = P_{\tau}e^{f_{av}\Delta t}$) once an estimate for f_{av} had been obtained from numerical integration of Eq. 8. Riley chose the approximation $f_{av} = f(\tau + \Delta t)$, which is exact only if $f(t)$ is constant for $\tau < t < \tau + \Delta t$, but otherwise incurs an error on the order of Δt (e.g., reducing Δt by half reduces the error by a factor of 2).

While Riley provides no rationale for his choice to separate the variables *a priori*, it has strength in that the error associated with the numerical method is limited to the ability to integrate $f(t)$ as opposed to the product $f(t)P(t)$. As the former quantity is less variable (Fig. 4b vs. 4d), his approach allows the use of a longer time-step in order to achieve an equal level of accuracy. Riley's choice of $\Delta t = 15$ days may seem grossly large in the

modern computational age, but one has to bear in mind that he was doing these calculations by hand and that evaluation even using this coarse temporal resolution of the annual cycle entailed significant labor. This choice does, however, make his use of $f_{av} = f(\tau + \Delta t)$ questionable because of the variation of $f(t)$ within each 15-day time period (Fig. 4b, and the values in Riley's table). Riley could have improved the accuracy of his estimates of f_{av} by solving Eq. 8 with one of the many numerical integration methods that existed in his day (e.g. Newton-Cotes, Gaussian etc.). For example, he could have used the so-called Mid-Point method which approximates f_{av} as the value at the mid-point of the interval (i.e., $f_{av} = f(\tau + \Delta t/2)$) or the Trapezoidal method which approximates f_{av} as the average of the value at each interval end point (i.e., $f_{av} = (f(\tau) + f(\tau + \Delta t))/2$). Both of these methods involve essentially the same computational effort as Riley's approximation, but with smaller error in that they are exact for an $f(t)$ that varies linearly over the time interval, and otherwise incur error on the order of Δt^2 (e.g. reducing Δt by half reduces the error by a factor of 4). It is not clear why Riley did not use one of these higher-order integration methods, nor whether he was even acquainted with them.

We investigated the extent to which Riley incurred errors during the numerical integration by comparing results obtained using his method of integration with those obtained by (1) using a very short Δt of 0.1 days and (2) when the two alternative integration methods, Mid-Point and Trapezoidal, are used (in each case with Δt of 15 days) (Fig. 5). Forcing variables were assumed to vary linearly within each 15-day period for these simulations. In order to get a fair comparison, in each case the model was initialized to ensure that P on Jan 1st was 3.323 g C m^{-2} (the effective initial condition in Riley's simulation based on his specification of P_0 : Fig. 3a). Riley's use of $f_{av} = f(\tau + \Delta t)$ meant that irradiance was relatively overestimated for each time step during the vernal increase in the early part of the year. The associated error increases with longer time steps and so lower phytoplankton growth is predicted with the 0.1-day time step compared to the 15-day time step and the spring bloom peaks 10 days later, and 15% lower, than in Riley's simulation (Fig. 5a). Without computers, the use of a 0.1-day time step was clearly impractical for Riley. If, however, he had kept his 15-day time step but instead used a more advanced integration method, such as the midpoint or trapezoidal, a level of accuracy similar to that using a time step of 0.1 day could have been obtained (Fig. 5b). Had he used an advanced integration method, the simulated mismatch in bloom timing may have motivated him to use different values for his tuned parameters. His results would, therefore, have likely been largely unaltered.

b. Parameter sensitivity

Sensitivity analysis is commonly undertaken to assess the robustness of model results and conclusions in the face of uncertain parameter values. No such analysis was demonstrated by Riley and so, in order to gain further insight into the performance of his model, we show in Figure 6 sensitivity of the predicted annual cycle of phytoplankton to parameters p

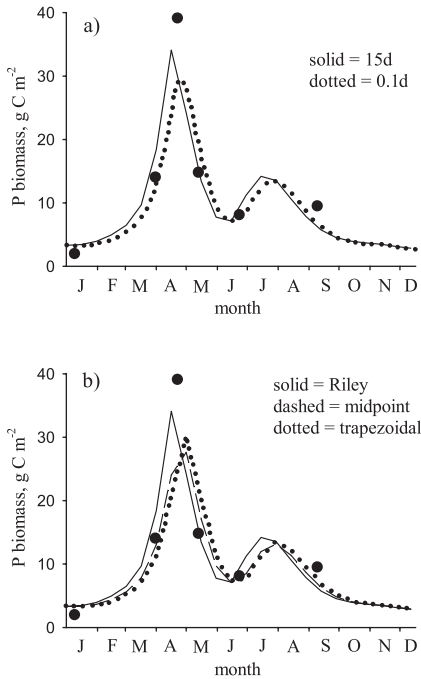


Figure 5. Comparison of model predictions for phytoplankton biomass as in the standard run of the model (Fig. 3a) with simulations using (a) 0.1 d (instead of 15 d) time step and (b) midpoint and trapezoidal integration methods. Data points as in Figure 3a.

(phytoplankton growth rate), g (grazing rate), r (temperature dependence of phytoplankton respiration) and P_0 (the initial phytoplankton concentration).

Even small changes in parameters p or g lead to the model diverging wildly from Riley's original run (Fig. 6a,b). Decreasing p or increasing g causes phytoplankton to die away during the latter part of the year. In contrast, increasing p or decreasing g disturbs the balance between phytoplankton growth and grazing to such an extent that phytoplankton proliferate unrealistically in the latter half of the year. Riley's model had a single state variable, P , with no inherent carrying capacity (no density dependence in the growth, respiration or grazing loss terms). Such aberrant model behavior is rendered less likely in models which use more than one state variable because of feedbacks between phytoplankton and the rest of the ecosystem, and prevents phytoplankton stocks from increasing *ad infinitum*. For example, when nutrients are dynamic such that they can get depleted as the phytoplankton population grows, the corresponding decrease in phytoplankton growth rate effectively acts as a density-dependence. Similarly, a dynamic balance between growth and grazing is maintained if zooplankton are represented explicitly as a state variable that responds directly to phytoplankton increase, e.g. giving rise to predator-prey oscillations (Popova *et al.*, 1997). No such feedback between system components takes place if, as in Riley's

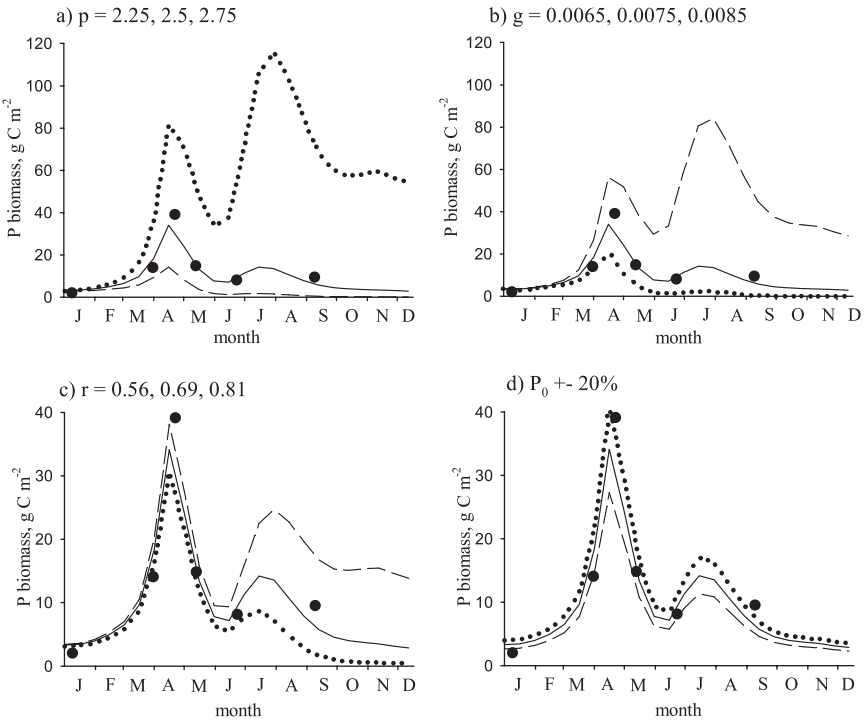


Figure 6. Sensitivity of phytoplankton biomass in Riley's (1946) model to parameters p (phytoplankton growth constant), g (grazing rate), r (phytoplankton respiration rate) and P_0 (initial phytoplankton biomass); standard run (solid line), lower bound (dashed), upper bound (dotted). Data points as in Figure 3a.

model, nutrients or zooplankton are imposed as external forcings. It is therefore apparent that p and g , as parameterized in Riley's model, have to be in perfect balance in order that the desired seasonal cycle of phytoplankton is obtained. One wonders how many simulations Riley worked his way through in order to achieve this goal.

Predicted phytoplankton dynamics in the latter part of the year were similarly affected by changing r , the temperature coefficient of respiration (Fig. 6c). Decreasing r leads to elevated phytoplankton production, the impact being greatest in the second half of the season because temperature is highest at that time. Finally, the model shows relatively little sensitivity to P_0 , although the magnitude of the bloom varied between 27.3 g C m^{-2} ($P_0 = 2.66 \text{ g C m}^{-2}$), 34.1 g C m^{-2} ($P_0 = 3.33 \text{ g C m}^{-2}$) and 40.9 g C m^{-2} ($P_0 = 3.99 \text{ g C m}^{-2}$).

5. In pursuit of excellence: Riley's modeling approach in context of contemporary oceanography

Riley's model was a masterpiece in its novel representation of the Georges Bank ecosystem, with the predicted seasonal cycle of phytoplankton showing close agreement with data

(Fig. 3a). The magnitude of Riley's achievement, however, lay not so much in fitting the data per se – as we have shown, this fit was sensitive to the values assigned to key parameters – but rather in bringing to the fore the new synthetic method and demonstrating its utility as a means of explaining and interpreting the dynamics of marine ecosystems. Riley's 1946 model showed how the seasonal cycle of phytoplankton at Georges Bank could be explained in terms of the interplay between phytoplankton growth rate and grazing, in a rigorous quantitative manner. Ask someone today just what modeling is all about and a likely reply is “making predictions on the basis of existing knowledge” (Anderson, 2010). We return to the subject of prediction later, but a more likely response from Riley would have been that models “help us to identify physiological and physical problems that have been neglected and are conceivably important,” and “frequently yield results that are not intuitively obvious” (Riley, 1984). Models quite simply provided a “way of thinking,” a means of clarifying thought (Riley, 1984). Or, as Gasol *et al.* (2008) and Anderson (2010) more recently put it, models allow us to synthesize existing knowledge and explore its ramifications, providing explicit quantitative descriptions to help clarify what we do and do not understand.

Riley knew all too well that new insight could only be gained from models if the theoretical principles applied are sound, underpinned by field data and physiological understanding of relevant processes. From the outset, he therefore confronted the issue of model complexity head on. Although he had the genius to see the potential merits of simple models, which are readily constrained by data and easy to conceptualize and analyze, this did not stop him from worrying about whether the assumptions made were too crude to be adequate representations of the real world. Indeed, Riley was remarkable in the extent to which he openly questioned the suitability of the simplifications that he imposed in his models. “At present this [modeling] can be done only tentatively,” he remarked, “with oversimplification of theory and without the preciseness of mathematical treatment that might be desired” (Riley, 1946). He worried about errors that occurred due to compromises in model construction, an example being the aggregation of all phytoplankton into a single state variable, “a sort of superspecies” (Riley, 1947).

On this kind of basis, simple models have provided an easy target for criticism over the years. Back in the 1970s, for example, Joel Hedgpeth, an expert on the seashore flora and fauna of southern California, published a paper with the controversial title “Models and Muddles” in which he referred to the “construction of elaborate diagrams and mystic-mathematical representations,” continuing, “...when taken with a grain of salt (preferably benzoate of soda), such models may stimulate further thought” (Hedgpeth, 1977). Model building in ecology is doomed to failure, it can be argued, because of the uniqueness and complexity in form and function of ecological systems (e.g., Peters, 1991). Riley's model of Georges Bank is, in contrast to the machinations of the skeptics, a triumphant demonstration of the role that simple models can play in ecology. It was to set alight a whole new field of research, paving the way for the nutrient-phytoplankton-zooplankton-detritus (NPZD) models that followed with key protagonists including John Steele (e.g., Steele, 1974), Joe

Wroblewski (e.g., Wroblewski, 1977) and Mike Fasham (e.g., Fasham *et al.*, 1990). Despite their simplicity, these models have by and large been successful at capturing bulk system properties such as chlorophyll and primary production which are constrained by nutrient availability, light and grazing, providing a robust platform for oceanographic work (Franks, 2002; Anderson, 2005). NPZD-type models continue to demonstrate their worth today in both regional and global general circulation modeling studies (e.g., Schmittner *et al.*, 2005; Gruber *et al.*, 2006; Okunishi *et al.*, 2007).

On what basis, then, have simple ecosystem models been apparently so effective? A possible answer is that, lowest-order, bulk properties and interactions tend to dominate the dynamics of marine ecosystems, at least as far as distributions of nutrients and phytoplankton are concerned. Provided light-dependent growth is included, most simple models should be able to predict the spring bloom that occurs in temperate high latitudes when the mixed layer shoals at the end of winter, providing an ideal light environment for algal growth. Of course, agreement with data often requires parameter tuning in which case the validity of equations and parameter values, and indeed the very robustness of modeling methodology, is rendered open to question. In Riley's model, for example, the crucial balance between phytoplankton growth and loss terms was achieved by adjusting the zooplankton grazing rate. One can take a cynical view of parameter tuning as a means of forcibly ensuring agreement with data (e.g. Passioura, 1996), the charge being that modeling is reduced to empiricism and modelers can produce any outcome they so desire (Aber, 1997). If potential falsification is at the heart of scientific practice (*sensu* Popper, 1963), and given that it may often be nigh impossible to falsify models (Franks, 2009), the very methodology of modeling is open to scrutiny (Anderson, 2010). The potential for compensating errors is all too real in the wake of parameter tuning, an example being that deficiencies in model physics have sometimes been offset by improvised biological parameterizations (Popova *et al.*, 2006). Of course one can argue that validation provides the necessary rigor, but the harsh reality is that few modeling studies undertake validation in the sense of critical testing against independent data (Arhonditsis and Brett, 2004).

One way to promote credibility, as Riley well knew, is to restrict the degree of under-determination by grounding models with sufficient data to underpin the chosen parameterizations, as well as to fit and compare the model: "A necessary prerequisite ... is a thorough knowledge of the physiology and ecology of particular species and ecological groups" (Riley, 1952). Adding complexity to models was fine by Riley, indeed desirable, but only within the confines afforded by data and physiological understanding. Riley was self trained as a jack-of-all-trades, including marine biology, physics and mathematics. Every avenue was pursued to try and ensure that realism was incorporated into the chosen assumptions, equations and parameters. As an ardent seafarer, he could tackle some of this head on. Riley is well known, for example, for his bottle experiments that examined the effects of nutrient supply, grazing, light and temperature on primary production and stocks of chlorophyll (e.g., Riley, 1941b). Riley's approach is in stark contrast to what Franks (2009) bemoans as the often mindless setting of parameters in models today, without critical thought or discussion.

Parameter values and functional forms may simply be taken from previous modeling papers and one may have to go back decades in the literature to find the original paper that documented the parameter in question, only to find that it had been set to provide a fit with data without regard to physiological or ecological relevance (Franks, 2009). A good example is provided by Fasham *et al.* (1990), who used the zooplankton multiple-prey functional response of Hutson (1984) because, in their particular application, it produced a more robust model as compared to other responses. They noted, however, that there is a peculiar effect in the Hutson formulation in that total grazing can increase as the concentration of one prey item approaches zero. Yet, despite Fasham pointing out this shortcoming and stating that “we know of no data that might lend support to any of these switching functions...the parameterization of zooplankton feeding preferences is a topic requiring further theoretical development,” decades of NPZD modelers have continued to use the Hutson formulation, citing the Fasham *et al.* ecosystem model.

Our experimental/observational knowledge base on the ecology of marine organisms has expanded greatly in the last few decades. Model complexity has proliferated in tandem, exemplified by the so-called plankton functional type (PFT) models which explicitly represent multiple plankton groups such as diatoms, coccolithophores and nitrogen fixers (e.g., Moore *et al.*, 2002; Gregg *et al.*, 2003; Le Quéré *et al.*, 2005). The argument is that realistic predictions can only be expected if key processes associated with system feedbacks are represented (Doney, 1999; Pomeroy, 2001). Yet, Riley’s emphasis on the requirement for physiological understanding is perhaps no less relevant today. There are many examples. Just recently Mayor *et al.* (2011), referring to contemporary stoichiometric models of trophic transfer by marine zooplankton, concluded that “our data highlight the need for a more detailed understanding of organismal physiology before ...models can be meaningfully constructed and parameterized”. Hood *et al.* (2006) suggested that representations of nitrogen fixation and calcification, based primarily on *Trichodesmium* and *Emiliania huxleyi*, are “incomplete” and that other important functional groups had not even been considered in open-ocean biogeochemical models. In the case of calcifiers, Anderson (2005) provocatively suggested that we are “running before we can walk” by attempting to parameterize these organisms in the current generation of general circulation models, given a lack of consensus within the scientific community as regards their niche in the marine ecosystem.

The problem is quite simply that even with current advances in knowledge, it often remains difficult to reliably characterize transfer functions and interactions within the ecosystem. To make matters worse, poorly understood ecology is by no means the only problem facing ecosystem modelers. Other difficulties include aggregating diversity within functional groups into meaningful state variables and constants, as well as sensitivity of output to the parameterizations in question and their physical and chemical environment. The last of these, dubbed by Anderson (2005) “all in the interactions,” may be particularly insidious. Predicted distributions of PFTs in global circulation models, for example, have been shown to be sensitive to both ecosystem model formulation (Anderson *et al.*, 2010)

and physics (Sinha *et al.*, 2010). Riley would undoubtedly agree with Oschlies (2000) that correctly representing physics is essential prior to “attempting to correct for a mismatch between model results and observations by adjusting the ecosystem model formulation”. Even today, disagreement between biogeochemical tracers and data in models, particularly circulation models, is often caused by deficiencies in physics rather than necessarily the ecosystem model parameterization. The move toward high resolution in circulation models, as well as improved parameterizations of mixing and other processes, thus remains a priority for the modeling community.

Successful prediction on the basis of theory can be thought of as the pinnacle of scientific achievement, a classic example being Einstein’s prediction that a ray of light from a distant star is deflected as it passes near to the sun. Contemporary society imposes a need for wide and varied predictions, everything from day-to-day changes in the weather, to the changing state of the economy, to next week’s football results, to the response of the environment to global warming. When it comes to prediction, however, there is a much greater emphasis on accuracy as compared to models developed purely for improving understanding. The trouble is that accurate prediction of one scenario does not mean that the model is correct and thereby transferrable to another, such that caution should be exercised when interpreting model predictions (Franks, 1995). In principle, better understanding should lead to improved parameterizations and more reliable predictions, but the reality is often less straightforward (Pace, 2001). Take the biogeochemistry of iron, for example, the importance of which has been established since John Martin proposed the iron hypothesis twenty years ago (Martin, 1990). Our understanding of iron biogeochemistry has forged ahead in leaps and bounds (Boyd and Ellwood, 2010; Breitbarth *et al.*, 2010), yet including iron in ecosystem models is problematic because its bioavailability is influenced by its various speciation and redox states, biological cycling and the different uptake strategies of phytoplankton bacteria. Although ecosystem models that include increased complexity in representation of the iron cycle are being developed (Weber *et al.*, 2007; Ye *et al.*, 2009), the current generation of ocean GCMs typically only include a single pool of dissolved iron and are therefore unable to account for the roles of ligand complexation and nonbiological processes (light and temperature) in governing concentrations of bioavailable iron, and thus the extent of phytoplankton iron limitation (Tagliabue *et al.*, 2009). Better understanding thus only leads to improved predictions where the processes in question can be effectively represented and parameterized.

Prediction requires that models be extrapolated beyond the bounds for which they are initially set up and tuned to. Riley was well aware that simplifying assumptions “place restrictions on the applicability of the equations” and he therefore urged caution as regards the “difficulty of deriving a system of mathematical equations subtle enough to meet the demands of widely varying environments and at the same time simple enough to be usable for practical application” (Riley *et al.*, 1949). The Georges Bank model, for example, useful as it was for gaining understanding of that system, was “too simplified to be suitable for general application” (Riley *et al.*, 1949). What would Riley think, then, of the implementation of

ecosystem models within GCMs used to predict global biogeochemical cycles and their response to changing climate? And are simple or complex ecosystem formulations to be preferred in this regard? On the face of it, complexity is superior because only by including it can the diversity in assemblages of marine communities be explicitly represented. The practical reality may, as Riley understood, be quite the opposite given the aforementioned problems of incompletely understood ecology and sensitivity to both model physics and the precise forms and parameterizations of the chosen equations. The result is a persistent tension in ecological studies between the need for increasingly detailed characterization of processes and that for accurate and the valid forecasts (LaDeau, 2010). Riley would probably agree with the views of Levins (1966) who argued that one has to sacrifice realism (model complexity), generality (e.g. size of the domain) or accuracy in ecological modeling studies. If this is indeed the case, accurate predictions are not to be expected in global GCMs incorporating complex ecosystem models, a sobering thought. He might equally have entertained the views of Anderson (2010) that, whereas models take us on a journey leading to insight and discovery, “a veil of measured prudence must descend upon us,” especially when definitive answers (accurate predictions) are required. Otherwise, as Riley put it, we may end up with “gee-whiz” models with fancy parameterizations, but which lose track of reality (Riley, 1984).

Just because modeling involves the use of approximations and simplifying assumptions does not mean that predictions are not of use to environmental managers and policy makers. The key is to ensure that the major system attributes are robustly captured within a practical framework, requiring investigation of the sensitivity of predictions to the various sources of model error including structure, formulations, parameter values and forcing, and the provision of quantitative assessment of associated uncertainties. The practical reality is far from straightforward and few studies systematically attempt to quantify these uncertainties. For starters, there is a pressing need to define suitable quantitative metrics (Allen *et al.*, 2007). In this context, it is often problematic even to decide which phenomena are most important to simulate accurately and therefore what the metrics need to measure (Gleckler *et al.*, 2008). While scientists often express confidence that today’s models can provide plausible quantitative predictions, it is a significant extra step to quantify the uncertainties associated with projected outcomes such as climate scenarios (Parker, 2009).

As for the way forward, Riley would likely advocate a cautious, stepwise approach, with strong interaction between modelers, field programs and those undertaking laboratory-based work. Bearing Levins’ credo in mind, the development of highly parameterized models for data rich local domains is an obvious starting point, an approach exemplified by the study of time series stations set up by the Joint Global Ocean Flux Study (JGOFS) community. The challenge is then to scale up and, despite the difficulties, at least the attempt should surely be made to develop robust ecosystem models for global applications (Fasham, 1995). Smarter approaches are coming to the fore such as adaptive models (e.g. Pahlow *et al.*, 2008), explicit representation of trade-offs (e.g., Yoshida *et al.*, 2003) and models with emergent community structure (e.g. Follows *et al.*, 2007). A promising future awaits us.

If he were with us today, however, Riley would no doubt remind us that, no matter how revolutionary and exciting these approaches are, they are no substitute for the ever present need for adequate grounding in data and knowledge.

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REFERENCES

- Aber, J. D. 1997. Why don't we believe the models? *Bull. Ecol. Soc. Am.*, 78, 232–233.
- Allen, J. I., P. J. Somerfield and F. J. Gilbert. 2007. Quantifying uncertainty in high resolution coupled hydrodynamic-ecosystem models. *J. Mar. Syst.*, 64, 3–14.
- Anderson, T. R. 2005. Plankton functional type modelling: running before we can walk? *J. Plankton Res.*, 27, 1073–1081.
- . 2010. Progress in marine ecosystem modelling and the “unreasonable effectiveness of mathematics.” *J. Mar. Syst.*, 81, 4–11.
- Anderson, T. R., W. C. Gentleman and B. Sinha. 2010. Influence of grazing formulations on the emergent properties of a complex ecosystem model in a global general circulation model. *Prog. Oceanogr.*, 87, 201–213.
- Arhonditsis, G. B. and M. T. Brett. 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modelling. *Mar. Ecol. Prog. Ser.*, 271, 13–26.
- Atkins, W. R. G. 1928. Seasonal variation in the phosphate and silicate content of sea water during 1926 and 1927 in relation to the phytoplankton crop. *J. Mar. Biol. Ass. U.K.*, 15, 191–205.
- Aumont, O., E. Maier-Reimer, S. Blain and P. Pondaven. 2003. An ecosystem model of the global ocean including Fe, Si, P co-limitations. *Global Biogeochem. Cycles*, 17, doi:10.1029/2001GB001745.
- Badoux, A. C., A. A. M. Noordeloos, M. J. W. Veldhuis and C. P. D. Brussaard. 2006. Virally induced mortality of *Phaeocystis globosa* during two spring blooms in temperate coastal waters. *Aquat. Microb. Ecol.*, 44, 207–217.
- Banase, K. 1994. Grazing and zooplankton production as key controls of phytoplankton production in the open ocean. *Oceanography*, 7, 13–20.
- . 2007. Do we live in a largely top-down regulated world? *J. Biosci.*, 32, 791–796.
- Bjerknes, V. F. K. 1898. Üeber einen hydrodynamischen Fundamentalsatz und seine Anwendung besonders auf die Mechanik der Atmosphäre und des Weltmeeres. *K. svenska VetenskAkad. Handl.*, 31, 35 pp.
- Boyd, P. W. and M. J. Ellwood. 2010. The biogeochemical cycle of iron in the ocean. *Nature Geoscience*, 3, 675–682.
- Breitbarth, E., E. P. Achterberg, M. V. Ardelan *et al.* 2010. Iron biogeochemistry across marine systems – progress from the past decade. *Biogeosciences*, 7, 1075–1097.
- Carney, H. J. 1987. [Field tests of interspecific resource-based competition among phytoplankton.](#) *Proc. Natl. Acad. Sci. USA*, 84, 4148–4150.
- Clarke, G. L. 1936. Light penetration in the western North Atlantic and its application to biological problems. *Rapp. Cons. Explor. Mer.*, 101, 1–14.
- Coles, V. J. and R. R. Hood. 2007. Modeling the impact of iron and phosphorus limitation on nitrogen fixation in the Atlantic Ocean. *Biogeosciences*, 5, 455–479.

- Cura, J. J. 1987. Phytoplankton, in Georges Bank, R. H. Backus, ed., MIT Press, Cambridge, MA, 213–218.
- Debes, H., K. Eliassen and E. Gaard. 2008. Seasonal variability in copepod ingestion and egg production on the Faroe shelf. *Hydrobiologia*, 600, 247–265.
- Doney, S. C. 1999. Major challenges confronting marine biogeochemical modeling. *Global Biogeochem. Cycles*, 13, 705–714.
- Durbin, E. G., R. G. Campbell, S. L. Gilman and A. G. Durbin. 1995. Diel feeding behavior and ingestion rate in the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Cont. Shelf Res.*, 15, 539–570.
- Ekman, V. W. 1905. On the influence of the earth's rotation on ocean currents. *Ark. Mat. Astr. Fys.*, 2, 52 pp.
- Fasham, M. J. R. 1995. Variations in the seasonal cycle of biological production in subarctic oceans: A model sensitivity analysis. *Deep-Sea Res. I*, 42, 1111–1149.
- Fasham, M. J. R., H. W. Ducklow and S. M. McKelvie. 1990. A nitrogen-based model of plankton dynamics in the oceanic mixed layer. *J. Mar. Res.*, 48, 591–639.
- Fleming, R. H. 1939. The control of diatom populations by grazing. *J. Cons. Int. Expl. Mer*, 14, 210–227.
- Follows, M. J., S. Dutkiewicz, S. Grant and S. W. Chisholm. 2007. Emergent biogeography of microbial communities in a model ocean. *Science*, 315, 1843–1846.
- Forget, M.-H., S. Sathyendranath, T. Platt, J. Pommier, C. Vis, M. S. Kyewalyanga and C. Hudon. 2007. Extraction of photosynthesis-irradiance parameters from phytoplankton production data: demonstration in various aquatic systems. *J. Plankton Res.*, 29, 249–262.
- Franks, P. J. S. 1995. Coupled physical-biological models in oceanography. *Rev. Geophys.* 33 (Suppl.), 1177–1187.
- 2002. NPZ models of plankton dynamics: Their construction, coupling to physics, and application. *J. Oceanogr.*, 58, 379–387.
- 2009. Planktonic ecosystem models: perplexing parameterizations and a failure to fail. *J. Plankton Res.* 31, 1299–1306.
- Franks, P. J. S. and C. Chen. 1996. Plankton production in tidal fronts: A model of Georges Bank in summer. *J. Mar. Res.*, 54, 631–651.
- 2001. A 3-D prognostic numerical model study of the Georges Bank ecosystem. Part II: Biological-physical model. *Deep-Sea Res. II*, 48, 457–482.
- Gasol, J. M., J. Pinhassi, L. Alonso-Sáez *et al.* 2008. Towards a better understanding of microbial carbon flux in the sea. *Aquat. Microb. Ecol.*, 53, 21–38.
- Gattuso, J.-P., B. Gentili, C. M. Duarte, J. A. Kleypas, J. J. Middelburg and D. Antoine. 2006. Light availability in the coastal ocean: impact on the distribution of benthic photosynthetic organisms and their contribution to primary production. *Biogeosciences*, 3, 489–513.
- Gentleman, W. 2002. A chronology of plankton dynamics *in silico*: how computer models have been used to study marine ecosystems. *Hydrobiologia*, 480, 69–85.
- Gleckler, P. J., K. E. Taylor and C. Doutriaux. 2008. Performance metrics for climate models. *Global Biogeochem. Cycles*, 113, D06104.
- Greenan, B. J. W., B. D. Petrie, W. G. Harrison, and P. M. Strain. 2008. The onset and evolution of a spring bloom on the Scotian Shelf. *Limnol. Oceanogr.*, 53, 1759–1775.
- Gregg, W. W., P. Ginoux, P. S. Schopf. *et al.* 2003. Phytoplankton and iron: validation of a global three-dimensional ocean biogeochemical model. *Deep-Sea Res. II*, 50, 3143–3169.
- Gruber, N., H. Frenzel, S. C. Doney, P. Marchesiello, J. C. McWilliams, J. R. Moisan, J. J. Oram, G.-K. Plattner and K. D. Stolzenbach. 2006. Eddy-resolving simulation of plankton ecosystem dynamics in the California Current System. *Deep-Sea Res.*, 53, 1483–1516.

- Harvey, H. W. 1934. Annual variation of planktonic vegetation, 1933. *J. Mar. Biol. Ass. U.K.*, *19*, 775–792.
- Hedgpeth, J. W. 1977. Models and muddles. *Helgoländer wiss Meeresunters*, *30*, 92–104.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *Canad. Entomol.*, *91*, 385–398.
- Hood, R.R., E. A. Laws, R. A. Armstrong *et al.* 2006. Pelagic functional group modelling: Progress, challenges and prospects. *Deep-Sea Res. II*, *53*, 459–512.
- Hutchinson, G. E. 1941. Limnological studies in Connecticut IV. The mechanisms of intermediary metabolism in stratified lakes. *Ecol. Monogr.*, *11*, 21–60.
- Hutson, V. 1984. Predator mediated coexistence with a switching predator. *Math. Biosci.*, *68*, 233–246.
- Kane, J. 2007. Zooplankton abundance trends on Georges Bank, 1977–2004. *ICES J. Mar. Sci.*, *64*, 909–919.
- Ketchum, B. H. 1939. The absorption of phosphate and nitrate by illuminated cultures of *Nitzschia closterium*. *Amer. J. Bot.*, *26*, 399–407.
- Kimball, H. H. 1928. Amount of solar radiation that reaches the surface of the earth on the land and on the sea, and methods by which it is measured. *Mon. Weath. Rev. Wash.*, *56*, 393–398.
- Kingsland, S. W. 1985. *Modeling Nature. Episodes in the History of Population Ecology.* Univ. Chicago Press, 267 pp.
- Kjørboe, T., J. C. S. Hansen, A. L. Alldredge, G. A. Jackson, U. Passow, M. G. Dam, D. T. Drapeau, A. Waite and C. M. Garcia. 1996. Sedimentation of phytoplankton during a diatom bloom: Rates and mechanisms. *J. Mar. Res.*, *54*, 1123–1148.
- Krümmel, O. 1907. *Handbuch der Ozeanographie. Band I. Die räumlich, chemischen und physikalischen Verhältnisse des Meeres.* J. Engelhorn, Stuttgart, 526 pp.
- 1911. *Handbuch der Ozeanographie. Band II. Die Bewegungsformen des Meeres.* J. Engelhorn, Stuttgart, 766 pp.
- LaDeau, S. 2010. Advances in modeling highlight a tension between analytical accuracy and accessibility. *Ecology*, *91*, 3488–3492.
- Le Quéré, C. 2006. Reply to horizons article ‘Plankton functional type modelling: running before we can walk’ Anderson (2005): I. Abrupt changes in marine ecosystems? *J. Plankton Res.*, *28*, 871–872.
- Le Quéré, C., S. P. Harrison, I. C. Prentice *et al.* 2005. Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biol.*, *11*, 2016–2040.
- Letelier, R. M., D. M. Karl, M. R. Abbott and R. R. Bidigare. 2004. Light driven seasonal patterns of chlorophyll and nitrate in the lower euphotic zone of the North Pacific subtropical gyre. *Limnol. Oceanogr.*, *49*, 508–519.
- Levins, R. 1966. The strategy of model building in population biology. *Am. Sci.*, *54*, 421–431.
- Lotka, A.J. 1956. *Elements of Mathematical Biology*, Dover Press, NY, 465 pp.
- Marshall, S. M., A. G. Nicholls, and A. P. Orr. 1935. On the biology of *Calanus finmarchicus*. Part VI. Oxygen consumption in relation to environmental conditions. *J. Mar. Biol. Ass. U.K.*, *20*, 1–27.
- Martin, J. H. 1990. Glacial-interglacial CO₂ change: the iron hypothesis. *Paleoceanography*, *5*, 1–13.
- Mayor, D. J., T. R. Anderson, X. Irigoien and R. Harris. 2006. Feeding and reproduction of *Calanus finmarchicus* during non-bloom conditions in the Irminger Sea. *J. Plankton Res.*, *28*, 1167–1179.
- Mayor, D. J., K. Cook, B. Thornton, P. Walsham, U. F. M. Witte, A. F. Zuur and T. R. Anderson. 2011. Absorption efficiencies and basal turnover of C, N and fatty acids in a marine Calanoid copepod. *Funct. Ecol.*, *25*, 509–518.
- Mills, E. L. 1989. *Biological Oceanography. An Early History, 1870–1960.* Cornell Univ. Press, Ithaca, 378 pp.
- 1995. From marine ecology to biological oceanography. *Helgoland. Meeresunt.*, *49*, 29–44.

- 2009. *The Fluid Envelope of our Planet. How the Study of Ocean Currents Became a Science*, Univ. of Toronto Press, 434 pp.
- Mohn, H. 1887. *The North Ocean, Its Depths, Temperature and Circulation*, The Norwegian North-Atlantic Expedition 1876–1878, II(2). Grøndahl & Son, Christiania, 212 pp.
- Monterey, G. I. and S. Levitus. 1997. *Climatological Cycle of Mixed Layer Depth in the World Ocean*. U.S. Gov. Printing Office, NOAA NESDIS, 5 pp + 87 figs.
- Moore, K. J., S. C. Doney, J. A. Kleypas, D. M. Glover and I. Y. Fung. 2002. An intermediate complexity marine ecosystem model for the global domain. *Deep-Sea Res. II*, *49*, 403–462.
- Moore, K. J., S. C. Doney and K. Lindsay. 2004. Upper ocean ecosystem dynamics and iron cycling in a global three-dimensional model. *Global Biogeochem. Cycles*, *18*, GB4028, doi: [10.1029/2004GB002220](https://doi.org/10.1029/2004GB002220).
- Okunishi, T., M. J. Kishi, Y. Ono and T. Yamashita. 2007. A lower trophic ecosystem model including iron fracture in the Okhotsk Sea. *Cont. Shelf Res.*, *27*, 2080–2098.
- O'Reilly, J. E. and C. Evans-Zetlin. 1987. Primary production, in *Georges Bank*, R. H. Backus, ed., MIT Press, Cambridge, MA, 220–233.
- Oschlies, A. 2000. Equatorial nutrient trapping in biogeochemical ocean models: the role of advection numerics. *Global Biogeochem. Cycles*, *14*, 655–667.
- Pace, M. L. 2001. Prediction and the aquatic sciences. *Can. J. Fish. Aquat. Sci.*, *58*, 63–72.
- Pahlow, M., A. F. Vézina, B. Casault, H. Maass, L. Malloch, D. G. Wright, D and Y. Lu. 2008. Adaptive model of plankton dynamics for the North Atlantic. *Prog. Oceanogr.*, *76*, 151–191.
- Park, T. 1939. Ecology looks homeward. *Q. Rev. Biol.*, *14*, 332–336.
- Parker, W. S. 2009. Confirmation and adequacy-for-purpose in climate modelling. *Proc. Aristotelian Soc.*, *83* (Suppl.), 233–249.
- Passioura, J. B., 1996. Simulation models: Science, snake oil, education, or engineering? *Agron. J.*, *88*, 690–694.
- Peters, R. H. 1991. *A Critique for Ecology*, Cambridge Univ. Press, 366 pp.
- Pomeroy, L. R. 2001. Caught in the food web: complexity made simple? *Sci. Mar.*, *65*, 31–40.
- Popova, E.E., A. C. Coward, G. A. Nurser, B. de Cuevas, M. J. R. Fasham, and T. R. Anderson. 2006. Mechanisms controlling primary and new production in a global ecosystem model. Part I. Validation of the biological simulation. *Ocean Science*, *2*, 249–266.
- Popova, E. E., M. J. R. Fasham, A. V. Osipov and V. A. Ryabchenko. 1997. Chaotic behaviour of an ocean ecosystem model under seasonal external forcing. *J. Plankton Res.*, *19*, 1495–1515.
- Popper, K. R. 1963. *Conjectures and Refutations*, Routledge and Kegan Paul, London, 412 pp.
- Raick, C., K. Soetaert and M. Gregoire. 2006. Model complexity and performance: How far can we simplify? *Prog. Oceanogr.*, *70*, 27–57.
- Richards, O. W. 1928a. The growth of the yeast *Saccharomyces cerevisiae*. I. The growth curve, its mathematical analysis, and the effect of temperature on the yeast growth. *Ann. Bot.*, *42*, 271–283.
- 1928b. Potentially unlimited multiplication of yeast with constant environment, and the limiting of growth by changing environment. *J. Gen. Physiol.*, *11*, 525–538.
- Richards, O.W. and G. A. Riley. 1937. The growth of amphibian larvae illustrated by transformed coordinates. *J. Exp. Zool.*, *77*, 159–167.
- Riley, G. A. 1939. Correlations in aquatic ecology. With an example of their application to problems of plankton productivity. *J. Mar. Res.*, *2*, 56–73.
- 1941a. Plankton studies. III. Long Island Sound. *Bull. Bingham Oceanogr. Coll.*, *7*, 1–93.
- 1941b. Plankton studies. IV. Georges Bank. *Bull. Bingham Oceanogr. Coll.*, *7*, 1–73.
- 1941c. Plankton studies. V. Regional summary. *J. Mar. Res.*, *4*, 162–171.
- 1942. The relationship of vertical turbulence and spring diatom flowerings. *J. Mar. Res.*, *5*, 67–87.

- 1943. Physiological aspects of spring diatom flowerings. *Bull. Bingham Oceanogr. Coll.*, 8, 1–53.
- 1946. Factors controlling phytoplankton populations on Georges Bank. *J. Mar. Res.*, 6, 54–73.
- 1947. Seasonal fluctuations of the phytoplankton population in New England coastal waters. *J. Mar. Res.*, 6, 114–125.
- 1952. Biological oceanography. *Survey of Biological Progress*, 2, 79–104.
- 1980. Interview of Gordon by Eric Mills, Halifax, Nova Scotia, 27 October, 1980. Available as MP3 file.
- 1984. Reminiscences of an oceanographer. Unpublished manuscript. Department of Oceanography, Dalhousie University. 136 pp.
- Riley, G. A. and D. F. Bumpus. 1946. Phytoplankton-zooplankton relationships on Georges Bank. *J. Mar. Res.*, 6, 33–47.
- Riley, G. A., H. Stommel and D. F. Bumpus. 1949. Quantitative ecology of the plankton of the western North Atlantic. *Bull. Bingham Oceanogr. Coll.*, 12, 1–169.
- Rose, K. A., B. A. Megrey, F. E. Werner and D. M. Ware. 2007. Calibration of the NEMURO nutrient-phytoplankton-zooplankton food web model to a coastal ecosystem: Evaluation of an automated calibration approach. *Ecol. Model.*, 202, 38–51.
- Ryther, J. H. 1956. Photosynthesis in the ocean as a function of light intensity. [Limnol. Oceanogr.](#), 1, 61–69.
- Saage, A., O. Vadstein and U. Sommer. 2009. Feeding behaviour of adult *Centropages hamatus* (Copepoda, Calanoida): Functional response and selective feeding experiments. *J. Sea Res.*, 62, 16–21.
- Schmittner, A., A. Oschlies, X. Giraud, M. Eby and H. L. Simmons. 2005. A global model of the marine ecosystem for long-term simulations: Sensitivity to ocean mixing, buoyancy forcing, particle sinking, and dissolved organic matter cycling. *Global Biogeochem. Cycles*, 19, GB3004, doi:10.1029/2004GB002283.
- Sinha, B., E. T. Buitenhuis, C. Le Quéré and T. R. Anderson. 2010. Comparison of the emergent behavior of a complex ecosystem model in two ocean general circulation models. *Prog. Oceanogr.*, 84, 204–224.
- Six, K. D. and E. Maier-Reimer. 1996. Effects of plankton dynamics on seasonal carbon fluxes in an ocean general circulation model. [Global Biogeochem. Cycles](#), 10, 559–583.
- Steele, J. H. 1974. *The Structure of Marine Ecosystems*, Harvard University Press, Cambridge, UK, 128 pp.
- Soetaert, K., P. M. J. Herman and J. Kromkamp. 1994. [Living in the twilight: estimating net phytoplankton growth in the Westerschelde estuary \(The Netherlands\) by means of an ecosystem model \(MOSES\)](#). *J. Plankton Res.*, 16, 1277–1301.
- Stross, R.G., S. W. Chisholm and T. A. Downing. 1973. Causes of daily rhythms in photosynthetic rates of phytoplankton. *Biol. Bull.*, 145, 200–209.
- Sverdrup, H. U. 1953. [On conditions for the vernal blooming of phytoplankton](#). *J. Cons. Int. Explor. Mer*, 18, 287–295.
- Sverdrup, H. U., M. W. Johnson and R. H. Fleming. 1942. *The Oceans. Their Physics, Chemistry, and General Biology*, Prentice-Hall, Englewood Cliffs, NJ, 1060 pp.
- Tagliabue, A., L. Bopp, O. Aumont and K. R. Arrigo. 2009. Influence of light and temperature on the marine iron cycle: From theoretical to global modeling. *Global Biogeochem. Cycles*, 23, GB2017, doi:10.1029/2008GB003214.
- Thomas, A. C., D. W. Townsend and R. Weatherbee. 2003. [Satellite-measured phytoplankton variability in the Gulf of Maine](#). *Cont. Shelf Res.*, 23, 971–989.

- Thomson, R. E. and I. V. Fine. 2003. Estimating mixed layer depth from oceanic profile data. *J. Atmos. Ocean. Tech.*, *20*, 319–329.
- Townsend, D. W. and A. C. Thomas. 2001. Winter-spring transition of phytoplankton chlorophyll and inorganic nutrients on Georges Bank. *Deep-Sea Res. II*, *48*, 199–214.
- . 2002. Springtime nutrient and phytoplankton dynamics on Georges Bank. *Mar. Ecol. Prog. Ser.*, *228*, 57–74.
- Von Arx, W. S. 1962. *An Introduction to Physical Oceanography*, Addison-Wesley, MA, 422 pp.
- Waku, M. and K. Furuya. 1998. Primary production and community respiration in a warm streamer associated with Kuroshio warm core ring in spring. *J. Oceanogr.*, *54*, 565–572.
- Walsh, J. J., T. E. Whitledge, J. E. O'Reilly, W. C. Phoel and A. F. Draxler. 1987. Nitrogen cycling on Georges Bank and the New York Shelf, *in* *Georges Bank*, R. H. Backus, ed., MIT Press, Cambridge, MA, 234–246.
- Wassmann, P. 1994. Significance of sedimentation for the termination of *Phaeocystis* blooms. *J. Mar. Syst.*, *5*, 81–100.
- Weber, L., C. Völker, A. Oschlies and H. Burchard. 2007. Iron profiles and speciation of the upper water column at the Bermuda Atlantic Time-series Study site: A model based sensitivity study. *Biogeosciences*, *4*, 689–706.
- Wroblewski, J. S. 1977. A model of phytoplankton bloom formation during variable Oregon upwelling. *J. Mar. Res.*, *35*, 357–394.
- . 1982. *Selected works of Gordon A. Riley*. Dalhousie Univ., Nova Scotia, Canada, 489 pp.
- Ye, Y., C. Völker and D. A. Wolf-Gladrow. 2009. A model of Fe speciation and biogeochemistry at the Tropical Eastern North Atlantic Time-Series Observatory site. *Biogeosciences*, *6*, 2041–2061.
- Yoshida, T., L. E. Jones, S. P. Ellner, G. F. Fussmann, and N. G. Hairston Jr. 2003. Rapid evolution drives ecological dynamics in a predator–prey system. *Nature*, *424*, 303–306.

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