

far beyond the limits for which it was intended. At the lower limit it extrapolates to the origin, which is almost certainly incorrect. As chlorophyll increases  $k_{wc}$  reaches a maximum at  $C = 125$  and then decreases, becoming negative at very high concentrations, an obviously unacceptable result.

However, despite theoretical flaws, the equation as a whole has statistical validity beyond the limits for which it was originally intended. As I reported earlier (Riley 1956), data by Conover (1954) on red tides in Long Island Sound also fit the curve. Her largest value,  $314 \text{ mg C m}^{-3}$ , gives a calculated  $K$  of 5.3, as compared with an observed value of 5.5. Incidentally the computed  $k_c$  is 0.0167, which is close to Bannister's constant, or alternatively, the results would be satisfied if  $k_c$  is 0.016, and  $k_{wc}$  levels off at about 0.45.

Practical application of Bannister's production equation to a particular body of water ordinarily would require measurements of light, chlorophyll, and extinction coefficients. However, its use in theoretical models poses more difficult requirements. These commonly involve a system of interrelated equations for nutrients, phytoplankton and zooplankton, and the results require simultaneous solution of the equations. Transparency is in part a biological variable and logically can be included in

the system if a suitable equation can be found for relating phytoplankton and transparency. I used my 1956 equation in one such model (Riley 1965), and although the problem needs to be re-examined with a new and better set of data, I think I have demonstrated a possibility of applying the same principles to modern models.

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#### Reply to comment by G. A. Riley

As discussed in my paper on production equations (Bannister 1974a), the extinction coefficient  $k_w$  must include the contributions of pure water, components such as inorganic silts and pigments and also organic materials not originating directly or indirectly from phytoplankton, and components such as zooplankton, their feces, algal cell walls, and pheophytins, all of which are, broadly speaking, algal derivatives. Dr. Riley suggests that, at any instant,  $k_{wc}$ , the contribution to the total

extinction made by algal derivatives, might be an essentially constant function of the concentration  $C$  ( $\text{mg Chl } a \text{ m}^{-3}$ ) of the phytoplankton existing at that instant. He also suggests that this function,  $k_{wc} = f(C)$ , might be generally applicable to any mixed layer.

I cannot help resolve the question of whether there is a single general function, or, if there is, whether the expression that Riley derives from his empirical equation for the total extinction  $K$  is the function

desired. I would, however, argue that such a general function is unlikely to originate in the way he envisions. He visualizes that  $k_{wc}$  is determined primarily by refractory algal derivatives which decay very slowly in the water, and he sees a single algal bloom as contributing only a little to a large "background" of materials accumulated from earlier blooms. According to this view, the value of  $k_{wc}$  is determined mainly by previous algal production not by the contemporary algal concentration. Also, whatever the increment added during the course of a single bloom, a slow decay rate means that  $k_{wc}$  would increase throughout the bloom, even in the late stages when algal concentration is falling. Such behavior is not consistent with a constant, general relation between  $k_{wc}$  and the instantaneous algal concentration  $C$ . Such a general relation might exist if the algal derivatives decayed rapidly, that is, with a time constant comparable to the algal generation time. In this case, the concentration of algal derivatives would rise and fall more or less in step with algal concentration or production. If a general relation does exist between  $k_{wc}$  and  $C$ , I would prefer to believe that components such as zooplankton and pheophytin, which can be expected to respond rapidly to algal concentration, and not slowly decaying components such as algal cell walls, are primarily responsible for  $k_{wc}$ .

I also would like to clarify what difficulties arise, as a result of the contribution of algal derivatives to  $k_w$ , in using my production equations and steady state theory (Bannister 1974a, b). At any instant, the value of  $k_w$  in a given mixed layer can be

easily calculated provided that my estimate of the value of  $k_c$  is accepted (Dr. Riley does so in deriving his expression for  $k_{wc}$ ), and that routine measurements of the transmission  $T$ , depth  $d$ , and algal concentration  $C$  of the mixed layer are made. Then,  $k_w = (1/d) \ln(1/T) - k_c C$ . Evaluation of  $k_w$  therefore offers no impediment to testing the ability of my production equations or theory to describe a given steady state. A dependence of  $k_w$  on algal concentration would be an obstacle to using my theory to predict the properties of an algal crop at times when  $k_w$  can't be evaluated experimentally. Thus, for example, one couldn't predict crop density in winter if the only available value of  $k_w$  is for summer. Dr. Riley's derived expression for  $k_{wc}$  could overcome this obstacle, provided his expression can be shown to be general. Dr. Riley's comment that use of my production equations in theoretical models "poses more difficult requirements" because it is one of a set of equations to be solved simultaneously does not seem to me to identify any deficiency of my production equations, but rather emphasizes that one equation of the set must specify the dependence of  $k_w$  on  $C$ .

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