COMMENT

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Spring bloom initiation and Sverdrup's critical-depth model

There is overwhelming evidence that the development of spring phytoplankton blooms is a function of light supply and the depth of vertical mixing. When stating this fact, it is common practice to cite the critical-depth model presented in quantitative terms by Sverdrup (1953), who reasoned

> at the compensation depth, . . . , gain and loss balance each other. . . . The condition for an increase of the total population is that the total production P must exceed the total destruction by respiration, R, . . . on an average for 24 hours. . . . This implies that there must exist a *critical depth* such that blooming can occur only if the depth of the mixed layer is *less* than the critical value. [p. 287]

That Sverdrup implicitly included zooplankton in the terms "total population" and "total respiration" is not evident from the paragraphs in which the model is introduced. In the section in which the assumptions underlying the model are listed, however, it becomes clear that Sverdrup had zooplankton respiration on his mind all along. We quote from the seventh.

> The compensation depth is defined as the depth at which the energy intensity is such that the production by photosynthesis balances destruction by respiration. This energy level may depend upon the temperature because photosynthesis and respiration may not stand in the same relation to temperature, and it must depend upon the composition of the plankton. It must, for instance, lie higher for a mixed population of phyto- and zooplankton than for a pure phytoplankton population. [p. 289]

Accordingly, Sverdrup did consider the influence of zooplankton when testing his model with observations carried out in the Norwegian Sea.

Gran and Braarud (1935), who first introduced the concept of a critical depth (which they estimated to be 5–10 times the compensation depth), also included zooplankton respiration in the term. Modern renditions of Sverdrup's model, however, generally ignore zooplankton and consider only phytoplankton respiration. Indeed, it will come as a surprise to most readers familiar with the model that zooplankton was included in the original respiration term. Selection of the term respiration was unfortunate as it is not only the cause of the confusion (dealt with below) but is also inappropriate. What the earlier workers were actually referring to was not just respiration by the entire plankton community (expressible as units of O_2 consumed or CO_2 produced) but also feeding, which destroys cells but only partly finds expression in units of respiration. The subsequent mutilation of the model, presumably due to oversight, obviously has important consequences other than altering the position of critical depth in the water column. Thus, the original version will tend to give much shallower positions than latter-day ones based only on phytoplankton respiration.

The reasoning behind the critical-depth model, whether with or without the effect of zooplankton grazing, appears sound and lends itself to mathematical treatment; what we examine here is whether phytoplankton respiration can be a significant factor at the short time scales of bloom initiation. We will not attempt to review the literature on algal respiration rates but instead will develop a series of arguments based on various considerations showing that it must be of little importance in initiating bloom growth.

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One of the essential assumptions of the model is that respiration, in contrast to production, is constant with depth. In graphic representations of Sverdrup's model (e.g. Parsons et al. 1984; Tett and Edwards 1984) respiration is depicted as about 10% of maximal photosynthetic rate (P_{max}). This value is based on estimates from many investigators (Parsons et al. 1984; Langdon 1988). When applied to the critical-depth model, it implies that for a given population with a P_{max} equivalent to a doubling time of 1 d, cells caught below the critical depth (as defined by the modern rendition) and still attempting to photosynthesize will respire half their biomass in 6 d. It is very unlikely that such a phenomenon actually happens. Indeed, there is no evidence that phytoplankton respiration is constant with depth.

Phytoplankton respiration is differentiated into photo- and dark respiration. As the respiration rate below the compensation depth determines the position of the critical depth, it follows that mainly dark respiration is relevant to the model. Dark respiration in turn can be subdivided into growth and maintenance (Raven and Beardall 1981). The former results from work necessitated by the mechanisms of cell growth and division (e.g. synthesis of various cellular materials, division, and relocation of organelles). Thus, growth respiration occurs following harvesting of sufficient light energy. Maintenance respiration, on the other hand, represents the energy demand of a cell not undergoing growth and can be defined as the energy needed to maintain "viability and, more particularly, the ability to resume growth at a rapid rate as soon as a missing resource (e.g. light or some nutrient) is restored"; this energy "is used inter alia for resynthesizing unstable macromolecules and for the active transport which recovers ions which have leaked through a membrane" (Raven and Beardall 1981, p. 71). It follows that, in the modern rendition, the rate of maintenance respiration will be important when estimating the position of the critical depth.

Respiration rates are commonly derived from measured photosynthesis–light relationships (P vs. I curves) by extrapolating alpha (the photosynthetic rate per unit biomass per unit irradiance) onto the linear irradiance axis. This procedure generally yields an intercept equivalent to ~10% of P_{max}, which is equated with respiration. Measurements of growth rates at very low light levels are difficult, but the few experiments carried out to date show that the relationship between photosynthesis and light deviates from a straight line and curves toward the origin. Experiments have been conducted, for example, with the diatom *Phaeodactylum* (Geider et al. 1985, 1986), cyanobacteria (Gibson 1987), and the green macroalga *Ulva lactuca* (Sand-Jensen 1988). According to Gibson (1987, p. 187) "the implication of these results is that 'maintenance energy' is a mathematical abstraction and the 'cost' of maintaining a cell varies with growth rate." The results obtained with *Ulva* are particularly interesting as this alga is often regarded as a ruderal sun plant, implying that it has a high respiration rate. Weight loss of *Ulva* kept in total darkness was extremely small, however, and corresponded to a half-life of the carbon content of 58 d. The compensation point for growth was observed at incident light as low as 2.48 μmol quanta m^{-2} s^{-1} (Sand-Jensen 1988). Even lower values were obtained for *Phaeodactylum* (Geider et al. 1986).

The implications of the above results for positioning compensation depth should be obvious. In contrast to the original definition, compensation depth—the lower boundary of the euphotic zone—is now generally regarded as the depth where production and respiration of a given cell are just balanced. The high degree of fluctuation of the underwater light field has made accurate specification of the compensation depth difficult. The rule-of-thumb approach most widely used is to equate this depth with the 1% (of subsurface light) depth, although some workers use 0.1%. Indeed, there is no general agreement on how to define the depth of the euphotic zone in relation to the light field, even when the latter has been accurately measured. Estimates will easily vary by 30% between scientists. The fact that at least some algae are capable of growing, albeit very slowly, at very low light levels indicates that the depth of the euphotic zone—sensu stricto—has been underestimated to

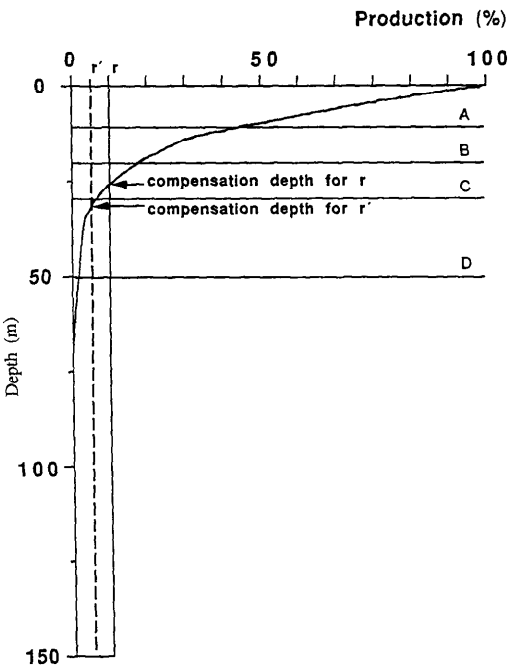

Fig. 1. Sverdrup's model in its modern rendition, where r and r' represent phytoplankton respiration at 10 and 5% of P_{max} (=100%). Whereas compensation depth increases by only 6 m (by a factor of 0.23) from r to r', critical depth doubles from 150 to 300 m (latter not shown). A, B, C, and D levels correspond to Fig. 2.

date. Because light supply decreases exponentially with depth, correcting respiration rate (from 10% of P_{max}) by a factor of 2 or 10 will lower compensation depth (approximately) by a factor of 0.2 or 2 respectively. The effect on critical depth will be much greater, however, as it will increase by the same factor that respiration is decreased (Fig. 1). A factor of 2–10 increase in critical depth will shift it well below the depth of winter mixing in most waters. This shift will render the critical-depth concept based on phytoplankton respiration useless as a tool in predicting induction of the spring bloom. The depths given in Fig. 1 are representative for spring in boreal shelf systems. They put the relationship between a 30-m-thick euphotic zone and its critical depth into perspective.

Let us, nevertheless, assume that maintenance respiration is indeed of significance in determining the timing of the bloom. Then, species with a low respiration rate would also have a deeper critical depth and begin growth earlier. Such species should dominate the active phytoplankton community by late winter and build up a competitive advantage for domination of the spring bloom. Field observations indicate, however, that the winter community is generally dominated by nanoflagellates, whereas the spring bloom is dominated by diatoms (Takahashi et al. 1978; Erga and Heimdal 1984). Compared to the long winter, spring bloom induction occurs on an event scale and obviously selects for species with a fast growth rate rather than a low respiration rate, even though these properties are not necessarily mutually exclusive. In other words, the steepness of the slope of alpha rather than position of I_c (on a P vs. I diagram where I_c is light intensity at the compensation point) confers the competitive advantage in the early stages of the spring bloom. In this case, factors other than the position of the critical depth must dominate induction of spring bloom growth.

As all high-latitude phytoplankton species survive through winter, their maintenance respiration must be low or they must switch to a "resting mode." Survival experiments have shown that diatoms, as vegetative cells or spores, can maintain viability under cold, dark conditions for months and even years (Smayda and Mitchell-Innes 1974; Durbin 1978; Hollibaugh et al. 1981). The evolutionary pressure to keep respiration low is obvious. We can well assume that every temperate and polar phytoplankter can survive from its reserves for periods upward of several months. Whether it is in the form of resting spores or vegetative cells (including resting stages) seems immaterial, as not all typical bloom diatoms are known to form spores (Hargraves and French 1983). Further, diatom resting spores are also capable of photosynthesis when exposed to light (Hargraves and French 1983), indicating that the respiratory cost of maintaining a physiologically active biochemical machinery is not as high as widely assumed, at least not in the diatoms. What will be of importance, however, are the factors triggering the switch from maintenance to growth respiration. The point we are making here is that the level of maintenance respiration cannot gain special importance in regulating the timing

of the spring bloom. Use of the critical-depth concept diverts attention to the lower reaches of the euphotic zone, whereas spring bloom induction is governed by processes occurring close to the surface.

Sverdrup's (1953) first assumption (p. 288) was that "there exists a thoroughly mixed top layer." Little is known, however, about the rate and intensity of vertical mixing in relation to input of kinetic energy. Lal and Lee (1988), using a novel method (cosmogenic P isotope tracers), found that (p. 753) "the mixed layer is not well mixed in the timescale of 2–3 weeks" at a station in the Pacific (off Santa Catalina Island). Although we cannot generalize from these data at present, field observations indicate that the timing and rate of spring bloom growth is controlled by the weather: cloudy and windy weather delays induction; calm, sunny weather advances it. During periods of low winds and high insolation, warming of the upper few meters can occur. This temporary stabilization of a shallow mixed layer is accompanied by rapid biomass buildup within it (e.g. von Bodungen et al. 1981).

In the presence of an adequate nutrient supply, phytoplankton growth rates are functions of irradiance, which decreases exponentially with depth. Typical spring irradiance levels permit maximal division rates only in the upper 10–20 m; rates are substantially lower below this level. It follows that population growth will attain its maximal potential relative to the light regime if the portion of the population dividing at maximal rates is retained in that layer; daughter cells will continue to divide at rates of those of the parent cells if they are accumulated within the layer rather than diluted downward to less favorable depths (Fig. 2). At constant surface light input, we have used a cell division rate of 1 d^{-1} in the layer above depth A (10 m) and 0.3, 0.1, and 0 div. d^{-1} in layers A–B, B–C, and C–D (from Fig. 1). Curve A represents the sum of these division rates over time. The other curves represent mixing depths varying across 20 m (B), 30 m (C), and 50 m (D) where average division rates in each of these mixed layers will be ~0.5, 0.25, and 0.1 div. d^{-1}. These values are representative and not arbitrarily assumed. For the sake of simplicity, however, light inhibition and self-shading have not been considered. Their inclusion will not affect the substance of our arguments.

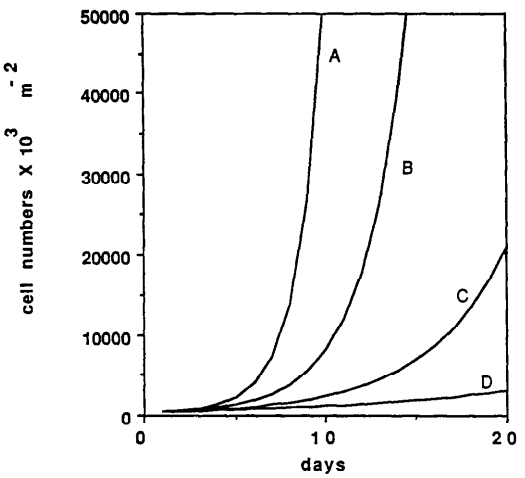

Fig. 2. Curves A–D represent population growth rates in a 50-m water column with mixing depths of 10, 20, 30, and 50 m (levels A, B, C, D from Fig. 1). Cell division rates explained in text. An initial seed stock of 10 cells $liter^{-1}$ for the entire water column has been used.

Because wind-induced kinetic energy (sensu Margalef 1978) in the water column is dissipated more rapidly in shallow, enclosed than in deep, open areas, temporary stratification arises earlier and layers are shallower in the former than in the latter type of environment. The idealized curves given in Fig. 2 explain why, following abatement of stormy weather, appearance of the spring bloom is much more rapid in topographically protected areas as compared to open-ocean waters. In the former, population growth rates will be in the range between curves A and B whereas in more open waters, the B–C range will tend to prevail. It seems safe to assume that zooplankton grazing can suppress populations growing at rates between type-C and -D curves.

These theoretical considerations are substantiated by observations of the rates of spring bloom growth in neighboring localities sharing essentially the same weather and zooplankton populations but with differing topography. In the protected Belt Sea region of the southwestern Baltic, salinity stratification is shallow (~10 m), and under

optimal weather conditions spring bloom initiation occurs as early as late February with culmination in mid-March. Prolonged stormy weather has been observed to delay the bloom to mid-April, when, after the advent of calm, sunny weather, the period between bloom induction and culmination can be as short as 10 d (Smetacek 1985). Salinity stratification in the adjacent Bornholm Sea is much deeper (60 m), and spring bloom development occurs some 4–6 weeks later than in the Belt Sea. It has been observed to begin before the advent of a stable thermocline, however, and under conditions of temporary thermal stabilization of the upper 5–10 m (von Bodungen et al. 1981). Kaiser and Schulz (1978) compared the timing of spring bloom initiation in different regions of the southern Baltic and concluded that the spring bloom began only after the mixing depth corresponded to the thickness of the euphotic layer, which they estimated at ~20–25 m. They concluded that the use of the term critical depth (Kaiser and Schulz 1978, p. 169) "did not appear apt for explaining the causes for the differences in the times at which mass development of phytoplankton begins in different regions of the Baltic."

In open and shelf waters, great horizontal variability is recorded during the growth phase of the bloom, often accompanied by local changes in species dominance. A causal relationship between stock size and structure of the water column is not always obvious. We suggest that the short-term past history of the surface layers due to the effects described above easily can give rise to such structures. Thus, a high biomass accumulation in a warm, shallow surface layer will result in horizontal and vertical patchiness of biomass reflecting the local hydrography. Strong biomass variation would also be expected in a frontal zone. Such complex structures in the relationship between biomass distribution and mesoscale hydrography have indeed been found in detailed studies of spring bloom growth in the Norwegian Coastal Current (Rey 1981; Peinert 1986), on the Bering Sea shelf (Sambrotto et al. 1986), in the Irish Sea (Fasham et al. 1983), and in association with meltwater lenses in the Ross Sea (Smith and Nelson 1985) and the Bransfield Strait, Antarctica (von Bodungen et al. 1986). In all these cases the mixed-layer depth was in the range of 20 m and hence corresponded more closely with the layer of maximal production than with the critical depth.

There will be an understandable reluctance to revert to the original definition of compensation depth, particularly as there is little to be gained by it. Zooplankton grazing pressure is highly variable and difficult to measure. Besides, it follows from the above arguments that retention of daughter cells in the most productive layer is the primary condition for induction and subsequent growth of the spring bloom. The role of zooplankton grazing can be judged only on this basis. Thus, if grazing pressure is assumed constant over a wide region, then differences in the accumulation rate of phytoplankton biomass will still be due to the dynamics of the most productive layer. Type-C or -D curves might well be suppressed by grazing pressure, whereas a type-A curve would be impossible to suppress, as it would require exact gearing of feeding intensity to the weather. Sand-Jensen (1988) argued that the depth distribution of *Ulva* is regulated by the growth-grazing ratio rather than just growth. Invertebrate grazing on *Ulva* is often intensive and may suppress colonization at depths where growth is slower than grazing. Sand-Jensen (1988) concluded (for macroalgae, p. 191) that "it follows that slow-growing, grazing-resistant species may dominate at great depths not because of a greater ability to photosynthesize and grow in the shade, but due to an ability to maintain their biomass." Defining critical depth sensu Sverdrup as the ratio between growth and grazing rates in pelagic environments will be difficult because of the number of variables impinging on this ratio (e.g. light field, physiological adaptation, phytoplankton seeding strategies, selective grazing, and parasitism).

Sverdrup (1953) himself was aware of the shortcomings of his model, stating that (p. 290) "the rapidity with which a given population may grow depends on how much the thickness of the top layer deviates from

the critical value." The argument is continued in the following paragraph which we cite in full.

> In the second place a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate. In this case the plankton may be unevenly distributed at the end of the daylight hours, with greater concentration above the compensation depth where production has taken place. During the night hours mixing may not be complete and when daylight again makes photosynthesis possible, the concentration of plankton may still be greater near the surface. In these circumstances the production will be greater than according to our assumptions, and the population may increase as long as the conditions prevail. A similar development may take place even with strong turbulence if the phytoplankton displays a positive phototaxis. [p. 290–291]

As shown above, this sequence of events is a more realistic representation of bloom development than the critical-depth model.

The concept of critical depth sensu Sverdrup is logically sound. We conclude, however, that this model is relevant only on an evolutionary scale, reflected in the fact that only a few species tend to dominate blooms. These species have responded to the necessity of lowering respiration rates and coupling growth performance to rapid changes in ambient light intensity—which is why they have succeeded in colonizing a specific type of environment that arises periodically in early spring. The critical factor for bloom initiation is not only spatial but also temporal. We can speak of a *critical period* of stabilization of a shallow layer long enough to permit accumulation of sufficient algal cells so as to overwhelm grazer populations. The *critical depth* of importance for bloom development lies in the upper, rather than the lower, third of the euphotic zone. The critical depth derived from phytoplankton respiration alone will be species-specific and vary by a factor of 10 or more. From an ecological viewpoint, its accurate estimation will not be worth the trouble. The original definition of critical depth averages over 24 h. If we average over a whole year we find that in all water columns (including the underlying benthos) production is always greater than respiration. Thus, the critical depth, on an annual basis, lies below the depth of the biosphere; all ecosystems contribute at least some organic carbon to the sedimentary fossil record, even if it amounts to only a few $\mu g\ C\ m^{-2}\ yr^{-1}$.

The fact that most scientists are not even aware of the discrepancy between Sverdrup's original model and its latter-day versions strongly suggests that it is put to little if any practical use. Its predictive ability in the context of spring bloom growth has, to our knowledge, been explicitly challenged by only a few workers (e.g. Kaiser and Schulz 1978). Its implicit acceptance is reflected in the way it is routinely cited and in the prominence it receives in teaching programs and textbooks. It is time we adopted a more critical attitude toward this model instead of continuing to inflict it as a matter of course on innocent graduate students.

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From image analysis to chemical analysis of bacteria: A long-term study?

The automated analysis of epifluorescence microscopy (EFM) images is becoming a valuable tool for determining the size distribution and the biovolume of planktonic bacteria (Sieracki et al. 1985; Bjørnsen 1986; Bjørnsen et al. 1988). Although no absolute calibration has yet been achieved, recent advancements suggest that the results obtained by automated image analysis are getting closer to the truth (Sieracki et al. 1989; Psenner in press; Schroeder and Krambeck in press). But measurement of bacterial carbon remains an unsolved problem. A better knowledge of the carbon content of aquatic bacteria would constitute a decisive link between studies on bacterial production and on interactions between bacteria, autotrophs, and grazers (Bird and Kalff 1987; Scavia 1988). In both cases the size-dependent distribution of bacterial