

# Subsurface Chlorophyll Maximum Layers: Enduring Enigma or Mystery Solved?

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## Keywords

deep chlorophyll maximum, phytoplankton, carbon-to-chlorophyll ratio, thin layers, turbulence, stratification, growth, acclimation, behavior, primary production

## Abstract

The phenomenon of subsurface chlorophyll maximum layers (SCMLs) is not a unique ecological response to environmental conditions; rather, a broad range of interacting processes can contribute to the formation of persistent layers of elevated chlorophyll *a* concentration (Chl) that are nearly ubiquitous in stratified surface waters. Mechanisms that contribute to the formation and maintenance of the SCMLs include a local maximum in phytoplankton growth rate near the nutricline, photoacclimation of pigment content that leads to elevated Chl relative to phytoplankton biomass at depth, and a range of physiologically influenced swimming behaviors in motile phytoplankton and buoyancy control in diatoms and cyanobacteria that can lead to aggregations of phytoplankton in layers, subject to grazing and physical control. A postulated typical stable water structure characterizes consistent patterns in vertical profiles of Chl, phytoplankton biomass, nutrients, and light across a trophic gradient structured by the vertical flux of nutrients and characterized by the average daily irradiance at the nutricline. Hypothetical predictions can be tested using a nascent biogeochemical global ocean observing system. Partial results to date are generally consistent with predictions based on current knowledge, which has strong roots in research from the twentieth century.

## 1. INTRODUCTION

Vertical profiles of chlorophyll *a* concentration (Chl), whether measured directly on discrete samples or estimated using in situ fluorometers, are seldom uniform; much more often than not, there is a subsurface maximum that is neither random nor ephemeral. Instead, these subsurface Chl maxima generally represent ecologically significant features of the planktonic ecosystem—contiguous layers of phytoplankton that are nearly ubiquitous in stratified waters and that have attracted focused examination since benchmark modeling studies by Gordon Riley and John Steele (Riley et al. 1949; Steele 1956, 1964; Steele & Yentsch 1960) and some of the first continuous vertical profiles of chlorophyll fluorescence that revealed previously unappreciated features in the vertical distributions of phytoplankton (Strickland 1968).

My studies of subsurface chlorophyll maximum layers (SCMLs) began nearly 40 years ago under the supervision of Richard W. Eppley, one of the most influential biological oceanographers of the twentieth century (Weiler et al. 1990). His guidance on how to approach this scientific problem is as appropriate now as it was then. The scenario, edited for brevity and undoubtedly colored by impressionistic recall, was roughly as follows:

J.J.C.: Dick, I'm really interested in studying chlorophyll maximum layers.

R.W.E. (feigning ignorance): What do you mean by that? [Translation: Define the phenomenon of interest.]

J.J.C.: We've been collecting vertical profiles of fluorescence, and lots of them show subsurface maxima.

R.W.E.: So? [Translation: What is it about the phenomenon that you find interesting?]

J.J.C.: I want to describe the mechanisms of their formation and maintenance.

R.W.E.: It's already been done. [Translation: If you want to study something, do your background research first. It probably has been looked at before, and it's your job to identify gaps that should be filled.]

J.J.C. retires to the library, does a fair amount of reading over many days, and returns to explain, to the best of his ability, what is known about chlorophyll maximum layers and some uncertainties that remain. Ideas flow. Then:

R.W.E.: What's your hypothesis?

Thus begins the journey.

A hypothesis is a proposed explanation for a phenomenon; the phenomenon of primary interest here is SCMLs, which are defined below. Here, I review the development of several hypotheses that have been proposed to explain SCMLs, in an attempt to describe what we think we know and what remains unexplained. Are SCMLs an enduring enigma, or a mystery solved? The answer may lie in what we think we know but actually do not.

Rather than attempting a comprehensive assessment of recent research, I focus considerable attention on older publications that established the theoretical framework for describing and explaining SCMLs. The justification for this approach is expressed very well by twenty-first-century graduate students: "The value of a theory is not determined by whether or not it is correct, but rather in the framework that it provides to guide thinking and test new ideas in the field" (Fischer et al. 2014, p. 232).

## 2. DEFINING THE PHENOMENON OF INTEREST

To constrain the scope of this review, here I define SCMLs as local maxima of Chl that form in layers and are maintained by ecological interactions that operate on timescales on the order of a day

or longer; these include autecological processes such as the growth, photosynthetic acclimation, and sinking or swimming of phytoplankton over scales of meters, as well as grazing control that can strongly modulate concentrations of phytoplankton over days to weeks. The corresponding vertical scales of SCMLs are from approximately one meter to tens of meters. Horizontal length scales in turn range from the (sub-)mesoscale (i.e., approximately 2 km, associated with frontogenesis, to the scale of eddies, 20–100 km; Lévy 2008) to the extent of oligotrophic biomes (>1,000 km; Karl 1999).

The terminology for layers of elevated Chl is not particularly complicated, but it requires some review to provide context. The terms deep chlorophyll maximum and chlorophyll maximum layer are commonly used descriptors that are useful in searches of the literature, but because not all subsurface layers are deep and the development of layers at the sea-surface interface (e.g., Cullen et al. 1989) is beyond the scope of this review, I use the term SCML here. Because an SCML can form independently of a maximum in phytoplankton biomass through changes in the chlorophyll content of phytoplankton relative to their biomass as organic carbon (Fennel & Boss 2003, Steele 1964), I make an important distinction between SCMLs and subsurface biomass maximum layers (SBMLs) (e.g., Beckmann & Hense 2007) when appropriate.

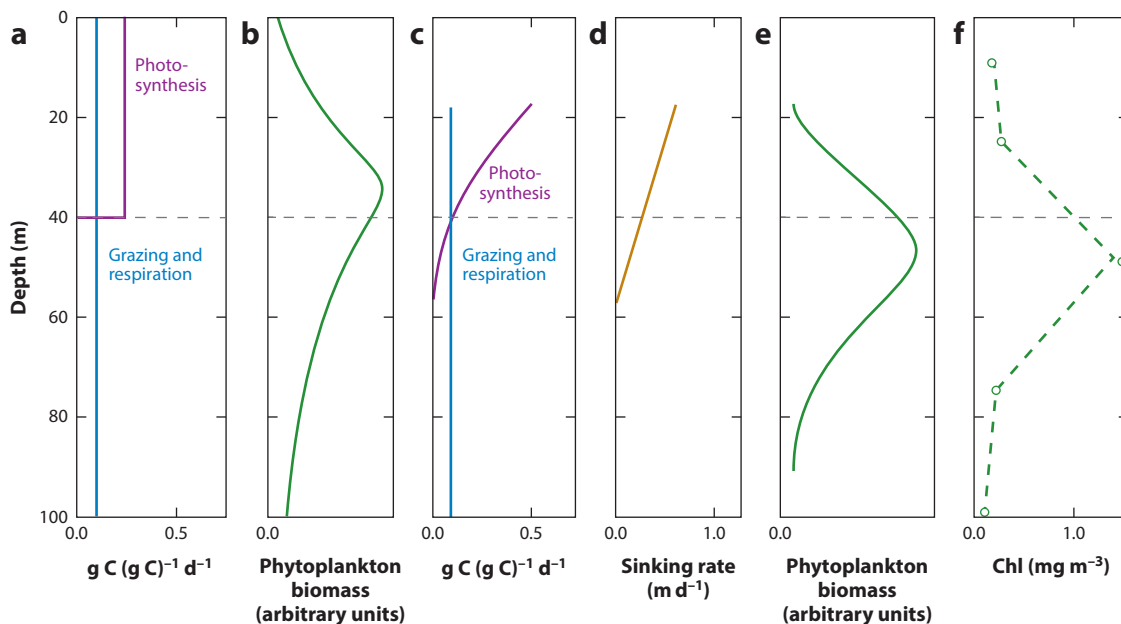
So-called thin layers of phytoplankton (see, e.g., Cowles 2003, Durham & Stocker 2012) are generally formed by biological-chemical-physical interactions on vertical scales of 1 m or less and are strongly influenced by stratification, shear, and sometimes nutrient gradients (e.g., Rines et al. 2010). In their excellent review of recent research, Durham & Stocker (2012) classified deep chlorophyll maxima (and generic SCMLs by inference) as occurring on scales of tens of meters with relatively weak gradients of phytoplankton concentration; they cited my review (Cullen 1982) for support, despite my discussion of studies showing intense thin layers of phytoplankton thought to be associated with variable sinking rates of diatoms with depth (Derenbach et al. 1979), and the apparent aggregation (Falkowski et al. 1980) or organized vertical migration (Kiefer & Lasker 1975) of motile phytoplankton in layers with a thickness of a few meters or less. I decline to cede the vertical scales of 1–10 m (fine scale, *sensu* Steinbuck et al. 2010) to thin-layers researchers, although I am happy to share it with them. The present review focuses on interactions of swimming and sinking behavior of phytoplankton with light and nutrients that can contribute to the formation and maintenance of SCMLs as defined here. I refer readers to the thin-layer literature (Cowles 2003, Durham & Stocker 2012, Sullivan et al. 2010 and references therein) for additional novel and fascinating observations and interpretations of biological, physical, and chemical interactions that influence microscale vertical distributions of phytoplankton and thus some interpretations of SCMLs.

Capitulating to the impracticality of reviewing mechanisms responsible for structuring the vertical distributions of phytoplankton in all marine environments, I focus primarily on one-dimensional processes that have an important influence on the vertical structure of chlorophyll across the trophic gradient from the stable oligotrophic biomes of the central gyres to productive coastal waters, referring tangentially to complex two- or three-dimensional interactions that can have a strong influence on the distributions of phytoplankton in stratified coastal ecosystems. These processes have been studied intensively as part of the Global Ecology and Oceanography of Harmful Algal Blooms (GEOHAB) program (Berdalet et al. 2014 and the special issue of *Deep-Sea Research Part II* in which it appeared) and the Layered Organization in the Coastal Ocean (LOCO) initiative (reviewed in a special issue of *Continental Shelf Research*; see Sullivan et al. 2010); these publications include a wealth of citations not considered here and vice versa. Such is the consequence of an enormous literature.

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**Phytoplankton biomass:** the biomass of phytoplankton, here expressed as organic carbon ( $C_p$ , in, e.g.,  $\text{mmol C m}^{-3}$ ) or nitrogen ( $N_p$ , in  $\text{mmol N m}^{-3}$ )

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**Figure 1**

Before the introduction of flow-through fluorometry (Lorenzen 1966), the chlorophyll *a* concentration (Chl)—along with salinity, nutrients, and sometimes light and primary productivity (Barber & Hiltling 2002)—was generally measured in discrete samples from five to eight depths in a vertical profile. Temperature was measured with reversing thermometers on sample bottles, and bathythermographs could provide complementary continuous profiles. Guided by such observations, which had a vertical resolution of approximately 10 m, by 1960 Riley, Steele, and others had developed a theoretical framework to describe the formation and maintenance of subsurface biomass maximum layers as the result of interacting influences of light and nutrients on the growth and sinking of phytoplankton (see Sections 3.1 and 3.2). The benchmark study by Riley et al. (1949) could explain a subsurface maximum of phytoplankton biomass associated with the sinking of phytoplankton (panels *a* and *b*), but as shown by Steele & Yentsch (1960)—who produced this figure and provided the experimental foundations for including variable sinking rate in their model—a subsurface peak of biomass could form below the daily compensation depth (*gray dashed lines*) only if sinking rate decreased deeper in the water column (panels *c–e*), providing an explanation for observations of Chl at an oceanic station (panel *f*). Figure adapted from Steele & Yentsch (1960).

### 3. EARLY OBSERVATIONS AND MODELS

Before Carl Lorenzen's (1966) introduction of *in vivo* flow-through fluorometry, measurements of the vertical distributions of Chl were sparse, with samples typically taken at five to eight depths per profile (**Figure 1**). Nonetheless, as described in the following three sections, the theoretical foundations to explain the formation and maintenance of SCMLs were for the most part established 50 years ago.

#### 3.1. Growth, Sinking, and a Subsurface Maximum of Biomass

As entertainingly and informatively explained by Wendy Gentleman (2002), models of plankton dynamics began with Richard Fleming (1939) and then developed rapidly under Riley's leadership. Although Riley's early models explicitly considered light penetration and photosynthesis (e.g., Riley 1946), he focused on describing the seasonal cycle of phytoplankton as influenced by environmental factors and grazing, and he did not resolve the vertical structure. This changed with the magnificent study by Riley, Stommel & Bumpus (1949), which dynamically linked

## EUPHOTIC DEPTH

The euphotic zone extends to the euphotic depth ( $z_{eu}$ , in meters; also called the compensation depth), defined by the compensation irradiance ( $E_c$ ) at which photosynthesis just balances losses to cellular respiration (Geider et al. 1986, Langdon 1987);  $E_c$  is appropriately reported as average photosynthetically available radiation (PAR) over 24 h (in  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) or as a cumulative value (in  $\text{mol photons m}^{-2} \text{ d}^{-1}$ ). In many environments habituated by oceanographers, estimates of  $z_{eu}$  correspond roughly to the depth at which surface PAR is reduced to 1% of its surface value ( $z_{1\%}$ , in meters) (e.g., Lee et al. 2007, Ryther 1956), so the equivalence of  $z_{1\%}$  and  $z_{eu}$  has been established with some experimental support (e.g., Marra 2004). But considering that—even if polar regions are ignored—daily solar insolation ( $E_o$ ) varies by well over two orders of magnitude as it is influenced by latitude, season, and cloud cover (Kirk 2011), it does not make sense to assume implicitly that  $E_c$  covaries in lockstep with  $E_o$  at a constant ratio of 1:100. Lorenzen (1976, p. 176) identified this as one of the “fallacies” in the use of  $z_{1\%}$  as a measure of  $z_{eu}$ , and Karl Banse (2004) elaborated, making a strong case for abandoning the practice. I agree, adding that the depth of 1% of surface irradiance, or the corresponding attenuation coefficient for that depth interval ( $K$ , per meter), will retain its utility as a key scaling factor for light transmission in models of depth-integrated primary productivity (e.g., Behrenfeld & Falkowski 1997, Cullen et al. 2012, Lee et al. 2007, Platt & Sathyendranath 1993) even after inappropriate references to euphotic depth—found here and there—are eliminated.

nutrients, phytoplankton, zooplankton, and carnivores in a vertically structured system in which phytoplankton could sink and turbulent diffusion influenced distributions of both nutrients and phytoplankton. Uniform production in the surface layer, influenced by the interaction of sinking and mixing, produced a subsurface maximum of phytoplankton biomass, by implication an SBML (Figure 1a,b), that could not occur below the maximum depth at which positive growth of phytoplankton was possible.

Building on the work of Riley and quickly establishing his own leadership role in the numerical modeling of plankton dynamics, Steele (1956) described and then modeled seasonal changes in the vertical structure of phytoplankton in Fladen Ground. Removing the steady-state restriction of Riley et al. (1949), he described temporal dynamics from spring through fall, including the deepening of the SBML resulting from phosphate depletion near the surface, thereby displacing downward the depth of maximum photosynthetic rate, which in his framework was equivalent to growth rate. This work thereby established the hypothesis relating the depth of the SBML to the stratum of optimum growth rate—nutrient limited above, light limited below.

### 3.2. Nutrient-Regulated Sinking Rate of Diatoms and a Deep Biomass Maximum

In the 1950s, it was well recognized that subsurface maxima of Chl occur commonly below the depth of maximum photosynthesis and sometimes below the euphotic depth (see sidebar Euphotic Depth). A new hypothesis was needed to describe the formation of such a deep biomass maximum.

Analyzing a large set of vertical profiles of particle concentration inferred from optical measurements of forward scatter, Jerlov (1959) identified interacting roles of vertical mixing and the variable sinking rate of phytoplankton in maintaining deep SBMLs, but he could not firmly establish a basis for predicting a reduction of sinking rate deep in the water column. Assessing progress to date (Figure 1), Steele & Yentsch (1960) showed that, in agreement with Jerlov, an SBML could form below the compensation depth if the sinking rate of phytoplankton slowed with depth. Importantly, they presented results from laboratory experiments that demonstrated a strong influence of nutrition on sinking: The sinking rate of a marine diatom in nutrient-deficient

## AN UNDERAPPRECIATED CONTRIBUTION

John Steele's "A Study of Production in the Gulf of Mexico" (Steele 1964) has arguably not received the recognition it deserves. During a conversation with Steele in August 2013, I praised his paper for being comprehensive, insightful, and fundamentally correct—but I questioned the title, which I thought was vague. He replied that the title was chosen to acknowledge that he was funded to work on the Gulf of Mexico! Despite the general title and some inconsistencies that might have been typographical errors, Steele's underappreciated study, highlighted in **Figure 2**, is a benchmark contribution that (a) succinctly summarized progress to date; (b) identified a major unresolved issue (variation in the ratio of Chl to phytoplankton carbon); (c) developed a theoretical framework for explaining the phenomenon, relying on innovations reported in his formidable 1962 study (Steele 1962); (d) compared predictions with observations; and (e) discussed the limitations of his approach. Remarkably, he accomplished this using less than 10 pages of text.

cultures decreased considerably when the cultures were reenriched in the dark. These results and modeling allowed them to relate the physiologically influenced sinking rate of diatoms to seasonal changes in the vertical distributions of Chl and the formation of an SBML near the nutricline in late summer.

### 3.3. Acclimation of Phytoplankton to Light and Nutrients to Form a Subsurface Chlorophyll Maximum

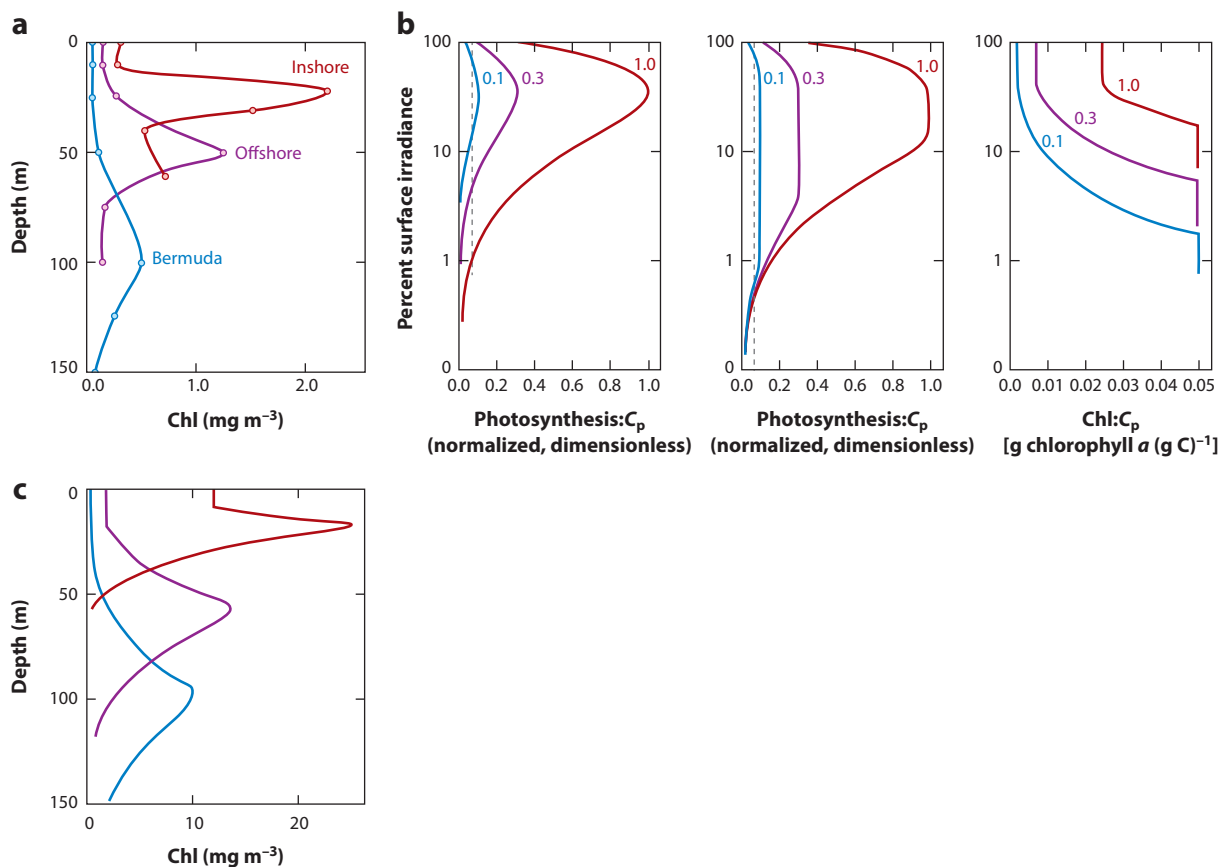
Steele (1964) recognized that sinking seemed to be unimportant in highly stable waters typical of the tropics, not only because the phytoplankton that they were able to enumerate were typically motile, but also because (presaging Margalef 1978) sinking implies a net downward flux of nutrients out of the euphotic zone that "appears to be an extremely inefficient response of a population living in such very stable nutrient-limited regions" (p. 213). Following suggestions by Riley et al. (1949), he thus explored the possible influence of the light adaptation of chlorophyll content and photosynthetic capabilities (now called photoacclimation) on the vertical structure of Chl, whereas previously only the vertical structure of biomass had been modeled. To do so (see sidebar An Underappreciated Contribution), he applied formulae from his groundbreaking 1962 paper (Steele 1962) to describe the influence of light and nutrients on the Chl:C<sub>p</sub> ratio and photosynthetic performance of phytoplankton in the context of a model of vertical structure that included both grazing and carnivory (**Figure 2**). In this second of two studies (Steele 1962, 1964) that were more than 30 years ahead of their time (cf. Geider et al. 1997, Taylor et al. 1997), Steele reproduced changes in the depth and magnitude of the SCML across a trophic gradient that were generally consistent with statistical analyses to come (Herbland & Voituriez 1979), and he generated estimates of the variation of Chl:C<sub>p</sub> as a function of light and nutrients that could produce subsurface maxima of Chl that were not maxima of biomass. Another long-standing hypothesis to explain the formation and maintenance of SCMLs had been established.

### 3.4. Limitations of the Early Observations and Models

As explained by physical oceanographer Walter Munk (2002) in his arguments for the establishment of a global ocean observing system, much of the twentieth century could be called a "century of undersampling" in which "physical charts of temperature, salinity, nutrients, and currents were so unrealistic that they could not possibly have been of any use to the biologists. Similarly, scientists could find experimental support for their favorite theory no matter what the theory claimed"

**Nutricline:** a general term for the gradient of nutrient concentration that represents the boundary between the nutrient-depleted surface layer and deeper, nutrient-rich waters; specific examples include the nitracline and the phosphocline

**Nitracline:** the boundary between the nitrate-depleted surface layer and deeper, nutrient-rich waters; it is commonly defined by a threshold concentration such as 0.1  $\mu\text{mol kg}^{-1}$  or 1.0  $\mu\text{mol kg}^{-1}$ , with units sometimes reported as  $\mu\text{g-at N L}^{-1}$



**Figure 2**

Early researchers knew that vertical profiles of chlorophyll *a* concentration (Chl) did not correspond exactly to profiles of phytoplankton biomass; the ratio of Chl to phytoplankton carbon (Chl:C<sub>p</sub>, or its reciprocal) varied with physiological status (photoacclimation) in ways that they were not yet able to generalize quantitatively. Steele (1964) was the first to tackle the problem of photoacclimation and its role in subsurface chlorophyll maximum layer (SCML) formation. (a) He began by illustrating well-recognized general trends of the depths and magnitudes of the SCMLs in stable midlatitude waters: a higher Chl and shallower maximum near the shore (approximately midshelf in the Mid-Atlantic Bight), a lower Chl and deeper SCML in less productive offshore waters near the shelf break, and the deepest SCML and much lower Chl in oligotrophic waters of the Sargasso Sea near Bermuda. (b) Building on his model of growth, photosynthesis, and photoacclimation in phytoplankton (Steele 1962), he described the acclimation of the photosynthesis-versus-irradiance relationship and Chl:C<sub>p</sub> as a function of light exposure and nutrient limitation (dimensionless, as labeled on the profiles). The left subpanel shows gross photosynthesis and respiration (*dashed line*) for unacclimated phytoplankton, the middle subpanel shows the same for acclimated phytoplankton, and the right subpanel shows the corresponding Chl:C<sub>p</sub> for the three nutritional states. (c) Theoretical profiles were generated by applying the physiology equations in a numerical simulation that included light attenuation by chlorophyll, grazing, and carnivory. Figure adapted from Steele (1964), with an assumed 10 × transcription error in the axis labels for Chl:C<sub>p</sub> corrected in the right subpanel of panel *b*.

(pp. 1–2). But as shown below, early theories to explain SCMLs have largely stood the test of time, although, owing to limitations imposed by sampling, the benchmark studies were fundamentally proofs of concept that had to await further validation. The major limitations of the studies up to the mid-1960s included the lack of systematic observations across a range of environmental regimes and seasons, the impracticality of sampling on vertical scales less than approximately 5–10 m, poor resolution of the influences of grazing, and sketchy experimental foundations for describing the



photoacclimation, buoyancy regulation, and vertical swimming behavior of phytoplankton. This was about to change.

#### **4. INSIGHTS FROM CONTINUOUS VERTICAL PROFILES MEASURED WITH A PUMP AND HOSE**

Biological oceanography was revolutionized in the 1960s with the introduction of new sampling technologies (Cullen 2012), including Lorenzen's (1966) method for measuring chlorophyll fluorescence *in vivo* using a flow-through system, which was applied to vertical profiles by using a pump and hose (Strickland 1968). It was soon established that in coastal waters, high concentrations of phytoplankton could be found in layers approximately 2–5 m or less in thickness (**Figure 3**). Vertical resolution was constrained by a smearing of the signal during transit in the hose, which could be roughly assessed during the calibration of the lag time in the pumped system. In my research group, lag time was determined by sending a graduate student over the side with a can of tomato juice, which was forcibly emptied near the hose inlet while colleagues watched for sharks—the signal was smeared, but not badly.

Conventional sampling continued to yield important data on the distributions of SCMLs that helped to establish the near ubiquity of the layers and to evaluate competing hypotheses to explain them, especially in the open ocean (Venrick et al. 1973), but continuous profiles using a pump and hose provided real-time observations of fluorescence while it was being measured and thus the opportunity to collect water for species identification from peaks as they were encountered. Consequently, subsurface layers of dinoflagellates were soon identified in a wide range of environments (e.g., Falkowski et al. 1980, Lasker 1975, Pingree et al. 1975), sometimes with evidence of diel vertical migration (Eppley et al. 1968, Kiefer & Lasker 1975, Tyler & Seliger 1978).

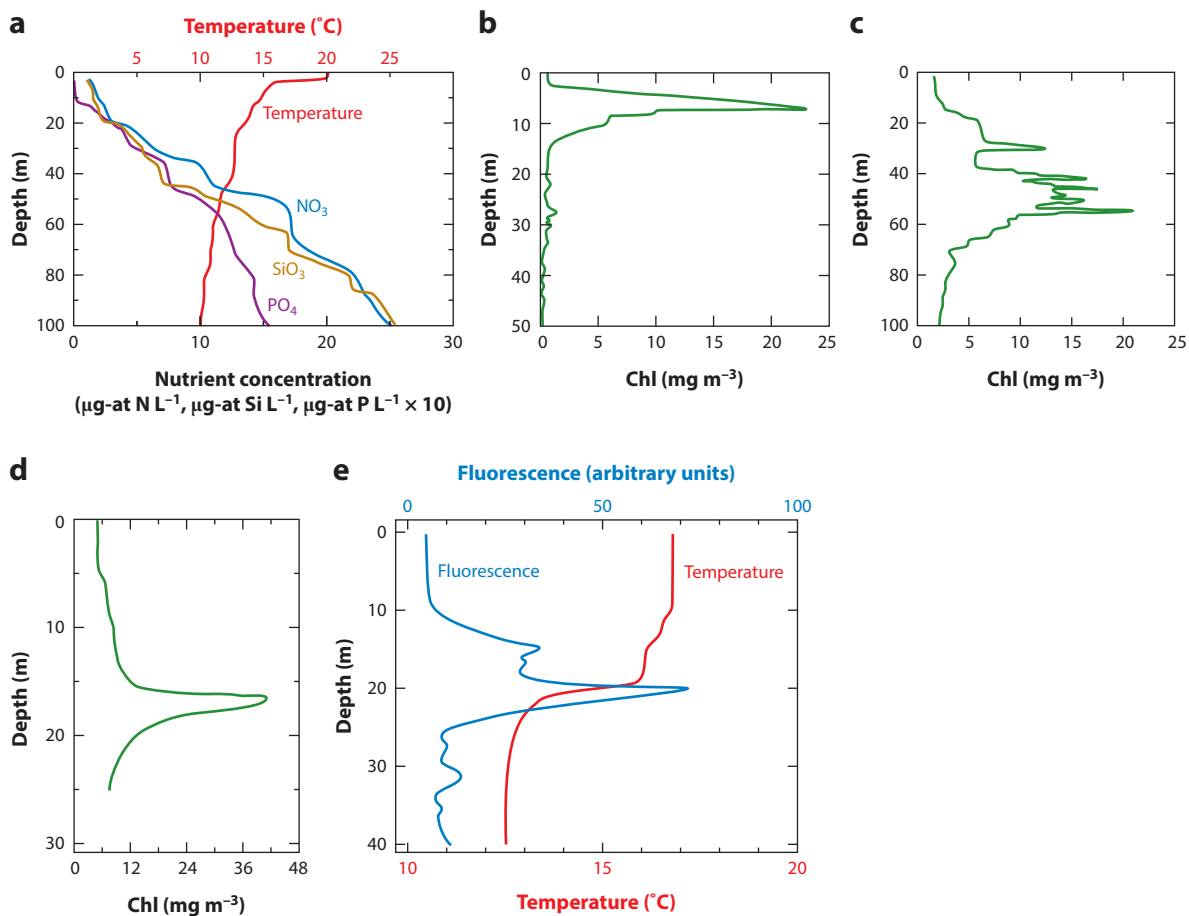
Although the vertical movements and diel vertical migration of dinoflagellates in layers were well recognized (Hasle 1950), the newly available high-resolution observations of the vertical distributions of individual species—demonstrating depth regulation influenced by environmental conditions—solidified an additional hypothesis to explain the formation of SCMLs: the vertical aggregation of motile phytoplankton under physiological control (e.g., Cullen 1985, Harris et al. 1979, Tyler & Seliger 1981). This stimulated many studies on the swimming behaviors of phytoplankton and their interactions with environmental factors, some of which are described below.

Diatoms were also observed in association with subsurface layers (**Figure 3b,c**). Cullen et al. (1982) suggested that the observed aggregations of pennate diatoms may have been associated with a reduced sinking rate near a nutrient gradient, as predicted by Steele & Yentsch (1960). The buoyancy regulation hypothesis was explored fairly thoroughly in lake systems (Heaney et al. 1989) but only sporadically in marine environments in the context of SCMLs (e.g., Bienfang et al. 1983, Lande & Wood 1987). However, the ecological differentiation of diatom species in different strata of the open ocean, including the deep chlorophyll maximum, was well described (e.g., Venrick 1988).

#### **5. THE EVOLUTION OF HYPOTHESES: TYPICAL STABLE WATER STRUCTURE**

The SCML phenomenon is not a unique ecological response to environmental conditions; rather, a broad range of interacting processes can and generally do contribute to the formation of persistent subsurface layers of elevated Chl. When I reviewed this topic more than 30 years ago (Cullen 1982), I proposed a classification of SCMLs to guide the discussion. Here, I update this classification to structure a selective overview of what has been and can be learned about the vertical structures of





**Figure 3**

Flow-through fluorometry fundamentally changed research on vertical distributions of chlorophyll *a* concentration (Chl). (*a–c*) In 1967, the Food Chain Research Group at the Scripps Institution of Oceanography conducted an extensive study of La Jolla Bay (Strickland 1970) in which they used a pump and hose to sample the water column for continuous records of temperature, nutrients (panel *a*), and chlorophyll fluorescence (panels *b* and *c*) and detected nearly ubiquitous subsurface layers of elevated Chl inferred from fluorescence. The sharp subsurface Chl maximum layer in panel *b* was observed during a bloom of the centric diatom *Leptocylinthus danicus*, whereas several diatom species dominated the integrated sample in panel *c* (Eppley et al. 1970). (*d*) Because water could be collected from the stream to enumerate the phytoplankton, aggregations of identified species in relatively thin layers (<5 m) were soon documented in many environments. Kiefer & Lasker (1975) observed a subsurface layer of the dinoflagellate *Akashiwo sanguinea*—at the time called *Gymnodinium splendens* or *Gymnodinium nelsonii*, and later called *Gymnodinium sanguineum* (see Rines et al. 2010)—in one of the earliest studies showing subsurface and sometimes migratory layers of motile phytoplankton (but see Hasle 1950). (*e*) Continuous profiles of fluorescence and temperature revealed a strong association between density structure and phytoplankton, here dominated by the dinoflagellate *Gymnodinium aureolum*, which at the time was called *Gyrodinium aureolum* and since then has gone by several other names (see Hansen et al. 2000). It is important to keep track of changes in taxonomic identification because alternative species identifications might be used over time in research on the same species. Panels *a–c* adapted from Strickland (1970); panel *d* adapted from Kiefer & Lasker (1970); panel *e* adapted from Pingree et al. (1975).

## REVIEWING A LITERATURE THAT IS TOO BIG TO REVIEW

When I last reviewed SCMLs in 1982 (Cullen 1982), the relevant literature seemed manageable: A Web of Science topic search on “(chlorophyll or phytoplankton) and (maximum or maxima) and (deep or subsurface or layer) and (ocean or marine or lake or lacustrine)” yields 256 publications up to that year. I can now see that the 1982 article was selective and likely missed some important insights, particularly from the limnological literature. Still, it was reasonably comprehensive. As of April 2014, the same search yields 3,023 titles since 1900, including 1,258 in the past 10 years. Considering that research on food web interactions and the variable chlorophyll content, swimming behavior, and buoyancy of phytoplankton is also relevant, a comprehensive evaluation of the literature on SCMLs is unrealistic. This review highlights older yet highly relevant literature that is threatened with oblivion from disuse; my intention is to provide future studies of SCMLs with appropriate foundations, consistent with Eppley’s guidance for initiating research (see Section 1) and the argument that established theory can play an important role in guiding thought and in the testing of new ideas (Fischer et al. 2014).

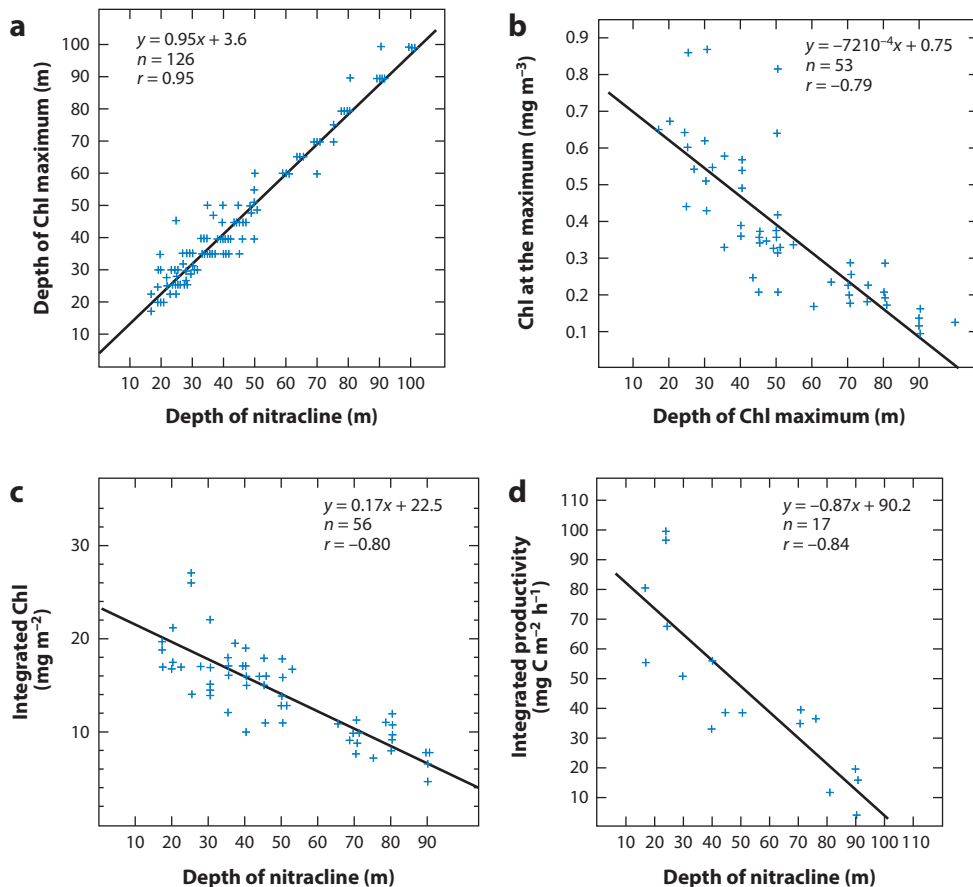
Chl and phytoplankton biomass. Regrettably, a comprehensive review of the literature on SCMLs is no longer practical (see sidebar *Reviewing a Literature That Is Too Big to Review*).

### 5.1. Identifying the Phenomenon

Herbland & Voituriez (1979) presented a statistical analysis and ecological interpretation of 126 vertical profiles (28 with measurements of primary productivity) from the tropical Atlantic Ocean, thereby defining a typical tropical structure (TTS) of stably stratified waters in which nitrate is depleted in the mixed layer (**Figure 4**). The depth of the Chl maximum was statistically the same as the top of the nitracline, consistent with phytoplankton growing where the combination of light and nutrients is optimal (e.g., Anderson 1969, Klausmeier & Litchman 2001, Steele 1956) and with the layer acting as a nutrient trap, ensuring nitrate depletion above (Banse 1987, Jamart et al. 1977, Taylor et al. 1986). The subsurface maximum of primary productivity coincided with that of Chl and with the nitracline except at the more oligotrophic stations, where the nitrate-depleted layer was deeper than 60–70 m and a subsurface peak of primary productivity could not be resolved. Observations at stations influenced by vertical advection—downwelling at a convergence or equatorial upwelling—deviated from TTS, confirming that the TTS phenomenology applies principally to stable waters structured by variability in vertical mixing.

Herbland & Voituriez (1979) related TTS variability to the stability of the water column. Charles Yentsch (1974, 1980) (**Figure 5**) postulated that baroclinicity—the tilting of isopycnals to bring deeper, nutrient-rich water in closer contact with the surface layer (Yentsch 1980)—would enrich phytoplankton stocks such that vertical profiles of Chl (**Figure 5b**) and depth-integrated Chl (**Figure 5c**) could be related to density through the nitrate–density relationship (Yentsch 1974). As incisive analyses have subsequently demonstrated in more detail (e.g., Lévy 2003, McGillicuddy & Robinson 1997, Williams & Follows 2003), the topography of isopycnals as influenced by ocean dynamics can thus significantly modulate the vertical structure of Chl from what it would be if it were influenced only by stratification countering vertical mixing.

The trophic gradient examined by Herbland & Voituriez (1979) did not extend to the most oligotrophic waters, in which the SCML is very deep and attributable mostly to photoacclimation of chlorophyll content rather than to a peak of biomass (Fennel & Boss 2003, Kiefer et al. 1976, Steele 1964, Taylor et al. 1997). Further, the TTS syndrome is confined not to the tropics but, rather, to waters that remain stable long enough for the ecological relationships to develop

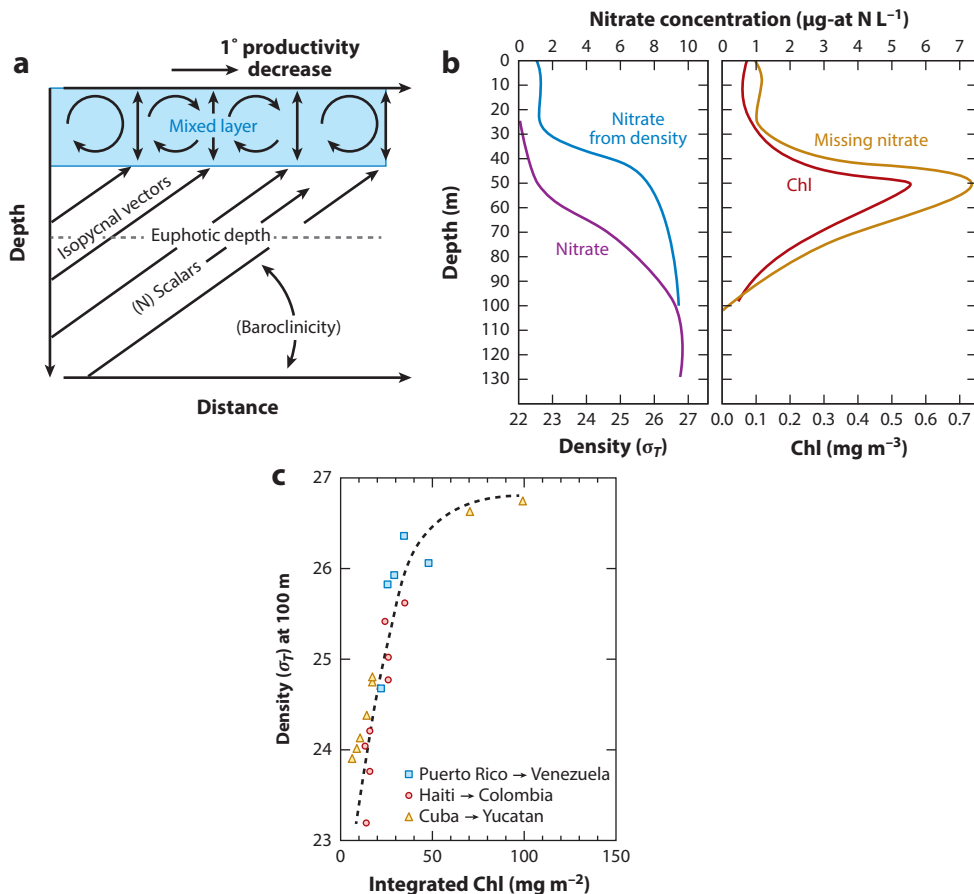


**Figure 4**

Herbland & Voituriez (1979) described a typical tropical structure of stably stratified waters in the tropical Atlantic Ocean, presenting statistical relationships in the vertical structure of chlorophyll *a* concentration (Chl) that were consistent with trends reported and simulated by Steele (1964) for three profiles representing a trophic gradient (**Figure 2**). (*a*) The depth of the subsurface Chl maximum was statistically indistinguishable from the depth of the nitracline ( $z_{\text{ncline}}$ ), consistent with vertical structure being closely related to the transport of nutrients through vertical mixing. (*b*) Chl at the maximum was inversely proportional to the depth of the maximum, as though lower vertical fluxes of nutrients supported smaller populations of phytoplankton because the nitracline was poised at lower light levels, where nutrient-saturated growth rates and corresponding steady-state grazer-controlled concentrations of phytoplankton would be lower (cf. figure 6 from Beckmann & Hense 2007). (*c,d*) In turn, both depth-integrated Chl (panel *c*) and primary productivity (panel *d*) were inversely proportional to the depth of the nitracline. Figure adapted from Herbland & Voituriez (1979).

(e.g., Estrada et al. 1993 and references therein). Consequently, I propose that the term typical stable water structure (TSWS) is more appropriate than TTS as a framework for describing and explaining how interactions of nutrient flux and irradiance influence the vertical structure of Chl.

I begin by addressing the vertical structure of phytoplankton biomass and then the process of photoacclimation. In Sections 5.4 and 7, I discuss where, when, and how the swimming behavior and buoyancy regulation of phytoplankton likely influence the vertical structure of Chl.



**Figure 5**

Yentsch (1974, 1980) related patterns of chlorophyll *a* concentration (Chl) to baroclinicity, which (a) as illustrated here, he described as the tilting of isopycnals associated with ocean circulation that brought nutrient-rich deeper water in communication with the surface layer. (b) Using density as a proxy for the concentration of nitrate at a deep boundary, he calculated the “photosynthetic uptake of nitrogen” as the difference between the deep nitrate concentration expected on the basis of density,  $[\text{NO}_3(\sigma_T)]$  (cf. McGillicuddy & Robinson 1997), and the measured nitrate concentration,  $[\text{NO}_3]$ , and related the result, labeled here as “missing nitrate,” to accumulated chlorophyll. (c) The strong relationship between depth-integrated Chl and density at 100 m in the tropical Atlantic is consistent with baroclinicity having a strong influence on the accumulation of phytoplankton biomass and on primary productivity. Yentsch’s intuitive grasp of the fundamental relationships between the physically driven topography of isopycnals, the nutrient enrichment of surface layers, and mesoscale patterns in the vertical structure and primary productivity of phytoplankton—effectively reviewed and examined further by Balch et al. (1997)—is slowly being validated further by modern analyses and models. Panel *a* adapted from Yentsch (1980); panels *b* and *c* adapted from Yentsch (1974).

## 5.2. Hypotheses to Explain the Vertical Structure of Phytoplankton Biomass

Based on the evidence and insights illustrated in **Figures 4** and **5** and supported by studies discussed in this review, I propose that TSWS represents the consistent responses of the epipelagic system to variations in the nutrient flux from below, which can be related to the depth of the nutricline

## A DIAGNOSTIC OF THE SUBSURFACE BIOMASS MAXIMUM LAYER

- *Hypothesis*: Based on observations and models reviewed here, it can be hypothesized that in stable systems, the SBML is located near the top of the nutricline, where the energy absorbed for photosynthesis and growth of phytoplankton matches the requirement for phytoplankton to consume the vertical flux of the limiting nutrient. Above the SBML, the accumulation of phytoplankton biomass is limited by nutrient supply; light limits growth rate below. In the oligotrophic extreme, the vertical flux of nutrients is too low to support a pronounced layer of elevated phytoplankton biomass.
- *Diagnostic*: Consistent with models of light absorption and photosynthesis (e.g., Bidigare et al. 1987), the energy absorbed for photosynthesis and growth of phytoplankton at the nitracline is  $\bar{a}_{\text{ph}} \cdot \bar{E}_{\text{ncline}}$ , where  $\bar{a}_{\text{ph}}$  (per meter) is the coefficient for absorption of light by phytoplankton, appropriately weighted for the irradiance spectrum, and  $\bar{E}_{\text{ncline}}$  is the average daily irradiance at the nitracline (in  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ ) or the equivalent daily exposure (in  $\text{mol photons m}^{-2} \text{ d}^{-1}$ ). The vertical flux of nutrients, e.g., nitrate (in  $\text{mol nitrate-N m}^{-2} \text{ d}^{-1}$ ), is a first-order measure of new production and thus the trophic status of the surface layer. It follows that the average irradiance at the nitracline is a useful diagnostic for examining relationships between the vertical structure of phytoplankton biomass and trophic status;  $\bar{E}_{\text{ncline}}$  is a more direct measure of the influence of light on phytoplankton dynamics than either the depth of the nitracline or its relative light level (see sidebar Euphotic Depth), and it is relatively easy to measure or estimate.

or, more appropriately, to the light level at that depth (in  $\text{mol photons m}^{-2} \text{ d}^{-1}$ ) (cf. Letelier et al. 2004; see sidebar A Diagnostic of the Subsurface Biomass Maximum Layer). The nutrient flux from below need not be exclusively from vertical mixing—e.g., as could be characterized by profiles of nutrients and turbulence (Lewis et al. 1986, Sharples et al. 2001)—and upwelling (Halpern et al. 1989); rather, it can be supplemented by transport along sloped isopycnals (**Figure 5a**) and by even more indirect processes (Jenkins & Doney 2003), some of which, such as eddies (McGillicuddy et al. 2007), would represent episodic perturbations in TSWS. Under relatively stable conditions (an admittedly fuzzy criterion), the result is a system poised by the upward rate of nutrient transport to the photic zone, in which the SBML acts as a nutrient trap (Banse 1987, Jamart et al. 1977, Taylor et al. 1986). If the flux is small, then low rates of nutrient uptake (new production) associated with a layer of phytoplankton growing relatively slowly at low irradiance will consume the supply; as the flux increases, higher rates of new production by phytoplankton growing more rapidly, and possibly attaining higher concentrations at higher irradiance, establish the balance between the supply of nutrients and the demand.

The proposed hypothesis is that TSWS—the syndrome identified by Herbland & Voituriez (1979) and Yentsch (1980, 1974), among many others (**Figures 4** and **5** and Section 6)—is structured by the vertical flux of nutrients to the surface layer balanced by the growth of phytoplankton, with the following consequences, presented as postulates:

1. The light level at the nutricline ( $\bar{E}_{\text{ncline}}$ , in  $\text{mol photons m}^{-2} \text{ d}^{-1}$ ) is positively, though not linearly, related to the vertical flux of nutrients (in, e.g.,  $\text{mol nitrate-N m}^{-2} \text{ d}^{-1}$ ). The depth of the nitracline ( $z_{\text{ncline}}$ ) is thus inversely related to nutrient flux, but the relationship between  $\bar{E}_{\text{ncline}}$  and nutrient flux should be stronger.
2. Because the SBML acts as a nutrient trap (Banse 1987, Taylor et al. 1986), the rate of new production in the SBML is strongly related to upward nutrient flux that is trapped and is thus also strongly related to  $\bar{E}_{\text{ncline}}$ . It follows that  $\bar{E}_{\text{ncline}}$  is an indicator of water column new production.

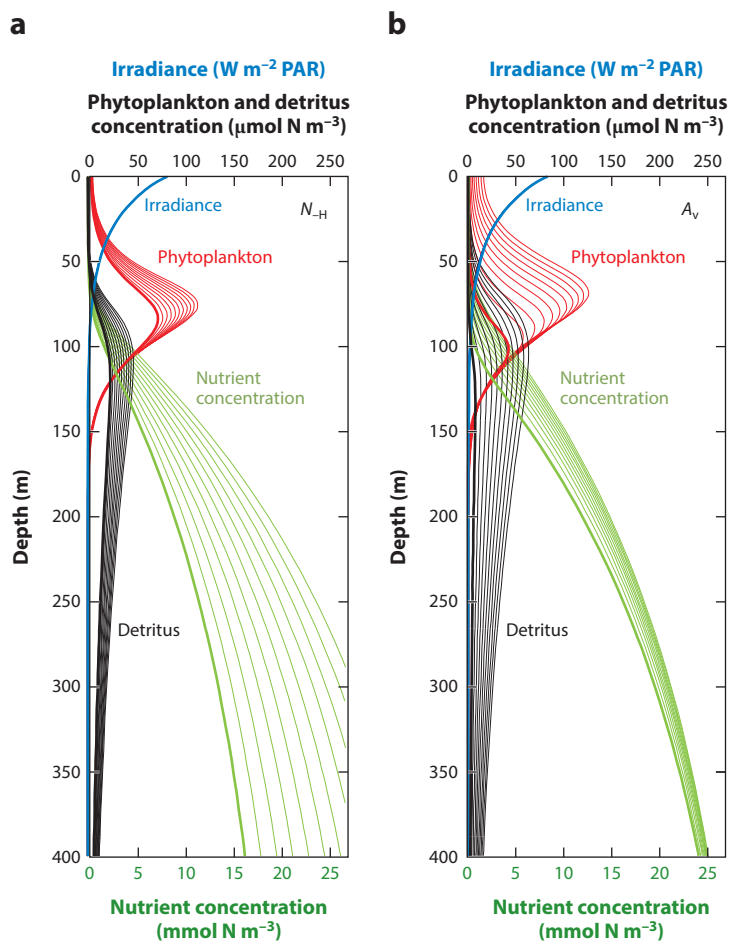
3. The depth of the SBML is very close to  $z_{\text{ncline}}$ , the boundary between nutrient-limited and light-limited strata. Generally, the specific growth rate of phytoplankton that can be supported at this depth is a function of  $\bar{E}_{\text{ncline}}$  and is thus higher when both irradiance and nutrient fluxes are higher.
4. Maximum phytoplankton biomass (e.g.,  $C_p$ , in  $\text{mmol C m}^{-3}$ , or  $N_p$ , in  $\text{mmol N m}^{-3}$ ) in the SBML is positively related to  $\bar{E}_{\text{ncline}}$  and to the rate of new production and is thus inversely related to  $z_{\text{ncline}}$ , consistent with observations indicating that higher fluxes of new nutrients drive food webs with higher ratios of export to total production (e.g., Eppley & Peterson 1979) and that the depth of the nutricline is a strong predictor of phytoplankton community composition and export flux (Cermeño et al. 2008). That is, in food webs poised at a high  $\bar{E}_{\text{ncline}}$ , higher concentrations of phytoplankton support the higher fluxes of organic matter to grazing and other losses.
5. Following established trends with new production across a trophic gradient, integrated phytoplankton biomass (in  $\text{mmol phytoplankton C m}^{-2}$ ) and integrated primary productivity (in  $\text{mmol C m}^{-2} \text{ d}^{-1}$ ) (but see Estrada et al. 1993) are also positively related to  $\bar{E}_{\text{ncline}}$  and thus inversely related to  $z_{\text{ncline}}$ .
6. At the oligotrophic extreme in waters with very low rates of vertical mixing, a pronounced SBML does not form, new production is very low, and a range of nutritional strategies of phytoplankton (Clegg et al. 2012) support the persistence of a deep community of phytoplankton at low concentrations regulated by grazing thresholds (see, e.g., Strom et al. 2000), extending roughly to the compensation depth and the nutricline, which might be deeper than the compensation depth if accessed by migrating phytoplankton (cf. Richardson et al. 1998, Villareal et al. 1996, White et al. 2006).

The central hypothesis and supplementary postulates about specific TSWS features are not new, of course, except perhaps for the explicit focus on daily photon flux at the nutricline (cf. Letelier et al. 2004, Mignot et al. 2014) rather than on its depth per se (Cermeño et al. 2008). Optical depth (see Babin et al. 1996, Uitz et al. 2006) is a useful proxy for daily irradiance at depth if seasonal or latitudinal variations in insolation are not important.

The general features of TSWS can be reproduced by many numerical models, each of which is designed to explore particular questions. A sensitivity analysis by Beckmann & Hense (2007) examined the two hypothesized drivers of vertical structure in phytoplankton: variations in vertical diffusivity (e.g., Herbrand & Voituriez 1979) and variations in nutrient concentration in the source water for vertical mixing (e.g., Yentsch 1974, 1980) (**Figure 5c**), both of which influence the vertical nutrient flux that is hypothesized to drive TSWS. The authors intentionally focused on the vertical structure of phytoplankton biomass rather than that of Chl, so their results are directly relevant to this discussion. Their finding—that the abundance and productivity of phytoplankton generally change with the supply rate of nutrients and available light (illustrated in **Figure 6**)—is consistent with the proposed TSWS hypothesis, except for postulate 6, which was not examined.

The phenomenology of TSWS implies bottom-up control, even though it has been abundantly clear for many decades that grazing is the principal agent countering the growth of phytoplankton, particularly in stable systems, and that this grazing must have a fundamental influence on their distributions (reviewed by Banse 1995, 2013). In stable one-dimensional systems approaching a steady state, the top-down and bottom-up perspectives might be reconciled if it is established that increased fluxes of new nutrients to phytoplankton and corresponding increased losses to grazing and sinking can be supported only by higher concentrations of phytoplankton growing at higher rates (postulate 4).





**Figure 6**

Beckmann & Hense's (2007) model of the vertical structure of phytoplankton biomass, which was intentionally designed to exclude the effects of photoacclimation on the ratio of chlorophyll *a* concentration to phytoplankton biomass ( $\text{Chl}:C_p$ ) and described grazing with a simple quadratic term, generates trends in solutions that are consistent with typical stable water structure. Phytoplankton (red), detritus (black), and irradiance (blue) follow the upper scale; phytoplankton does not sink, whereas detritus sinks and is regenerated. Nutrient concentration (green) follows the lower scale. For each property, the leftmost, thick line represents the results for the minimum parameter value, and the thin lines show increments of 1/10th the modeled range. (a) An increase in nutrient concentrations in deep water ( $N_{-H}$ ) leads to a shoaling of the subsurface biomass maximum layer and an increase in its magnitude, along with a shoaling of the nutricline and increases in depth-integrated biomass and (not shown) integrated productivity. (b) An increase in vertical diffusivity ( $A_v$ ) generates similar trends. This model, along with many others that use admittedly oversimplified grazing functions, generates results that are consistent with bottom-up mechanisms structuring the vertical profile of phytoplankton biomass. But consistency is not a validation of simple bottom-up control: In their study, Beckmann & Hense (2007) ascribed significant importance to detrital sinking and remineralization rates. More broadly, it has been authoritatively argued for decades that, because losses to grazing often match or exceed gains from growth, top-down control of phytoplankton must play a large role in pelagic ecology (Banse 1995, 2013). Additional abbreviation: PAR, photosynthetically available radiation. Figure adapted from Beckmann & Hense (2007).

## FLUORESCENCE IS NOT CHLOROPHYLL

That chlorophyll fluorescence is an imprecise measure of Chl (Cullen 1982) is well established, so caution is warranted when inferring the vertical structure of Chl from profiles of fluorescence, which are now available in abundance. The calibration of fluorescence from autonomous sensors on profiling floats and ocean gliders is particularly problematic because coincident sampling for in situ validation is impractical or impossible; because data from these platforms will be used to test general theory, novel calibration techniques are required. New approaches have been introduced (e.g., Mignot et al. 2011; Xing et al. 2011, 2012) and will surely be refined. Optical assessment of the red absorption peak of chlorophyll has significant advantages, and this method is suitable for autonomous sampling (Roesler & Barnard 2014).

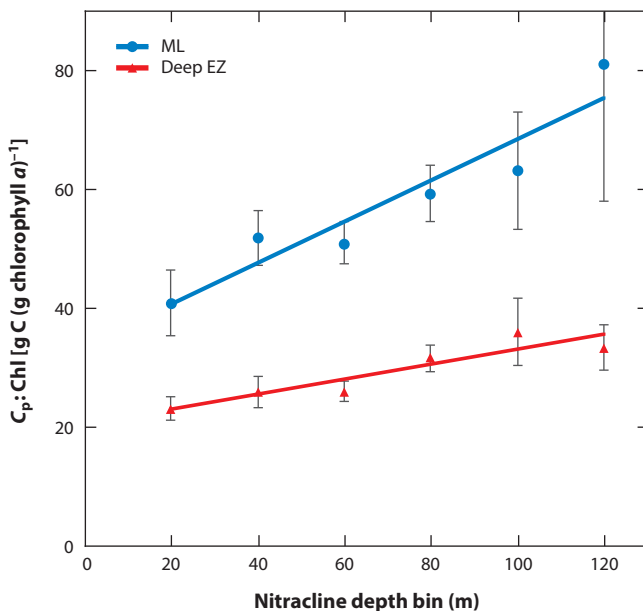
### 5.3. Acclimation and Adaptation of Pigment Content and the Vertical Structure of Chlorophyll

According to postulate 6, there is no biomass maximum near the nitracline at the oligotrophic extreme. Rather, it is at this extreme that the contribution of photoacclimation to the vertical structure of Chl (Section 3.3) dominates, producing the upper gradient of the SCML; inadequate light for growth accounts for the decline with depth below the peak. Accepting that many assessments of TSWS have relied or will rely on vertical profiles of Chl (as estimated from fluorescence; see sidebar Fluorescence Is Not Chlorophyll), it is appropriate to include variability in pigment content (Chl: $C_p$  or its reciprocal) resulting from both photoacclimation (physiological regulation) and changes in community composition attributable to adaptation (see Falkowski & LaRoche 1991) in a TSWS for Chl. Two additional postulates expand the hypothetical framework:

7. In all stably stratified waters, Chl: $C_p$  is higher in the SCML than in the nutrient-depleted surface layer owing to the acclimation of phytoplankton to lower light and an increased nutrient supply (e.g., Fennel & Boss 2003 and many others). Like other TSWS features, the ratio of Chl: $C_p$  in the SCML to that near the surface is related to the vertical flux of nutrients and the depth of the nitracline; it is greatest at the oligotrophic extreme, where the contrast between the high-light, low-nutrient surface community and the low-light, higher-nutrient deep community is greatest. Consequently, the contribution of photoacclimation to the ratio of Chl in the SCML relative to that near the surface is relatively weak in more eutrophic waters, where the accumulation of biomass accounts for the SCML, and strong in oligotrophic waters, where increased Chl: $C_p$  accounts for the subsurface maximum of Chl.
8. The Chl: $C_p$  of cyanobacteria is inherently lower than that of most eukaryotes (Geider 1992), so their increased relative abundance in the SCML of oligotrophic waters relative to that of more eutrophic waters can mask the predicted increase of Chl: $C_p$  in the SCML associated with reduced  $\bar{E}_{\text{ncline}}$  across a trophic gradient.

These postulates are generally consistent with data and interpretations presented in a recent study by Taylor et al. (2014) (**Figure 7**).

Appropriate assessment of postulates 7 and 8 in the context of TSWS would require a comprehensive review of models, measurements, and optical estimates (e.g., Behrenfeld & Boss 2003, Cetinić et al. 2012, Mignot et al. 2014) of  $C_p$ :Chl (or Chl: $C_p$ ) in the context of recent studies employing newer methods for determining the carbon content of phytoplankton (e.g., Graff et al. 2012, Li et al. 2010, Taylor et al. 2014). None of this is possible here, although the study by Fennel & Boss (2003) is an excellent point of reference; the foundational literature is considered



**Figure 7**

Patterns in the ratio of phytoplankton biomass to chlorophyll  $a$  concentration ( $C_p:Chl$ ) measured over six years in the California Current Ecosystem (Taylor et al. 2014) illustrate trends that are generally consistent with model results and with less comprehensive (and sometimes less certain) sets of observations over the past 50 years, including estimates from the same region (Cullen et al. 1982, Li et al. 2010). Generally,  $C_p:Chl$  increases nonlinearly with growth irradiance in nutrient-replete phytoplankton, increases with nutrient limitation of growth at a given light level, and is consistently higher for cyanobacteria compared with eukaryotes (Geider 1992). Stations are binned along a trophic gradient according to nitracline depth (mesotrophic to oligotrophic);  $C_p:Chl$  is calculated for the mixed layer (ML) and deep euphotic zone (deep EZ), which corresponds to the SCML. The trend in mixed-layer  $C_p:Chl$  is consistent with acclimation to reduced nutrient supply (Babin et al. 1996) and an increased relative abundance of cyanobacteria (Taylor et al. 2014) in progressively more oligotrophic surface waters. Assuming that the subsurface chlorophyll maximum layer (SCML) (deep EZ sample) is near the nitracline and that  $\bar{E}_{ncline}$  decreases with its depth, the increase in  $C_p:Chl$  in the SCML with  $z_{ncline}$  is consistent with postulate 8—a floristic shift from diatoms and larger eukaryotes in more eutrophic waters toward cyanobacteria in oligotrophic waters ( $C_p:Chl$  increases) having a greater influence than the acclimation of nutrient-replete phytoplankton to lower irradiance in the oligotrophic SCML ( $C_p:Chl$  decreases). In the same region, measured  $C_p:Chl$  in SCMLs dominated by dinoflagellates near a shallow nitracline was much higher than this trend (Cullen & Horrihan 1981, Cullen et al. 1982), as expected (Chan 1978). Figure adapted from Taylor et al. (2014), which includes a discussion of these influences.

carefully, and many subsequent studies that are relevant to this discussion cite it, so they are easy to find.

#### 5.4. Variable Sinking Rate with Depth

As outlined in Section 3.2, Steele & Yentsch (1960) established the hypothesis that SBMLs could be produced if the sinking rate of phytoplankton decreased when they encountered the nutricline. Jamart et al. (1977) parameterized this effect in a notably comprehensive time-dependent simulation of the vertical structure of phytoplankton growth, Chl, and nutrients; a thorough sensitivity analysis (Jamart et al. 1979) later showed that SCML formation could be simulated using many

combinations of parameters, including some that omitted a nutrient-dependent sinking rate, so at the time there was no compelling case to include the added complexity to numerical models. Subsequently, Fennel & Boss (2003) carefully considered the need for nutrient-dependent sinking in their model of the vertical structure of Chl in oligotrophic waters and concluded, consistent with Steele (1964) and Bienfang et al. (1983), that changes in sinking rate with depth are not an important structuring mechanism in oligotrophic waters (where losses to the system from sinking are inherently low; see Eppley & Peterson 1979, Margalef 1978).

Deferring consideration of neutral buoyancy and the vertical migration of nonmotile phytoplankton,<sup>1</sup> we can predict the influence of variable sinking rate on TSWS based on a ninth postulate:

9. The SCML is accentuated when the sinking rate of nutrient-stressed phytoplankton is reduced upon reaching the nutricline. Because the ratio of export production to total production and, thus, the losses of phytoplankton to sinking decrease as a function of vertical nutrient flux (new production), the potential influence of variable sinking rate on the vertical structure of Chl decreases in more oligotrophic waters.

Lande & Wood (1987) considered a special case of nutrient-influenced sinking in which a reduced sinking rate associated with enhanced nutrient concentrations just below the mixed layer not only could produce an SCML below the mixed layer, but also could result in enhanced resuspension into the mixed layer, thereby improving growth conditions.

As recognized by Jamart et al. (1979), observations of vertical structure alone are unlikely to resolve hypothesized influences of variable sinking. The ninth postulate might be useful as a reminder that the mechanism can only be important where sinking losses of phytoplankton are significant, as they may be in more productive upwelling situations or perturbed systems. For example, phytoplankton blooms can be terminated with rapid sinking of phytoplankton biomass, often facilitated, if not forced, by aggregation (Passow et al. 1994, Smetacek 1985). The pulse of sinking phytoplankton can appear as a transient but pronounced subsurface layer (Briggs et al. 2011, Platt & Rao 1970) that has important consequences for the ecology and biogeochemical cycles of the sea but does not persist, and thus is not considered in detail here.

## 6. HOW TYPICAL IS TYPICAL STABLE WATER STRUCTURE?

The TSWS framework is a compilation of postulates—most of them well established—that have the advantages of making sense and having strong support from observations and models. But comprehensive validation will be a challenge, and it is explicitly recognized and abundantly evident that some or many of the TSWS postulates do not apply to strongly perturbed systems (upwellings, spring blooms, and complex coastal hydrographies) where SCMLs are observed, so the utility of the framework can be questioned. The value in TSWS (and its conceptual components—TTS, photoacclimation of  $C_p$ , and variable sinking) may lie in the cases where it succeeds in explaining observations, thereby supporting the underlying hypotheses and the diagnostic and predictive models that are based on them. More important, perhaps, is that much can also be learned when TSWS fails, leading to the development and testing of alternate hypotheses.

Estrada et al. (1993) examined vertical distributions of Chl, phytoplankton species, nutrients, and primary productivity in the Mediterranean and interpreted their results in the context of TTS and established knowledge about the seasonal succession of phytoplankton in the region. Letelier

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<sup>1</sup>Diatoms and filamentous cyanobacteria can glide along surfaces, but for the purposes of this review, motility is synonymous with swimming.

et al. (2004) carefully examined the seasonal dynamics of the SCML in the oligotrophic North Pacific Subtropical Gyre, providing strong foundations for some of the TSWS postulates and also quantifying the influences of perturbations. These studies and many others are relevant to the testing of TSWS, but here I focus selectively on the potential for global assessment using the rapidly developing global array of autonomous bio-optical profiling platforms (Johnson et al. 2009).

The need to refine global estimates of primary productivity in the ocean by remote sensing led to comprehensive examinations of the vertical structure of Chl. Morel & Berthon (1989) described consistent changes in subsurface Chl distributions as a function of Chl at the surface (see also Platt & Sathyendranath 1988). Their publication serves as a benchmark for the study of the vertical structure of Chl. As subsequently confirmed by Uitz et al. (2006), observations of the vertical structure of Chl, grouped by trophic status (**Figure 8**), describe the trends predicted for TSWS biomass distributions (**Figure 6** and Section 5.2) but with the additional contribution of photoacclimation (Section 5.3). A recent examination of fluorescence profiles from stratified waters (Mignot et al. 2011), rooted in the study by Morel & Berthon (1989), revealed statistical relationships consistent with TTS and TSWS (**Figure 9**). Notably, these studies were confined to case 1 waters, where phytoplankton and covarying substances are responsible for changes in optical properties. The excluded case 2 waters include many coastal systems where complicated hydrodynamics and freshwater inputs can obviate development of TSWS.

Profiling floats and gliders (Johnson et al. 2009) are capable of providing global observations of the vertical distributions of Chl (see sidebar Fluorescence Is Not Chlorophyll) and, when interpreted cautiously, estimates of  $C_p$  from optical measurements (e.g., Fennel & Boss 2003, Gernez et al. 2011, Kitchen & Zaneveld 1990, Mignot et al. 2014). Because these profiling systems are also capable of measuring nitrate concentration, irradiance, oxygen (which can be related to new production; Riser & Johnson 2008, Shulenberger & Reid 1981), temperature, and salinity, the stage has been set for comprehensive assessments of TSWS predictions of the vertical distributions of both Chl and  $C_p$  in relation to integral (or average) daily irradiance, density structure, and estimates of the vertical flux of nutrients. Rapid progress is already being made. I suggest that there may be value in converting the proposed TSWS postulates into quantitative predictions and testing these predictions against observations from autonomous profilers, paying particular attention to estimates of available light in absolute units ( $\text{mol photons m}^{-2} \text{ d}^{-1}$ ) because they are better than either depth or a percentage of surface irradiance as indicators of the influence of light on the epipelagic balance (e.g., Banse 1987, Letelier et al. 2004; see also sidebars Euphotic Depth and A Diagnostic of the Subsurface Biomass Maximum Layer). If measurements of daily solar irradiance at the surface are not available, then using relative light penetration to represent depth (e.g., optical depth; Babin et al. 1996, Morel & Berthon 1989) will account for much of the variability in structure resulting from light. However, as already established for the euphotic depth (Banse 2004; see also sidebar Euphotic Depth), estimates of daily photon flux are much more relevant for ecological prediction and possibly critical for appropriate assessment of  $\bar{E}_{\text{ncline}}$  as a diagnostic of trophic status.

## 7. BEHAVIORAL AGGREGATION OF PHYTOPLANKTON IN LAYERS

As with the photoacclimation of Chl: $C_p$  (Section 5.3), behavioral aggregation of phytoplankton in layers merits extensive discussion that cannot be presented under the constraints of this review. Durham & Stocker (2012) provided an excellent review of interactions between physical processes and the behavior of phytoplankton, including several on the microscale, that have important influences on the dynamics of thin layers. Newly described mechanisms such as gyrotactic

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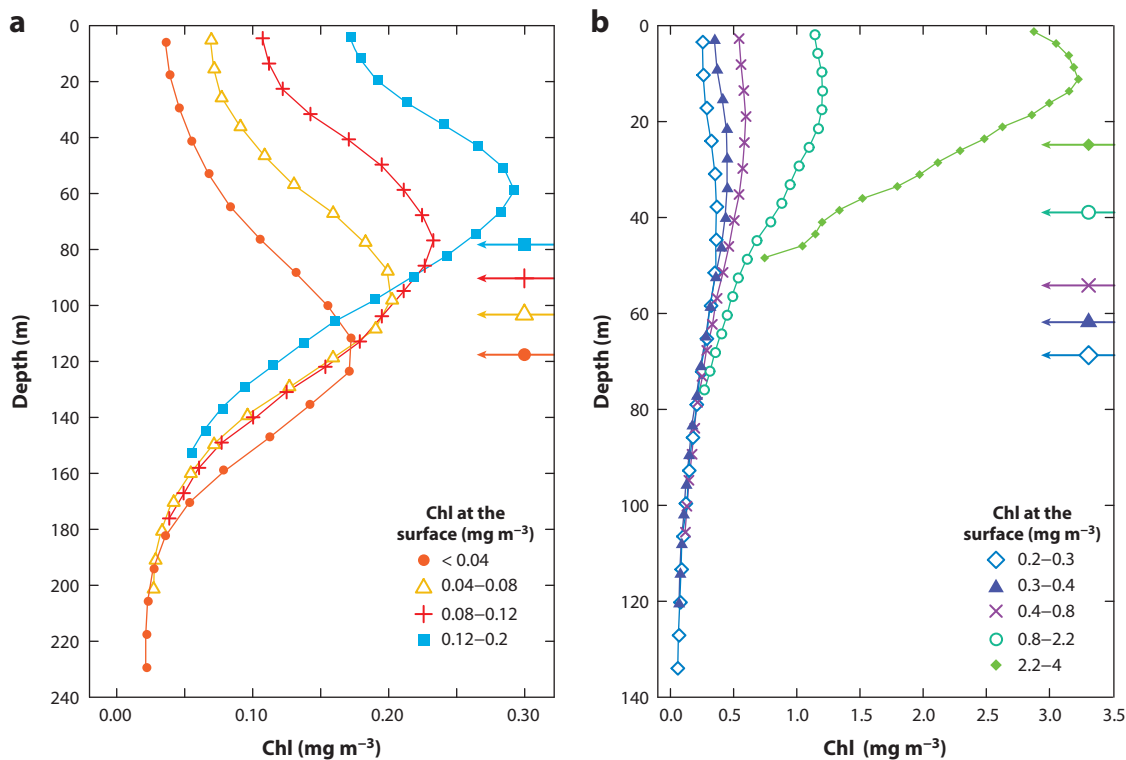
### Case 1 waters:

a bio-optical classification in which variability in optical properties is due to chlorophyll and covarying substances, generally of biological origin (Morel 1988)

### Case 2 waters:

waters in which the optical properties are influenced not only by phytoplankton but also by other substances, such as suspended sediment and colored dissolved organic matter, that vary independently from phytoplankton (IOCCG 2000)

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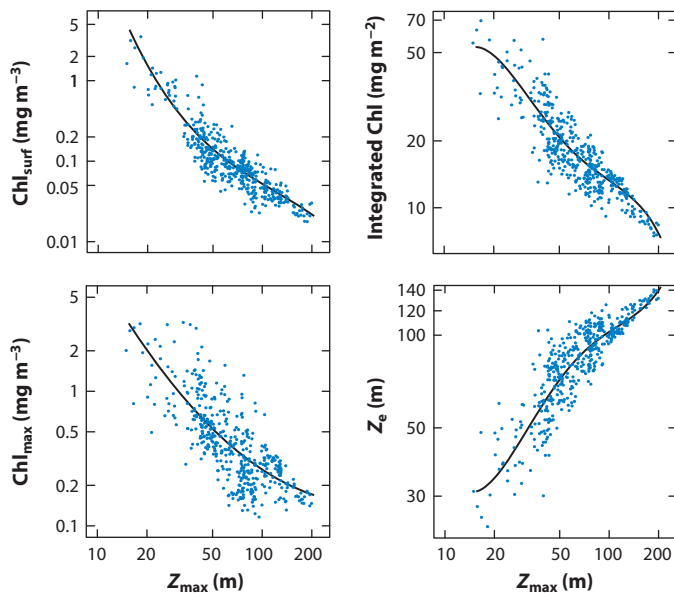
**Figure 8**

Vertical profiles of chlorophyll *a* concentration (Chl) from 1,821 stations in stratified waters illustrate consistent changes in the vertical distributions of Chl with trophic status, categorized here by Chl at the surface. The positions of  $z_{1\%}$  (the depth at which surface photosynthetically available radiation is reduced to 1% of its surface value) are indicated with arrows and the symbols corresponding to each trophic category. Note the scale changes for both Chl and depth. These profiles show patterns of Chl that reflect both the vertical structure of biomass and changes in the ratio of Chl to phytoplankton biomass (Chl: $C_p$ ) with depth and location; the trends are consistent with the postulates of typical stable water structure. For comparison, **Figure 6** shows modeled patterns in the vertical structure of phytoplankton biomass, with no photoacclimation, as influenced by the creation of a trophic gradient by vertical nutrient flux. Figure adapted from Uitz et al. (2006).

trapping (Durham et al. 2009) and refined models of physical and biological controls on vertical gradients of phytoplankton (see sidebar Physical and Biological Controls of Vertical Gradients in Phytoplankton) have greatly enhanced the understanding and quantitative prediction of thin layers. The recent research on harmful algal blooms in stratified waters (reviewed by Berdalet et al. 2014) is well integrated with studies of thin layers, and the theoretical framework overlaps that for fine-scale SBMLs as defined here, so a great deal of complementary research applies.

Endorsing the conclusion of Fischer et al. (2014) that scientific progress has at times been slowed by a lack of awareness of relevant research within or outside of a given field of study, and appreciating that it is now effectively impossible to develop and maintain that awareness (see sidebar Reviewing a Literature That Is Too Big to Review), I offer a few examples of publications on swimming behavior and buoyancy regulation—some well recognized, others not—that might help to guide future studies of layer formation by phytoplankton. Cullen & MacIntyre (1998) discussed three broad niches of phytoplankton: mixers, migrators, and layer formers—phytoplankton that aggregate in persistent subsurface layers. Here, I discuss layer formers and phytoplankton that





**Figure 9**

Continuous profiles of chlorophyll *a* concentration (Chl) estimated from fluorescence (calibrated with the pigments determined by high-performance liquid chromatography) show trends consistent with typical tropical structure and typical stable water structure in 486 stations from case 1 waters ranging from the hyperoligotrophic South Pacific to the eutrophic Benguela upwelling (Mignot et al. 2011). The depth of maximum Chl is  $z_{\max}$ ; the variables related to it are Chl at the surface ( $\text{Chl}_{\text{surf}}$ ), Chl at the maximum ( $\text{Chl}_{\max}$ ), the depth at which surface photosynthetically available radiation is reduced to 1% of its surface value ( $Z_e$ ), and Chl integrated from the surface to  $Z_e$ . In principle, data from biogeochemical profilers could be used to examine predicted relationships between profiles of Chl, phytoplankton biomass from optical measurements, the depth and light level of the nitracline, and the physical structure of the water column, with complementary depth-resolved estimates of daily irradiance, primary production (Claustre et al. 2008), and new production (Riser & Johnson 2008). In a paper published after this review was submitted, Mignot et al. (2014) presented novel comparisons of vertical profiles recorded by floats equipped with bio-optical sensors.

form subsurface layers during migrations, with a focus on the behavioral traits of phytoplankton that would lead to the formation of persistent layers that would maintain consistent relationships with gradients of light and nutrients in the water column.

### 7.1. Accumulation of Swimming Phytoplankton in Layers

The active accumulation of motile phytoplankton in layers is common in stratified environments (e.g., Berdalet et al. 2014 and references therein), reflecting an ecological adaptation—depth regulation under physiological control—that is sometimes overwhelmed by physics [see the review by Kamykowski (1995)]. Single species can persist for long periods of time in subsurface strata (Eppley et al. 1984, Granéli et al. 1993, Kononen et al. 2003, Pingree et al. 1975), where active growth can be maintained, or they can migrate vertically (Eppley et al. 1968, Smayda 1997) in a behavior that in some cases has been related to deep nutrient acquisition (Cullen 1985, Ji & Franks 2007, Ralston et al. 2007) and also to vertical niche partitioning among species according to optimum light conditions (as shown for freshwater phytoplankton; Sommer 1982).

Ralston et al. (2007) carefully examined vertical migration for deep nutrient acquisition, comprehensively reviewing the relevant literature in support of their modeling effort. Recognizing

## PHYSICAL AND BIOLOGICAL CONTROLS OF VERTICAL GRADIENTS IN PHYTOPLANKTON

Deferring for now discussions of horizontal processes that are especially important in thin-layer research, there are two key questions about persistent subsurface layers of phytoplankton biomass: How are their magnitude and shape maintained, and what does this tell us about the ecological processes at play? In an impressive synthesis that includes a quantitative theoretical framework used to interpret advanced in situ measurements of phytoplankton and turbulence, Prairie et al. (2011)—the source of the title of this sidebar—described how physical and biological processes interact to determine the formation, maintenance, and destruction of vertical gradients of phytoplankton. Their discussion of ecological implications addresses important topics that are not explored effectively in this review, such as grazing and other food web interactions that depend on encounter rates. The paper by Prairie et al. (2011) is reminiscent of a remarkable study by Lande et al. (1989) that introduced a mathematical model of phytoplankton growth countered by diffusion and grazing that was used to interpret vertical profiles of phytoplankton (measured with flow cytometry) and turbulence, yielding estimates of phytoplankton growth rates; this article also provided a comprehensive introduction to the relevant literature and an insightful discussion that highlighted observations, approaches, and interpretations that are still highly relevant but not well recognized in recent research. Despite theoretical foundations and novel observations that qualify it for benchmark status, Lande et al.'s (1989) work seems to have had little influence on the development and validation of modern theory (but see Fennel & Boss 2003). It is still worth reading.

that vertical migration for nutrient acquisition need not be synchronized to the day/night cycle, as had been commonly studied in motile phytoplankton, they developed a model of dinoflagellate migration governed by nutritional status that predicts asynchronous vertical migration leading to persistent bimodal distributions, with maxima near the surface and in the nitracline, when an increased nutricline depth precludes synchronous diel vertical migration—which is limited to approximately 5–10 m for commonly occurring dinoflagellates, depending on their swimming speed. The asynchronous migration strategy had limits: For one set of parameters, vertical migration and deep nutrient acquisition could not maintain growth when the depth of the nutricline exceeded 60 m, suggesting that accumulation of vertically migrating dinoflagellates near the nutricline would not be an important contributor to SBMLs in oligotrophic waters with deep nutriclines. Working at the same time and using a similar modeling approach, but with different assumptions, formulations, and objectives, Ji & Franks (2007) revealed that a number of effective migration strategies could be developed in different regimes of mixing and internal waves.

Vertical migration for nutrient acquisition, whether synchronous or not, is commonly described as a transit between the surface and nutricline, but motile phytoplankton exhibit a broad range of migration patterns (reviewed by Cullen 1985 and Cullen & MacIntyre 1998), some of which include an upper daytime terminus in a subsurface layer that appears to correspond to an optimum irradiance (e.g., Cullen & Horrigan 1981, Heaney & Eppley 1981) but might also be described as high light avoidance (cf. Ji & Franks 2007). Extensive sampling in Monterey Bay, California (Ryan et al. 2010), revealed diel shifts in the position of subsurface layers consistent with this migration strategy; when the migrating populations were a significant component of the phytoplankton community, they produced SCMLs that were displaced upward from the nutricline during the day but were in it during the night. Notably, the relatively large (>10–20  $\mu\text{m}$ ) motile phytoplankton that are capable of these behaviors dominate the phytoplankton only in waters that typify eutrophic and mesotrophic conditions in TSWS.

## 7.2. Regulation of Buoyancy

As discussed in Section 4.2, early experimentation and modeling (Steele & Yentsch 1960), followed by observations of diatom layers using pumped profiles of fluorescence and an early in situ fluorometer (Derenbach et al. 1979), generated interest in the buoyancy regulation of diatoms, in part to examine the possible role of sinking in SCML formation (e.g., Bienfang et al. 1983, Davey & Heaney 1989, Richardson & Cullen 1995, and references cited within these papers) but also because of the significant role of sinking in ecological adaptation (Smayda 1970, Smetacek 1985) and biogeochemical fluxes (Michaels & Silver 1988). The research yielded many useful results on the control of buoyancy in diatoms, including changes that could drive vertical migration (Richardson et al. 1996, 1998; Villareal et al. 1996). In addition, Boyd & Gradmann (2002) compiled important information on the role of osmolytes in the regulation of buoyancy, complementary to calculations based on, e.g., carbohydrate ballast as influenced by nutrition and light (e.g., Richardson & Cullen 1995, White et al. 2006).

Subsequently, as research progressed on the motility and buoyancy of phytoplankton as processes that restore the sharpness of phytoplankton layers (Birch et al. 2009, Durham & Stocker 2012, Prairie et al. 2011, Stacey et al. 2007; see also sidebar Physical and Biological Controls of Vertical Gradients in Phytoplankton), the potential complexity of physiologically controlled buoyancy regulation of nonmotile plankton was greatly simplified. Cells were assigned the density of the water at a target depth and assumed to ascend or descend to it based on their form resistance and the difference between their unchanging density and that of the ambient water. That is, phytoplankton were assumed to act as isopycnic Swallow floats (see sidebar Is a Diatom a Swallow Float?). Given the indications that diatom layers are found near nutrient gradients, it seems promising to revive interest in studies of the influence of nutrients and light on the buoyancy regulation of diatoms.

### IS A DIATOM A SWALLOW FLOAT?

In a review of research on thin phytoplankton layers, Durham & Stocker (2012) highlighted systematic studies that included sensitivity analyses of the possible roles of cell size and buoyancy, and the associated rates of sinking or floating, in the accumulation of nonmotile phytoplankton in layers (Stacey et al. 2007, Steinbuck et al. 2010). Tracing their assumptions to a model of convergent swimming behavior (Franks 1992), Stacey et al. (2007) imposed a binary convergence model on nonmotile phytoplankton such that cell density is constant and equal to the water density at the center of a layer (i.e., cells are neutrally buoyant at the center). Rates of sinking from above or rising from below are determined by both the density of cells relative to that of the water and the effective cell diameter, according to Stokes's law. Physiological influences on the buoyancy of the phytoplankton (e.g., Steele & Yentsch 1960) were not included, so the general applicability of the approach merits further study. Nonetheless, the convergent buoyancy model has interesting implications on its own because it assumes that phytoplankton, notably diatoms, have the same compressibility as seawater—that is, they act as isopycnic rather than isobaric Swallow floats (technology described by Gould 2005 and Rossby et al. 1985). When I was a graduate student at the Scripps Institution of Oceanography in the 1970s, the eminent physical oceanographer Joseph Reid periodically asked me the intriguing question “Is a diatom a Swallow float?” He was referring to the possibility that siliceous diatoms seem to be relatively incompressible and might therefore accumulate on isobars, not necessarily on isopycnals. The physical properties of diatom frustules have been examined in an ecological context (Hamm et al. 2003), and clearly a diatom cannot be completely incompressible because it exchanges solutes with surrounding water, but, to the best of my knowledge, Reid's question has yet to be answered.

The ecology of buoyancy regulation in freshwater cyanobacteria, including the formation of persistent metalimnetic layers (e.g., of *Oscillatoria agardhii*; Konopka et al. 1993), has been well studied (Oliver 1994). Using buoyancy-control mechanisms (Walsby 1978) comparable to those used by vertically migrating diatoms (Richardson et al. 1996, Villareal et al. 1999), the filamentous marine cyanobacterium *Trichodesmium* may “mine” nutrients in oligotrophic waters through vertical migration to the phosphocline (White et al. 2006 and references therein). Although these examples of buoyancy control have important ecological and biogeochemical implications, they do not seem to contribute significantly to SCMLs in oligotrophic waters because the Chl profile is dominated by much smaller phytoplankton.

### 7.3. Motility, Buoyancy Regulation, and Typical Stable Water Structure

Examples of migratory behavior and layer formation by phytoplankton provide the foundations for three additional TSWS postulates that also apply to less stable coastal waters, where readily distinguishable layers of motile phytoplankton are common (see, e.g., Berdalet et al. 2014, Cullen 2008):

10. Swimming behavior or buoyancy regulation, under physiological control and defined by environmental cues such as a light gradient and the nutricline, can lead to an accentuation of the SCML (Lande et al. 1989, Prairie et al. 2011) or the formation of multiple layers.
11. Vertically migrating phytoplankton can form layers near the nutricline at night that move closer to the surface during the day. Where the nutricline is too deep to be reached during synchronized diel migration of motile phytoplankton, asynchronous migration can proceed, leading to bimodal distributions; buoyancy-regulating diatoms or cyanobacteria can carry out similar asynchronous migrations.
12. Vertically migrating phytoplankton influence the vertical structure of Chl to the extent that they dominate the phytoplankton assemblage; this is less likely in more oligotrophic waters, where populations of larger phytoplankton that can benefit from this strategy tend to be small.

The hypothesis for TSWS (vertical scale of approximately 1 m or greater) is that swimming behavior or buoyancy regulation commonly influences vertical distributions of phytoplankton, but pronounced layers form only when two conditions are satisfied: (a) The interaction of behavior with physical or chemical gradients allows strong relative concentrations to form, and (b) the availability of nutrients within the ambit of motile phytoplankton can support the development of persistent layers well above background concentrations. Excellent progress is being made toward putting quantitative constraints on the physical and biological controls of behaviorally induced layers of phytoplankton (Durham & Stocker 2012, Ji & Franks 2007, Prairie et al. 2011, Ralston et al. 2007, Rines et al. 2010). More experimentation on swimming behavior (e.g., Kamykowski 1995) and buoyancy regulation in studies that are informed by prior results, integrated with physical-biological models including growth and grazing, and validated with powerful new observation technologies will likely lead to rapid advances.

## 8. THE “NICHE” OF THE SUBSURFACE CHLOROPHYLL MAXIMUM LAYER?

The SCML is one of the most consistent features of planktonic ecosystems in stratified waters, and it is strongly related to physiologically significant gradients of light and nutrients. The principal mechanisms of formation and maintenance of the SCML are growth under an optimal combination of light and nutrients, physiologically controlled swimming behavior or buoyancy regulation,

and photoacclimation of pigment content. All are influenced by food web interactions and hydrodynamics, thereby defining a range of ecological niches and associated adaptations for SCMLs across the trophic gradient of TSWS, which I propose is defined by the balance between the vertical flux of nutrients and the light energy available for the growth of phytoplankton, as reflected in the average irradiance at the nutricline,  $\bar{E}_{\text{nutricline}}$ .

Clearly, there is no one “niche” of the SCML. Rather, the SCML represents a broad range of ecological settings that can be categorized by trophic status according to the following synopsis, the foundations of which can be found in previous sections of this review:

- At the eutrophic extreme, the vertical flux of nutrients nearly overwhelms the capacity of the planktonic system to consume it. Irradiance at the nutricline and the standing crop of phytoplankton are high and the nutricline and SCML are shallow; evolutionarily stable strategies for phytoplankton in the high-irradiance SCML include equal limitation by light and nutrients in the layer and behavioral aggregation at that optimum depth (Klausmeier & Litchman 2001). As described in Section 3.2, the SCML in these higher-energy situations can be augmented by reduced sinking rates of diatoms in the nutricline; Lande & Wood (1987) showed how this could lead to increased resuspension of the diatoms into the mixed layer—an adaptive advantage.
- As the vertical flux of nutrients decreases from the eutrophic extreme, either along a spatial gradient or owing to “decaying turbulence” (Margalef et al. 1979), irradiance at the nutricline can limit growth rate, so vertical migration for nutrient acquisition would offer advantages to phytoplankton that shuttle between the nutricline and the well-lighted surface layer, allowing them to grow faster than phytoplankton that remain in either stratum. Adaptations for phytoplankton that accumulate in the moderate-irradiance SCML rather than migrate include effective photoacclimation, which contributes to the development of a Chl peak, and a range of strategies that minimize losses (e.g., to grazing) (Verity & Smetacek 1996).
- Toward the oligotrophic extreme, in which irradiance at the nutricline and SCML is very low—approaching the compensation irradiance—the SCML is not a peak of biomass but rather a reflection of increased chlorophyll content of phytoplankton; adaptations for survival of phytoplankton in low light include optimization of growth rates, e.g., with mixotrophy, and minimization of losses. The niche can be characterized as hostile (Clegg et al. 2012).

Further elaboration on adaptations of SCML phytoplankton is beyond the scope of this review. My message here is that when adaptations to the SCML are studied, it is important to identify which segment of the trophic spectrum is being considered. In TSWS, trophic status and the niche of the SCML can be related to the irradiance at the nutricline.

## 9. CONCLUSIONS

Several esteemed colleagues of mine have remarked that the SCML is enigmatic. In what has been a decidedly and intentionally unconventional review emphasizing the foundational literature at the expense of recent research, I have traced a development of theory characterized more by evolution than surprise, at least for vertical scales of 1 m or greater. One could argue that for general trends of vertical structure across a trophic gradient, rather than being an enigma, the SCML is a mystery solved. But this may reflect unwarranted optimism as we emerge from Munk’s “century of undersampling” (see Section 3.4). Indeed, many observations of the vertical structure of Chl are consistent with established theory, much of it developed decades ago, but the systematic

formulation and comprehensive testing of hypotheses to explain the vertical structure of Chl across trophic gradients have yet to be completed.

We are now able to collect thousands of vertical profiles of biological, chemical, and physical properties well suited to testing the postulates of TSWS and the associated predictions of vertical structure in more complex coastal waters. Without a doubt, our current understanding will be unable to explain much that will be observed. It will be exciting to develop new theory to provide those explanations. I hope that the existing theory, tracing back to Riley, Yentsch, and Steele and buttressed with excellent observational, experimental, and theoretical work in the pre-PDF era, will be part of that development—because, as Yentsch (1980) wrote, “the problem is not to destroy present views but to include these in a larger, more comprehensive theoretical structure” (p. 30).

### SUMMARY POINTS

1. Subsurface chlorophyll maximum layers (SCMLs) are nearly ubiquitous in stratified surface waters. They are formed and maintained by a range of interacting processes, including enhanced growth of phytoplankton under an optimal combination of light and nutrients, physiologically controlled swimming behavior or buoyancy regulation, and photoacclimation of pigment content—all influenced by food web interactions and hydrodynamics.
2. The SCML is associated with the nutricline, the depth of which is determined by the balance between the vertical flux of nutrients and the light energy available for the growth of phytoplankton. The trophic status of the surface layer is reflected in the average daily irradiance at the nutricline, which can be used as a diagnostic.
3. The nature of the SCML varies across the trophic gradient. At the eutrophic extreme, it is primarily a peak of biomass maintained by growth and sometimes behavioral aggregation and retarded sinking. Vertical migration for nutrient acquisition can contribute to the SCML where the nutricline is deeper. At the oligotrophic extreme, the SCML is formed independently of a peak in phytoplankton biomass owing to the selection for low-light-acclimated phytoplankton with increased chlorophyll content relative to biomass.
4. Data from a nascent biogeochemical global ocean observing system can be used to test hypotheses underlying a proposed typical stable water structure; results to date are generally consistent with established theory. Unexplained variability may be reduced by describing the vertical structure of Chl and nutrients versus the average daily irradiance rather than depth.

### DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Drives home the message that percent surface irradiance is an inappropriate measure of light exposure when daily solar irradiance at the surface varies significantly, as it does with latitude, season, and cloud cover.

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In a sense, an update of Steele 1964—comprehensive, well rooted in the literature, and tested with modern optical observations.

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Written by graduate students, an excellent review of the legacy of a classic paper, demonstrating the value of building upon the older literature.

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Incisive analysis of the measured distributions of phytoplankton species in relation to turbulence, years ahead of its time and still full of useful insights.

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Comprehensive study illustrating ecological shifts related to vertical displacement of isolumines rather than to differences in percent surface irradiance.

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A recent study that relates vertical structure to isolumes, revealing patterns that appear to be generic and that the authors conclude are potentially characteristic of all areas where the SCML forms.

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Remembered best for its photosynthesis-versus-irradiance equations, this study includes a model of photoacclimation that was 35 years ahead of its time.

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Predicts the vertical structure of Chl across a trophic gradient, including the formation of an SCML due primarily to photoacclimation.

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Excellent example of Yentsch's deep appreciation of interdisciplinary oceanography and of oceanographers.

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**Errata**

An online log of corrections to *Annual Review of Marine Science* articles may be found  
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