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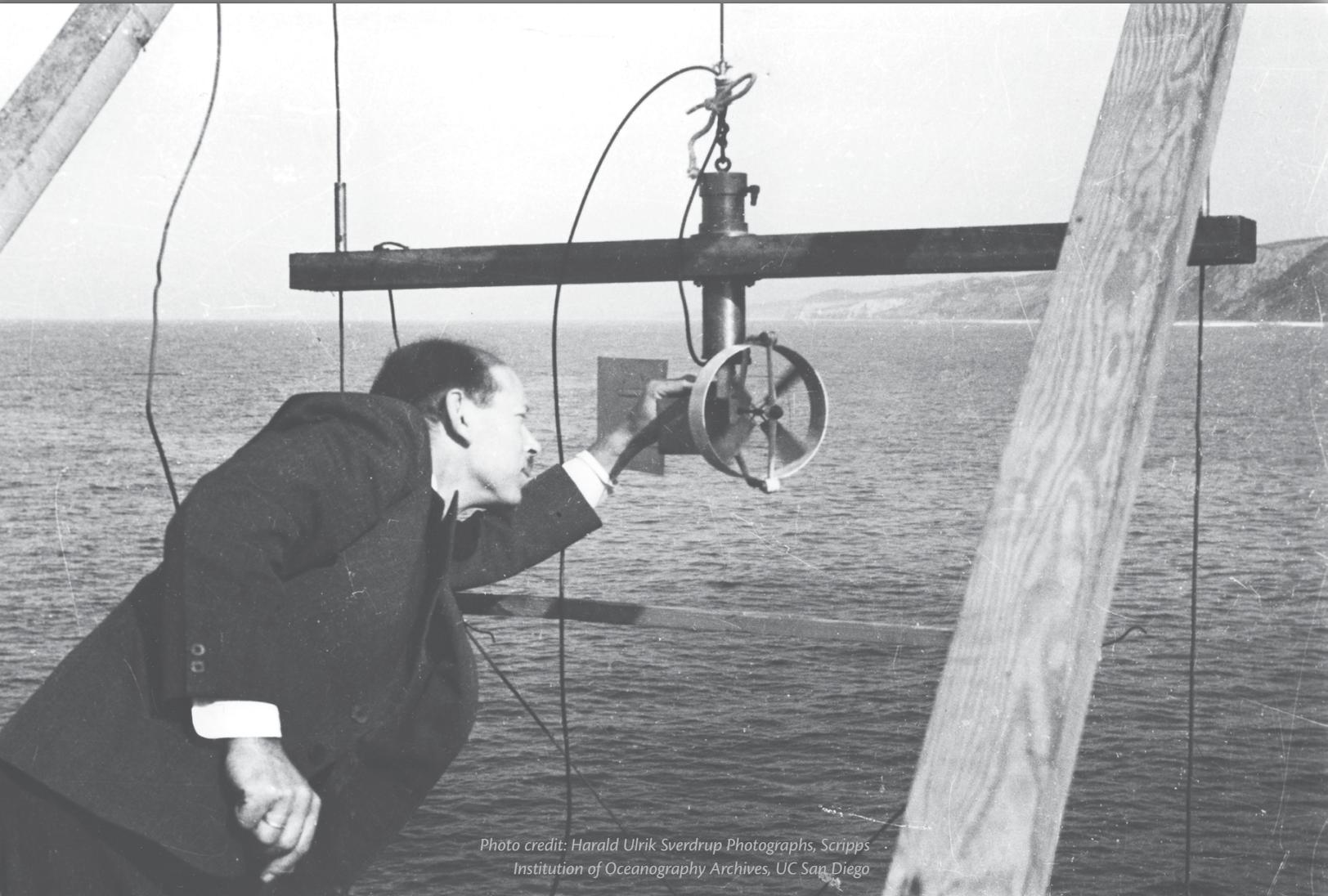
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# Sixty Years of Sverdrup

## A Retrospective of Progress in the Study of Phytoplankton Blooms

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*Photo credit: Harald Ulrik Sverdrup Photographs, Scripps  
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**ABSTRACT.** One of the most dramatic large-scale features in the ocean is the seasonal greening of the North Atlantic in spring and summer due to the accumulation of phytoplankton biomass in the surface layer. In 1953, Harald Ulrik Sverdrup hypothesized a now canonical mechanism for the development and timing of phytoplankton blooms in the North Atlantic. Over the next 60 years, Sverdrup's Critical Depth Hypothesis spurred progress in understanding of bloom dynamics and offered a valuable theoretical framework on which to build. In reviewing 60 years of literature, the authors trace the development of modern bloom initiation hypotheses, highlighting three case studies that illuminate the complexity, including both catalysts and impediments, of scientific progress in the wake of Sverdrup's hypothesis. Most notably, these cases demonstrate that the evolution of our understanding of phytoplankton blooms was paced by access not only to technology but also to concurrent insights from several disciplines. This exploration of the trajectories and successes in bloom studies highlights the need for expanding interdisciplinary collaborations to address the complexity of phytoplankton bloom dynamics.

## INTRODUCTION

*Perhaps no phenomenon in the natural economy of the Gulf [of Maine] so arrests attention (certainly none is as spectacular) as the sudden appearance of enormous numbers of diatoms in early spring and their equally sudden disappearance from most of this area after a brief flowering period.*

– Henry Bryant Bigelow, 1926

The drivers and the timing of phytoplankton blooms in the ocean have puzzled and captivated scientists since the advent of the field of biological oceanography (Mills, 1989). Sixty years ago, in 1953, Harald Ulrik Sverdrup, a Norwegian oceanographer and meteorologist, hypothesized a now canonical mechanism for the development and timing of phytoplankton blooms in the North Atlantic in his seminal paper “On conditions for the vernal blooming of phytoplankton.” Sverdrup's Critical Depth Hypothesis united concepts from physical and biological oceanography to formulate a quantitative relationship among the initiation of phytoplankton

blooms, light, and mixed layer depth. It has since become a central concept in biological oceanography.

Sixty years later, we (a group of graduate students) were challenged by our instructor (coauthor Sosik) to explore how this hypothesis influenced the rate of progress in understanding bloom dynamics. To fuel our debate, we traced bloom formation theories through time back to Sverdrup (1953). In this process, we realized that the path of these ideas through time was not as clear as we initially imagined, and defining the ensuing “progress” was one of the most challenging aspects of our task.

To start, we evaluated a naive definition of progress—one study makes a discovery, a later study builds upon it, this process iterates, and progress is made. We then looked for how and why new insights into phytoplankton blooms deviated from this “linear” type of progress. By examining the literature

citing Sverdrup (1953) over the ensuing 60 years, we found that progress is typically characterized by many stops and starts, with new insights gleaned by interweaving new and old ideas, debating theories, and implementing new technology and methods. Progress sometimes stalled when literature from previous studies or other fields was not incorporated, or important assumptions were left unaddressed. In contrast, progress accelerated as new technologies were developed, new regions of the ocean were explored, and scientists leveraged their creativity and re-explored old ideas. With Sverdrup's Critical Depth Hypothesis as a springboard and focal point, we trace several cases where linear progress seemed to occur, and then explore how the development of three modern hypotheses deviate from that relatively simple conception of progress. We particularly focus on the evolving interpretation of the Critical Depth Hypothesis and how seminal ideas and technologies impinged on the trajectory of progress. While this paper focuses on the field of phytoplankton bloom dynamics, other fields are likely to show analogous histories of progress.

## THE CRITICAL DEPTH HYPOTHESIS

Sverdrup (1953) simplified the general problem of phytoplankton bloom formation by assuming that phytoplankton growth is limited by light during pre-bloom months and that the amount of light a phytoplankton community is subject to is determined by the incident

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<sup>1</sup> A.D.F. and E.A.M. are co-first authors and led the effort to develop and write this paper. H.A., E.F.B., K.H.C., K.J.P., and S.Z.R. contributed substantively to researching and writing the manuscript and are listed alphabetically. E.A.M. researched and created figures. H.M.S. formulated original debate concept, facilitated discussion, and provided critical review and guidance.

irradiance, the coefficient of light extinction, and mixed layer depth. By incorporating the concepts of Gran and Braarud (1935), Sverdrup proposed that in the North Atlantic, deep mixed layers in winter months keep the phytoplankton in an unfavorable light environment and therefore limit production. A “critical depth” is defined as the bottom of a layer in which the total production of

organic matter by the phytoplankton community—from this depth to the surface—is equal to its destruction by respiration (Figure 1a). If phytoplankton are mixed evenly to depths that exceed the critical depth, loss exceeds production and there is a net loss of biomass. Conversely, when the mixed layer depth is shallower than the critical depth, phytoplankton have the potential to

bloom because the whole community experiences sufficient light levels to support net growth (Figure 1b). The Critical Depth Hypothesis is a simple, quantitative model that has provided a working and testable framework for the ensuing theoretical and empirical experiments over the years.

## PROGRESS FROM SVERDRUP'S FRAMEWORK

The model of bloom formation described in Sverdrup (1953) laid the foundation for several studies, both immediately after its publication and during the ensuing decades, that showed the type of straightforward advancement we might naively expect and describe as “linear” progress. For example, Semina (1960) demonstrated that bloom formation in the Bering Sea near Kamchatka was better explained by stability, nutrients, and grazing than light limitation, and Menzel and Ryther (1961) invoked the critical depth model to explain how the Sargasso Sea can sustain high growth despite a deep mixed layer (i.e., high water clarity). On the theoretical front, models by Steele (1962) and Steele and Menzel (1962) expanded upon Sverdrup's formulation by adding factors such as photoinhibition, nutrient limitation, and self-shading. Later efforts (e.g., Murphy, 1971) incorporated the Critical Depth Hypothesis within broader models that included feedbacks to determine whether light and/or other factors, such as nutrients or grazing pressure, were limiting.

As scientists gained information about new regions of the ocean, many studies still seemed to fit with a simple concept of progress, albeit more than three decades after publication of Sverdrup's original ideas. Literature citing Sverdrup (1953) was focused on regions around

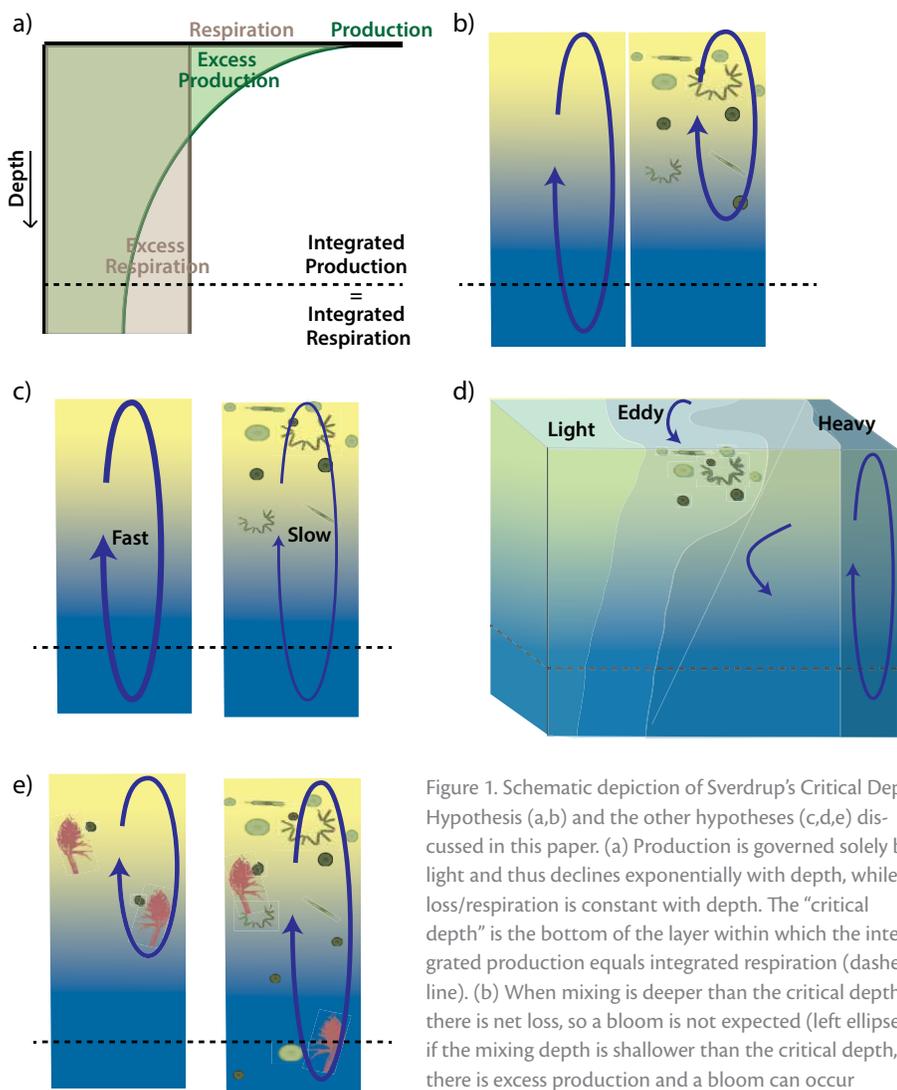


Figure 1. Schematic depiction of Sverdrup's Critical Depth Hypothesis (a,b) and the other hypotheses (c,d,e) discussed in this paper. (a) Production is governed solely by light and thus declines exponentially with depth, while loss/respiration is constant with depth. The “critical depth” is the bottom of the layer within which the integrated production equals integrated respiration (dashed line). (b) When mixing is deeper than the critical depth, there is net loss, so a bloom is not expected (left ellipse); if the mixing depth is shallower than the critical depth, there is excess production and a bloom can occur (right ellipse). Modified from Sverdrup (1953) (c) The

Critical Turbulence Hypothesis. Even if mixing is deeper than the critical depth, a bloom can form if the rate of mixing is slow enough that phytoplankton are retained in sunlit waters for suitably long periods (right ellipse). (d) Bloom initiation due to Stratification from Mixed Layer Eddies. The left-right gradient indicates light to heavy water from north to south (Northern Hemisphere). As the Coriolis effect induces eddies, lighter water is pushed above heavier water, creating shallow mixed regions where phytoplankton can grow. Adapted from Mahadavan et al. (2012) (e) The Dilution Recoupling Hypothesis. A deepening of the mixed layer (right ellipse) dilutes the predatory pressure on the phytoplankton, allowing a bloom to begin even if mixing is deeper than the critical depth.

the world (Figure 2) and elucidated mechanisms for different types of blooms. For example, Nelson and Smith (1991) apply the Critical Depth Hypothesis to ice-edge phytoplankton blooms in the relatively poorly studied Southern Ocean. With contemporary physiological and optical data, they reformulated Sverdrup's model to show that meltwater near ice margins caused strong stratification—a mechanism of mixed layer shoaling that Sverdrup mentioned—and therefore favorable mixing and irradiance conditions for pre-bloom phytoplankton.

Access to satellite data broadened the spatial scale for investigation of bloom dynamics. In 1996, Obata et al. combined data on mixed layer depth (available ca. 1982), attenuation coefficients (available ca. 1976), ocean color (high-quality analysis ca. 1993), and cloud cover (available ca. 1991) to investigate how the Critical Depth Hypothesis held up on a global scale. The results demonstrated that shoaling and deepening of the mixed layer relative to the critical depth could explain the initiation and termination of blooms in the North Atlantic and North Pacific, while lack of data limited explanatory power in other regions. Several years later, Siegel et al. (2002) built upon the work of Obata et al. (1996) to perform a novel inversion of Sverdrup's critical depth model, with the goal of quantifying the balance of biological production and loss processes that leads to bloom formation in the North Atlantic. Siegel et al. (2002) leveraged satellite observations of phytoplankton blooms, surface irradiance and estimated light penetration, and climatologies of mixed layer depth to estimate community compensation irradiance values, as implied by Sverdrup's formulation. The results suggest that

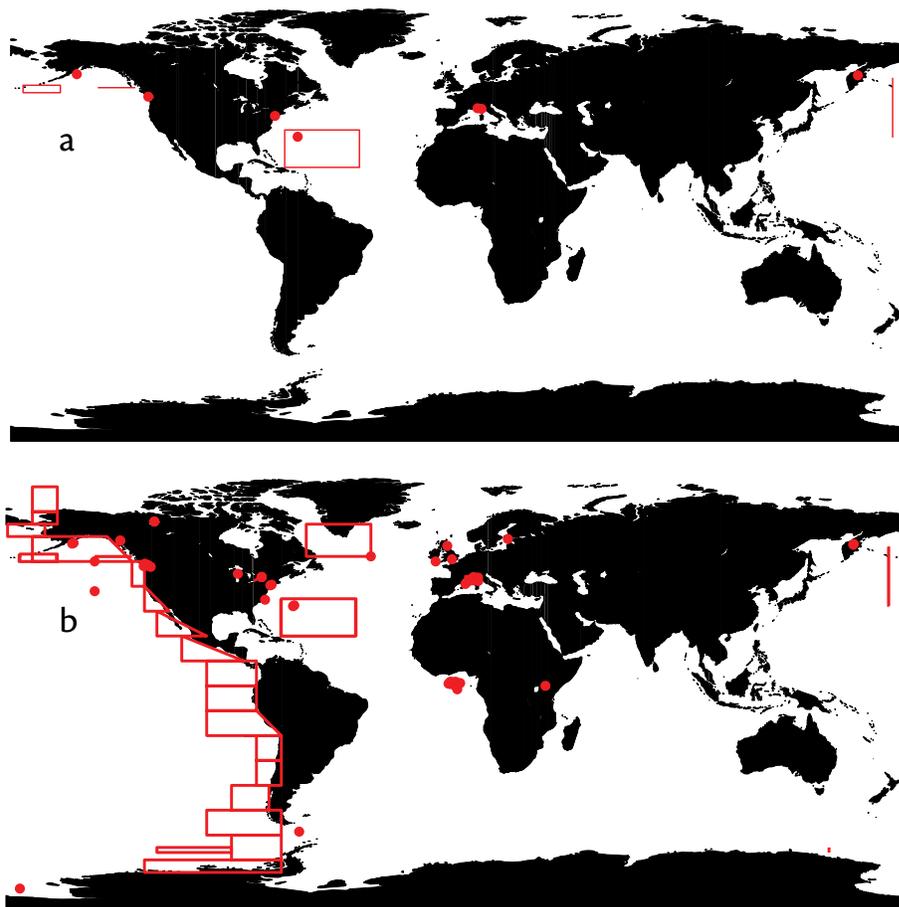


Figure 2. Geographical expansion of study sites that reference Sverdrup (1953) through (a) 1965 and (b) 1978. Sixty-nine studies were found on Web of Science and the locations of the 51 that were not modeling or review studies are marked. Note that 1978 marks the advent of the Coastal Zone Color Scanner, enabling satellite coverage of this indicator. Lines or polygons indicate regions that were sampled as part of a cruise track; dots indicate sampling at a single location. In the first 12 years after Sverdrup's publication (a), there were three main centers of study, all in coastal areas of the Northern Hemisphere. In the next 13 years (b), investigations expanded to the Southern Hemisphere, more open ocean locations, and polar habitats (Antarctic).

approximately half the total community loss of fixed carbon is due to phytoplankton respiration. Furthermore, these authors deduced that the accumulation of phytoplankton in the surface layer of the eastern North Atlantic basin south of 40°N is likely limited by nutrients (even following winter mixing), rather

than light—delineating a region where Sverdrup's assumptions and formulation do not appear to apply.

This story shows some of the complications that can arise in interpreting progress and how much detailed knowledge is required to interpret this progress. At first glance, the fact that

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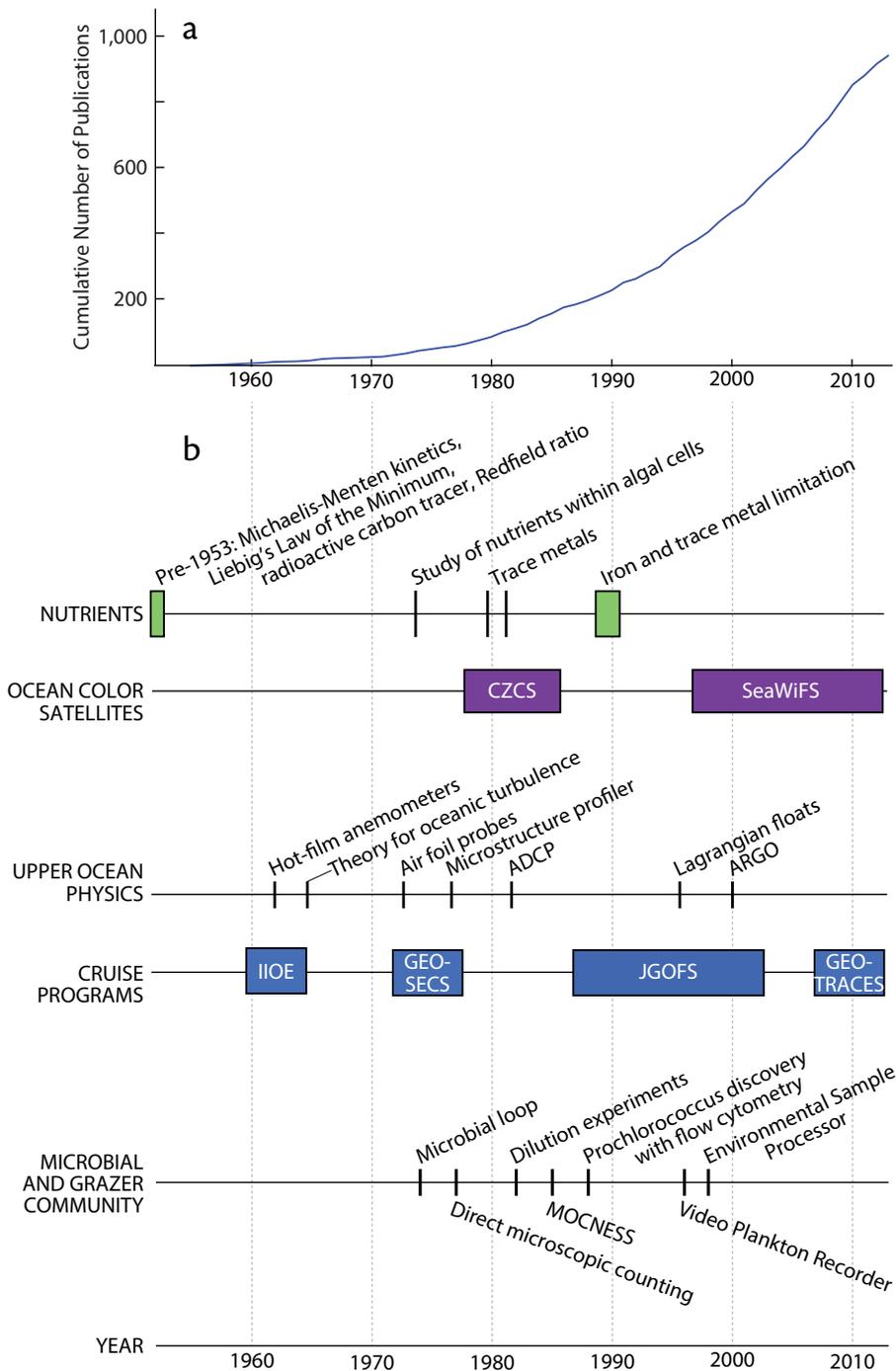


Figure 3. (a) Graph of Sverdrup (1953) citations over time. (b) Timeline of seminal achievements pertinent to the case studies highlighted in this paper and based on an extensive literature review (see Supplementary Bibliography). The achievements selected are all burgeoning theories or technologies that spurred research leading to a greater understanding of specific physical, chemical, and biological processes controlling phytoplankton bloom formation. Citations, in chronological order, are (for nutrients) Michaelis and Menten (1913), Redfield (1934), Browne (1942), Droop (1974), Huntsman and Sunda (1980), Fitzwater et al. (1982), and Martin et al. (1990); (for upper ocean physics) Grant et al. (1962), Ozmidov (1965), Nasmyth (1973), Thorpe (1977), and Oakey (1982); and (for microbial and grazer community) Pomeroy (1974), Hobbie (1977), Landry and Hassett (1982) and Fenchel (1982), Chisholm et al. (1988), Davis et al. (1996), and Scholin et al. (1998).

this study occurred nearly 50 years after Sverdrup (1953) and over 20 years after the advent of ocean color satellites might seem to suggest a lag after all the necessary pieces existed. While ocean color satellites had been available for decades, until SeaWiFS was deployed, the quality of those data was not sufficient to support the findings of Siegel et al. (2002). Better characterization of oceanic properties around the world (e.g., mixed layer depth) also contributed. Data availability must also be matched by scientific interest and inspiration. For example, the inversion of Sverdrup's model to calculate community compensation irradiances emerged from the "insight and imagination of Dave Siegel" (James Yoder, Woods Hole Oceanographic Institution, *pers. comm.*, March 31, 2013). These elements of the story show the importance of details that contribute to progress. Some aspects originated directly from Sverdrup's hypothesis—such as the formulation for community compensation irradiance—while other components came together from many technologies, observations, and unique inspirations of the scientists.

### COMPLEX PATHWAYS TO PROGRESS

The aforementioned studies illustrate how the application of Sverdrup's concepts, previous literature, and new technology could provide insights into the factors that regulate blooms in different parts of the world ocean. As citations of Sverdrup (1953) accumulated (Figure 3), these and other studies showed that the characteristic spring bloom is a mid- to high-latitude phenomenon (e.g., Cushing, 1959; Yoder and McClain, 1993; Obata et al., 1996; Siegel et al., 2002), and that Sverdrup's critical depth could not explain all bloom formations.

Sverdrup himself foresaw this when he stated that “a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate” and that his “conclusions may be greatly modified if grazers are present.” Consideration of these factors, coupled with observations of phytoplankton blooms occurring in the apparent absence of water column stratification (Heimdal, 1974; Schei, 1974; Townsend et al., 1992; Eilertsen, 1993; Backhaus et al., 1999; Dale et al., 1999; Körtzinger et al., 2008), led to insights into different bloom formation processes.

Historically, many researchers have looked to the role of nutrients in spring blooms. For example, Steele and Menzel (1962) conducted a theoretical study that used mixed layer depth and nitrogen uptake to describe a winter bloom. Anderson (1964) studied nutrient limitation and the influence of physical oceanographic processes in a North Pacific spring bloom. Walsh (1971) investigated stability and nutrient controls on the spatial and temporal distribution of phytoplankton and found silicate (replenished by upwelling and increased stability) to be associated with spring biomass increases. Conover (1975) demonstrated the role of nitrogen in mediating the size of a spring bloom. Apollonio (1980) invoked high nutrient concentration coupled with ice cover, incident radiation, and runoff to explain an unusual bloom timing. Franks (2002) reviewed nutrient-phytoplankton-zooplankton models, some of which also incorporate mixed layer depth as a mechanism for mediating light and nutrient levels. Moore et al. (2006) investigated iron limitation as a mediating factor in North Atlantic blooms. In addition, other controls on phytoplankton, such as photoperiod or cell dormancy, have

been investigated. Experiments demonstrating a photoperiodic response in the germination of spores and/or the onset of growth (Hollibaugh et al., 1981; Eilertsen, 1993; Eilertsen et al., 1995; Hansen and Eilertsen, 1995) suggest a probable mechanism for the onset of blooms that begin at approximately the same time in otherwise variable coastal and open waters. Figure 3 shows several seminal studies in these different areas, as well as historic technological advancements.

To illustrate the complexity evident in some of these pathways to progress, we selected three recent hypotheses that highlight the role that turbulent processes, large-scale eddies, and biological loss processes play in phytoplankton blooms. These hypotheses serve to elucidate how interpretation and use of Sverdrup’s hypothesis coevolved with a wide range of new technologies, theories, and observations: the Critical Turbulence Hypothesis uses insights and methodological improvements from physical oceanography to explore an alternate bloom initiation criterion, Stratification from Mixed Layer Eddies leverages a suite of new technologies and theories to refine the shoaling mechanism that can initiate blooms, and the Dilution Recoupling Hypothesis merges older ideas with novel biological observations from satellites to propose how trophic imbalances can initiate blooms. These studies use Sverdrup’s model as the primary theoretical basis and expand upon and/or challenge the model (Figure 1), while leveraging tools from various scientific fields. Tracing the concepts through time, we illustrate how new insights result from a combination of different elements, including observations of unexplained phenomena, advancements in technology and theory, and interweaving of new and old

ideas and approaches. These studies also demonstrate how the pace of scientific progress was slowed by factors ranging from lack of technology to a failure of knowledge to bridge fields.

## CRITICAL TURBULENCE HYPOTHESIS

The Critical Turbulence Hypothesis proposes a distinct set of conditions capable of initiating a bloom in light-limited conditions. The evolution of this hypothesis highlights how the combination of better observational tools, challenged assumptions, and synthesis of ideas from different parts of the literature can lead to significant progress in our understanding of phytoplankton blooms. In his hypothesis, Sverdrup imposed a “thoroughly mixed” water column but also recognized that “a phytoplankton population may increase independently of the thickness of the mixed layer if the turbulence is moderate” (Sverdrup, 1953). Decades later, the thoroughly mixed assumption was formally relaxed in the context of bloom formation by Huisman et al. (1999) and Taylor and Ferrari (2011). Consistent with Sverdrup’s mixed layer formulation, Huisman, Taylor, Ferrari, and colleagues hypothesized that if turbulence is low enough, phytoplankton in the well-lit surface layer will have an opportunity to bloom before being mixed down to unfavorable light conditions (Figure 1c). Our analysis suggests the journey from Sverdrup’s Critical Depth Hypothesis to these recent formulations was characterized by extended periods of slow progress punctuated by times of accelerated development.

At the time that Sverdrup wrote his 1953 paper, the basic concepts of turbulence were well developed. Over the ensuing decades, technological

developments for turbulence measurement and studies of phytoplankton physiology in the mixed layer led to a much greater understanding of both turbulence in the mixed layer and its effect on phytoplankton. Yet, the progression from these accomplishments to the more sophisticated characterizations of low turbulence bloom initiation in the late

Marra (1978a,b) investigated how fluctuation in the light environment can lead to different rates of photosynthesis. This led to questions on how natural vertical turbulence (or lack thereof) in the mixed layer would affect production (Gallegos and Platt, 1982) or support the acclimation of phytoplankton to different light levels (Tilzer and Goldman, 1978).

anemometers, airfoil probes, and fine-scale conductivity-temperature-depth (CTD) measurements—facilitated quantification of turbulence in less-energetic regions (Grant et al., 1968a,b; Osborn, 1974; Thorpe, 2005). It was not until the 1980s, however, that turbulent energy could be routinely measured in the upper ocean (Dillon and Caldwell, 1980; Oakey and Elliott, 1982). These results allowed Denman and Gargett (1983) to estimate the temporal and spatial scales for vertical displacements that phytoplankton could undergo in turbulent motion.

These advances in turbulence studies were not applied to the study of blooms, as the field's focus was still on photoacclimation. For example, the influential study by Lewis et al. (1986) simultaneously measured the rates of turbulent dissipation (with a free-fall microscale profiler) and the photoacclimative properties of phytoplankton, and showed that the degree to which phytoplankton acclimated to their light environment depended on whether the rate of acclimation was faster or slower than the rate of mixing. This work and relevant research outside of biology was not applied to the study of bloom formation during this time. For example, Moum et al. (1989) studied diurnal effects of heating and mixing, which can affect phytoplankton distributions, but the paper was only cited in physical oceanographic and geophysical journals, without mention of biota for the next six years (Web of Science cited reference search, <http://thomsonreuters.com/web-of-science-core-collection>). Smetacek and Passow's (1990) call to evaluate the importance of mixing rate, which they contended was poorly quantified, illustrates the failure of advances in physical measurements to bridge into the study of blooms.

“...WE FOUND THAT PROGRESS IS TYPICALLY CHARACTERIZED BY MANY STOPS AND STARTS, WITH NEW INSIGHTS GLEANED BY INTERWEAVING NEW AND OLD IDEAS, DEBATING THEORIES, AND IMPLEMENTING NEW TECHNOLOGY AND METHODS.”

1990s is characterized by periods of stagnation, largely as a result of slow information transfer between disciplines and alternate study foci.

Many scientists were interested in turbulence in the 1950s. Skellam (1951) and Kierstead and Slobodkin (1953) present investigations of the critical size of a patch in which phytoplankton could bloom in the face of turbulent diffusion away from that area. These studies paved the way for a growing interest in plankton patchiness (Okubo, 1980) and the interaction between turbulence and expected plankton distributions in the horizontal dimension (Platt, 1972; Okubo, 1980). During the late 1970s into the mid-1980s, attention was directed toward the relationship between exposure to variable light, due to vertical mixing within the water column, and phytoplankton physiology. For example,

Throughout this time, technological developments were important in advancing knowledge of turbulence in the mixed layer and its effect on phytoplankton. Through the 1960s, stratification was assessed at a few depths by either density or temperature differences (e.g., Aron, 1959; Nival, 1965; Walsh, 1971; Coste et al., 1972). These measurements, however, gave no information on how quickly mixing within this homogeneous layer occurred. Estimates of mixing were scarce and often calculated from atmospheric and water properties and not measured directly (e.g., Thomas, 1966). Before 1960, because turbulence could not be measured in places less energetic than tidal channels, little information existed for other parts of the ocean (Gregg, 1991). The development of new measuring devices and methods in the late 1960s and 1970s—hot film

In the following decade, observations of bloom phenomena that seemingly contradicted the Critical Depth Hypothesis accumulated. They spurred investigation into the causes of blooms and seem to have directed more attention to bloom phenomena. Townsend et al. (1992) described a phytoplankton bloom in the Gulf of Maine that preceded the onset of vertical water column stratification, and Eilertsen (1993) observed phytoplankton blooms in Norwegian fjords without any apparent stratification to depths greater than 200 m. During this time, researchers began to consider whether low levels of turbulence could possibly trigger a phytoplankton bloom (Fogg, 1991; Stramska and Dickey, 1994; Huisman et al., 1999, 2002; Ebert et al., 2001; Ghosal and Mandre, 2003). Huisman et al. (1999) expanded the theory by postulating a critical turbulence level for the onset of blooms. This progress and the questions it left unanswered (such as how atmospheric and oceanic conditions lead to low turbulence levels) led Ferrari to realize that descriptions of the effects of mixed layer turbulence were incomplete, and his group had the expertise to tackle a more comprehensive assessment (Raffaele Ferrari, Massachusetts Institute of Technology, *pers. comm.*, April 5, 2013). Taylor and Ferrari (2011) relate a critical turbulence diffusivity (level of turbulence at which a phytoplankton bloom could occur) to atmospheric forcing—which is easier to quantify at large scales. These authors showed that a bloom could be initiated at the end of winter by a reduction of air-sea fluxes—conditions that may often precede the shoaling of the mixed layer in spring.

Tracing the paths of progress that led to the Critical Turbulence Hypothesis, we identified technological

advancements and novel observations as essential developments. Equally intriguing was identification of aspects that appeared to slow progress—especially when interest in the field was elsewhere and researchers were unaware of relevant research either within the field, as with plankton physiological acclimation to turbulence, or outside it, as with many measurements of rates of upper ocean mixing. In addition, we found lags in progress may appear worse than they really are if there is a lack of relevant citations in the literature. For example, Taylor and Ferrari (2011) did not cite papers that considered the influence of turbulent mixing rates on phytoplankton growth or distribution (e.g., Denman and Gargett, 1983; Venrick et al., 1987; Owen, 1989), which creates a false impression of a lag in progress for those not familiar with the literature.

Overall, the slow transfer of ideas in parallel research tracks combined with the steady accumulation of observations and new technological and theoretical tools led to progress, with some periods of stagnation and other periods of rapid growth. The development of technology to measure turbulence and the focus of research interest were particularly important in advancing ideas about how critical turbulence can initiate blooms.

### STRATIFICATION FROM MIXED LAYER EDDIES

In Sverdrup's Critical Depth Hypothesis, the onset of stratification in the spring raises the depth of the mixed layer above that of the critical depth to initiate a bloom. This stratification was assumed to arise from surface heating due to increased radiation or decreased surface salinity in the spring. Mahadevan et al. (2012) found that this one-dimensional view of stratification could not fully

explain the timing of phytoplankton bloom phenomena in the North Atlantic. Their results showed that the start of the phytoplankton bloom south of Iceland did occur with the onset of stratification, consistent with Sverdrup's hypothesis; however, the initial stratification resulted not from warming of the sea surface but instead from eddies—large circular vortices of water caused by Earth's rotation—pushing well-mixed water into a shallow zone (Figure 1d).

Because bloom phenomena initiated by mixed layer eddies are likely to be more spatially and temporally patchy than those initiated from surface heating, novel technologies were required to sample at the requisite scales. To overcome this observational challenge, Mahadevan et al. (2012) relied on a suite of technologies: measurements were made from a subsurface Lagrangian float, Seaglider robots (self-propelled, buoyancy-driven autonomous underwater vehicles) sampling around the float, Argo floats (autonomous profiling floats), and Earth-orbiting satellites (see Figure 3 for the timing of technology developments). These measuring devices were critical, as observations from fixed points, such as ships or moorings, are ill suited for resolving patchy processes. They allowed characterization of the area and physical processes during the bloom and provided a climatological picture of the region (obtained from Argo floats that had been deployed for over eight years). Satellite images were used to characterize conditions preceding the eddy-driven slumping and the subsequent bloom.

Although these technological advances were critical for observing this patchy bloom, the theory and computational tools needed to understand submesoscale processes, such as mixed layer eddies, were also essential. New

satellite data had illustrated that mixed layer eddies were not rare events (Amala Mahadevan, Woods Hole Oceanographic Institution, *pers. comm.*, April 12, 2013). Although a relatively new area of research, understanding of submesoscale eddy processes (e.g., Mahadevan and Tandon, 2006; Boccaletti et al., 2007; Fox-Kemper et al., 2008) was central to the study by Mahadevan et al. (2012). Sophisticated three-dimensional models, which required the creativity and insight of researchers to recognize the importance of additional spatial dimensions and processes, enabled the testing of theories and ideas about processes occurring at the submesoscale. Mahadevan et al. (2012) use an ocean process model that resolves fine-scale features, including mixed layer eddies.

Beyond enabling technology and theory, the Mahadevan et al. (2012) study was sparked by observations of phytoplankton blooms that occurred either too early or too late to fit with a thermal stratification explanation. Rather than dismissing these seemingly anomalous blooms, these researchers set out to investigate and understand their dynamics. As with the Critical Turbulence Hypothesis, the emergence of a new theory was precipitated by observations that did not match the current dogma, development of appropriate observational and theoretical tools to attack the problem, integration and extension of old theories, and researchers who then pursued the challenge.

## DILUTION RECOUPLING HYPOTHESIS

In the 1940s, it was realized that blooms were the consequence of subtle imbalances between phytoplankton division rates and loss rates (Riley, 1946; Riley and Bumpus, 1946). These ideas formed

the foundation for quantitative modeling of planktonic ecosystems. In particular, the Critical Depth Hypothesis is a simplification of this framework, as the loss term in Sverdrup's model combines the effects of predation (i.e., grazing), respiration, and—as extrapolated by others—vertical export of sinking particles (e.g., Siegel et al., 2002; Behrenfeld, 2010) into a single rate assumed to be constant at all depths and times. Despite this apparent naiveté in the early days of phytoplankton biology, the effect of the loss term was being investigated. In particular, Cushing (1959) demonstrated that phytoplankton blooms are expressions of subtle imbalances in predator-prey relations rather than reflections of rapid cell division. Yet, the implication of the loss rate for bloom initiation received little or no attention until Smetacek and Passow (1990) stimulated its consideration. Later, with the provocative title “Abandoning Sverdrup's Critical Depth Hypothesis on phytoplankton blooms,” Behrenfeld (2010) motivated the scientific community to reevaluate the shortcomings of Sverdrup's loss term. This delay in attention to the loss term was in part due to a lag in the theory and technology required to understand the biological factors influencing phytoplankton at the microscale.

Characterization of the oceanic autotrophic and grazing community has advanced greatly since Sverdrup's 1953 publication (Figure 3). Early work investigating the importance of heterotrophic microbes in oceanic environments (then considered to be dominated by bacterial decomposers) concluded their role to be very minimal, as traditional methods of counting bacteria (e.g., culturing on agar plates) yielded only small numbers. In the 1970s, the alternative technique of direct microscopic counting with an

epifluorescence microscope (Francisco et al., 1973; Hobbie et al., 1977) led to reassessment and the conclusion that earlier methods grossly underestimated the large concentration of bacteria in the sea. Pomeroy, Azam, and colleagues (Pomeroy, 1974; Azam et al., 1983) challenged the canonical view of the marine pelagic food web by suggesting an alternate pathway of carbon flow from bacteria to protozoans to metazoans via the “microbial loop.” This theory raised many new questions that were unanswerable because of technical constraints, thereby spurring a revolution in marine microbial oceanography and the development of several important technologies to investigate plankton dynamics at the microscale. For example, flow cytometry enabled Chisholm et al. (1988, 1992) to discover a novel picoplankter (*Prochlorococcus*) that is now considered the most abundant autotroph in the world. The advent of dilution techniques allowed Landry and Hassett (1982) and Fenchel (1982) to determine that grazing by protists was responsible for holding bacteria and picoautotroph populations at relatively constant values.

These rapidly growing micrograzers respond quickly to increases in abundance of their phytoplankton prey but never “overgraze” because of feeding threshold effects that make it energetically unprofitable for the grazers to feed when the prey density drops below a given value (Strom et al., 2001). These grazing thresholds, multiple trophic levels, and patchiness are used to explain the lack of blooms in high nutrient, low chlorophyll areas (Strom et al., 2000). Other work on grazing rates (Landry and Hassett, 1982; Landry et al., 1995, 1997) showed that grazer control of pico- and nanophytoplankton was a typical pathway for fixed carbon and that this

recycling in the microbial food web is a significant fate for primary production in the open ocean. An alternative fate for picoplankton-based production is direct and grazer-mediated sinking as a result of picoplankton aggregation (Richardson and Jackson, 2007).

These technical breakthroughs were critical in demonstrating the important contribution of micrograzers to Sverdrup's loss term. The recent resurrection of the earlier concepts of Riley (1946), Nielsen (1958), and Cushing (1959) has paved the way for modern studies leveraging new technologies to investigate the coupling between phytoplankton growth and loss during bloom development. Notably, with observations from NASA's Coastal Zone Color Scanner (CZCS, 1978–1986), Banse (1992, 2002) showed that the annual North Atlantic phytoplankton bloom results from a mismatch between growth and loss processes, where growth is temporarily higher than loss. Additionally, the bloom terminates with either exhaustion of surface nutrients or overgrazing by heterotrophs, such that the rates of growth and loss are once again in balance.

To investigate whether this initial decoupling was a result of increased phytoplankton growth rates or decreased losses, Behrenfeld (2010) used a satellite record of phytoplankton biomass in the North Atlantic and merged concepts originally formulated by Cushing (1959), Evans and Parslow (1985), Banse (1992, 2002), and Marra and Barber (2005) into the Dilution Recoupling Hypothesis (Figure 1e). The synthesis of these fundamental ideas, combined with new technology and perspective, enabled the interplay among phytoplankton growth, grazing, and seasonal physical processes to be evaluated in greater detail. Behrenfeld (2010) argues that

bloom initiation occurs in the winter when the mixed layer is deepest, contrary to the Critical Depth Hypothesis. Deep mixing replenishes the surface ocean with essential nutrients for bloom formation and dilutes phytoplankton cell density, thus reducing the encounter rate between predator and prey during winter (Cushing, 1959; Strom et al., 2001).

As the mixed layer depth shoals and increasingly concentrates phytoplankton and grazer populations, the lagging grazer population eventually “recouples” with the phytoplankton population and can limit bloom extent and duration (Cushing, 1959). Advances in the spatial and temporal resolution of ocean data were instrumental in the refinement and evaluation of the Dilution Recoupling Hypothesis (Michael Behrenfeld, Oregon State University, *pers. comm.*, April 5, 2013).

Despite these advances, technology continues to be a limiting factor in our understanding of biological losses—for example, respiration rates remain poorly constrained, and we are now realizing viruses may play a larger role than previously thought (see Miki and Jacquet, 2008; Breitbart, 2012). Today, the development of novel in situ biological

sensors provides opportunities to explore the relationships between phytoplankton community growth and loss rates and physical processes at previously unprecedented resolution levels. For example, the Imaging FlowCytobot (Olson and Sosik, 2007) and the Environmental Sample Processor (Scholin et al., 1998) are capable of measuring abundance of

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plankton and microbes of certain sizes to the species level with imaging and genomic probes, respectively. Larger zooplankton can be identified with the Video Plankton Recorder (Davis et al., 1996) and their biomass estimated with acoustic profilers. Technological advances that enable extensive in situ observation of whole ocean communities have spurred estimates of community-level production and loss. Innovations in autonomous profilers to facilitate the in situ measurement of oxygen concentrations allow accurate estimates of net community production, or the net oxygen production minus the respiration from all trophic levels, and ultimately a better understanding of ecosystem carbon dynamics (Riser and Johnson, 2008). Additionally, advances in bio-optical measures of particle flux (such as those used by Claustre et al., 2008, and

Briggs et al., 2011) enable the estimation of gross community production, community losses, and net community production in surface waters. New instrumentation, combined with phytoplankton bloom models incorporating more biological detail, hold great promise in further elucidating the complex variables at play in bloom development.

dilution experiments. After the 1990s, focus shifted toward bulk measurements of phytoplankton blooms over large spatial and temporal scales with ocean color satellites. In recent years, as autonomous samplers capable of identifying individuals and genetic and chemical markers in the field have become a reality, focus may come full circle, back to

dynamics. On one hand, the literature review has demonstrated that much of the trajectory toward modern hypotheses of bloom initiation has drawn directly from Sverdrup's model. Indeed, his theory clarified and explicitly laid out the relationships between environmental variables and phytoplankton responses, providing a useful framework for the construction of testable hypotheses to expand the model's scope. At the same time, this review has also shown that scientific progress after Sverdrup's publication followed more complex trajectories. In particular, when field observations did not fit Sverdrup's framework, researchers were able to use his model to explore alternative mechanisms underlying bloom initiation. Following three specific cases studies revealed that, at times, this process was paced by technological developments and awareness of scientific insights across disciplines. In fact, we found examples where progress in understanding phytoplankton blooms was both catalyzed and delayed by the timing of methodological developments and interdisciplinary communication.

Beyond the Critical Depth Hypothesis, this review shows that perhaps 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. It is a testament to the value of Sverdrup's 1953 paper that even 60 years later it is interwoven into current investigations and in doing so, continues to spur progress. Going forward, the trajectories and successes in our understanding of bloom initiation in the wake of Sverdrup's publication underscore the importance of continued interdisciplinary collaborations and awareness to address the complexity of phytoplankton bloom dynamics.

“ BEYOND THE CRITICAL DEPTH HYPOTHESIS, THIS REVIEW SHOWS THAT PERHAPS 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. ”

In their recent review focused on the ecological complexity of phytoplankton blooms, Behrenfeld and Boss (2013) emphasize evidence of the continued controversy over factors controlling phytoplankton blooms. Yet, in comparison to the influence of abiotic factors such as turbulence and nutrients, the effects of grazing and other biotic factors on phytoplankton blooms have appeared in the literature about half as frequently since Sverdrup (1953) (Web of Science). Our review of the literature (see complete bibliography in Supplementary Material) suggests that this disparity is most likely due to limitations in methodologies to constrain ecosystem-level processes (Figure 3). In the 1980s and 1990s, understanding of grazer-phytoplankton dynamics at the community level was greatly advanced through

measuring community-level biological interactions. Technology has certainly spurred progress in our understanding of biotic factors on phytoplankton bloom initiation in the past, and looking forward, we see great promise in observational strategies that allow insight into concurrent biological, chemical, and physical processes over multiple spatial and temporal scales.

#### CONCLUSION

More than half a century ago, Sverdrup provided a framework for understanding the environmental conditions necessary to initiate a phytoplankton bloom. By following the path of Sverdrup's ideas to the present day, we tracked the interplay among technology, theory, observations, and inspiration that have led to our current understanding of bloom

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