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Phytoplankton bloom phenomena in the North Atlantic Ocean and Arabian Sea

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We review bio-optical and physical data from three mooring experiments, the Marine Light – Mixed Layers programme in spring 1989 and 1991 in the lceland Basin ($59^{\circ}N/21^{\circ}W$), and the Forced Upper Ocean Dynamics Experiment in the central Arabian Sea from October 1994 to 1995 ($15.5^{\circ}N/61.5^{\circ}E$). In the Iceland Basin, from mid-April to mid-June in 1989, chlorophyll-*a* concentrations are sensitive to small changes in stratification, with intermittent increases early in the record. The spring increase occurs after 20 May, coincident with persistent water column stratification. In 1991, the bloom occurs 2 weeks earlier than in 1989, with a background of strong short-term and diurnal variability in mixed layer depth and minimal horizontal advection. In the Arabian Sea, the mixing response to the northeast and southwest monsoons, plus the response to mesoscale eddies, produces four blooms over the annual cycle. The mixed layer depth in the Arabian Sea never exceeds the euphotic zone, allowing interactions between phytoplankton and grazer populations to become important. For all three mooring experiments, change in water column stratification is key in producing phytoplankton blooms.

Keywords: Arabian Sea, critical depth, North Atlantic, spring bloom, Sverdrup, zooplankton grazing.

Introduction

There has been a resurgence of interest in Sverdrup's (1953) critical depth hypothesis in recent years (e.g. Behrenfeld, 2010; Chiswell, 2011; Taylor and Ferrari, 2011), as exemplified by a special session at a recent Ocean Sciences Meeting (February 2014) and by this issue of the *Journal of Marine Science*. The most recent contributions indicate an ongoing interest in what has been called "one of the largest transient events on the planet" (Gillis, 1991): the North Atlantic spring bloom is the rapid increase in phytoplankton biomass that occurs in spring months because of the interacting conditions of high nutrients and the seasonal increasing solar irradiance.

There are few datasets that can be used to understand the initiation of the North Atlantic spring bloom. *In situ* data on hydrographic structure and biological response are sparse or non-existent

for winter or early spring, before seasonal restratification of the water column. Here, we reanalyse observational data from two moorings deployed in 1989 and in 1991 in the Iceland Basin $(59^{\circ}N/21^{\circ}W)$ (Figure 1a) that help illuminate the causes of the initiation of the North Atlantic spring bloom. We also use data from the Forced Upper Ocean Dynamics Experiment in the Arabian Sea in 1994–1995 (15.5°N and 61.5°E; Figure 1b). The Arabian Sea is a monsoon-dominated regime, with two energetic surface forcing seasons, and unlike the North Atlantic, has near-constant surface irradiance over the year and a more modest seasonal temperature range (20–30°C). In these respects, the Arabian Sea serves as a useful contrast to the North Atlantic. The moorings recorded both physical (e.g. irradiance and temperature) and biological (e.g. chlorophyll-*a*) properties at high temporal resolution

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Figure 1. (a) Site of the Marine Light—Mixed Layers ("ML – ML") mooring experiments in 1989 and 1991. (b) Map showing the site of the Forced Upper Ocean Dynamics Experiment in 1994 – 1995. The mooring data come from the marker designated as "WHOI" at $15.5^{\circ}N/61.5^{\circ}E$ [see Rudnick *et al.* (1997)].

(minutes and hours), allowing the covariability between physical and biological properties to be examined as the structure of the water column evolved from late winter to spring.

Data sources

Marine Light - Mixed Layers, 1989, Iceland Basin

The first Marine Light–Mixed Layers (ML–ML) mooring experiment took place in spring, 1989 (hereafter, "MLML89"; much of the data are publicly available, with assistance from the authors, at http://www. ldeo.columbia.edu/research/biology-paleo-environment/bioinfo). The mooring was deployed from 15 April (year day, or yd, 105) to 10 June (yd 161). Details of the mooring design, instrumentation, sensor

Table 1. Array of relevant instrumentation on the three moorings, MLML89, MLML91 (Iceland Basin), and the Forced Upper Ocean Dynamics Experiment in the Arabian Sea. 'Meas' refers to measurement type.

Relevant measurements in upper 250 m					
MLML89		MLML91		Arabian Sea	
Meas	Depth	Meas	Depth	Meas	Depth
Temp	2	Temp	2	Temp	1.5
MVMS	10	MVMS	10	Temp	5
MVMS	30	MVMS	30	MVMS	10
MVMS	50	MVMS	50	Temp	15
MVMS	90	MVMS	70	Temp	20
MVMS	110	Temp	80	Temp	25
MVMS	150	Temp	102	Temp	30
Temp	200	Temp	118	MVMS	35
MVMS	250	Temp	150	Temp	40
		Temp	166	Temp	45
		Temp	182	Temp	50
		Temp	198	Temp	55
		Temp	214	Temp	60
		Temp	230	MVMS	65
				Temp	72.5
				MVMS	80
				Temp	90
				Temp	100
				Temp	125
				Temp	150
				Temp	175
				Temp	200
				Temp	225
				Temp	250

MVMS, Multivariate Moored Sensor; temp, temperature sensor package.

calibration, and methods can be found in Stramska and Dickey (1992) and Dickey *et al.* (1994). Multivariate Moored Sensors (MVMSs; Dickey *et al.*, 1994) were put at 10, 30, 50, 90, 150, and 250 m. (See Table 1 for the array of sensors relevant to the data discussed. Sensors at 70 and 110 m failed, and are not included in the analysis.) Bio-optical observations at these depths included chlorophyll-*a* fluorescence, beam attenuation coefficient, and photosynthetic active radiation (PAR). Temperature and current velocities were measured at these same depths; salinity was measured only at 10 and 250 m. Meteorological data were collected at a surface buoy. We do not have data for all these variables for the full deployment period; but overall, the data retrievals were good.

Marine Light - Mixed Layers, 1991, Iceland Basin

The mooring for MLML91 collected data from 30 April (yd 120) until 6 September (yd 249), although we consider only data through yd 155. For MLML91, MVMSs were deployed at 10, 30, 50, 70, and 90 m. Temperature sensors were placed approximately every 20 m, starting at the surface, to 250 m (Table 1). Key references for background, methods, instrumentation, and mooring design are Plueddemann *et al.* (1993, 1995), Stramska *et al.* (1995), and Weller *et al.* (1990).

Forced Upper Ocean Dynamics Experiment, 1994–1995, Arabian Sea

The mooring for the Arabian Sea was similar in design to that deployed in MLML91, with MVMS units deployed at 10, 35, 65,

and 80 m, and temperature sensors placed at depth intervals of 5–10 m throughout the upper 250 m (Table 1). The mooring discussed here (Figure 1b) was at the central point of an array of five moorings, also part of the Forced Upper Ocean Dynamics Experiment. There were two deployments of 6 months each, the first from 16 October 1994 to 21 April 1995, and the second from 23 April to 25 October 1995. Key references for this programme are Rudnick *et al.* (1997), Dickey *et al.* (1998), Kinkade *et al.* (2001), and Weller *et al.* (2002).

Results

MLML89

The time evolution of the temperature and chlorophyll-*a* distributions from the various sampled depths are shown in Figure 2. Temperature (Figure 2a) is marked by periods of intermittent stratification and isothermal layers, culminating in spring restratification beginning about yd140 (May 20), and remains so for the remainder of the record.

There are periods of stratification early in the series (April to early May), followed by a few days where the sensors recorded nearly uniform temperatures, suggesting vertical mixing. The water column then begins to restratify, punctuated by a shallow mixing event (0–150 m) around May 18 (yd138). By yd145, the water column becomes stratified and remains so for the remainder of the record. Winds and windstress were highly variable throughout the time-series; the mixing event during May 18–May 20 (yd 138–140) was associated with the windstress event [see Dickey *et al.* (1994)].

The chlorophyll-*a* record (Figure 2b) essentially follows the temperature in character. There are early periods of vertical stratification where chlorophyll-*a* increases at all depths except the deepest (150 and 250 m), followed by a brief periods where chlorophyll values are nearly uniform. After this, the spring increase is almost completely confined to the shallowest three depths, 10, 30, and 50 m, with the values at 10 m exceeding for a short time, 3 µg chlorophyll-*a* 1^{-1} . The increases in near-surface chlorophyll-*a* near the end of the record (late May, early June, where June 1 is yd 152) come at the expense of chlorophyll-*a* deeper in the water column, an example of self-shading of the population [see Marra (2004)].

Contour plots are always an interpretation. The two episodic stratification events are best viewed with time-series plots of data from each of the depths to span the period covering both events



Figure 2. Contour plots of (a) temperature (°C) and (b) chlorophyll-*a* (μ g l⁻¹) for the MLML89 mooring experiment. There are no data from 110 m for chlorophyll-*a*. Time is presented as calendar dates (mm/dd) in (a) and as yd in (b).



Figure 3. Time-series from individual depths for mid-April to mid-May in Figure 2 with (a) temperature (°C) and (b) chlorophyll-*a* (μ g l⁻¹). The data have been smoothed, for clarity. The unsmoothed data are shown in Marra (2004).

(Figure 3). In both instances, the water column becomes progressively warmer at all depths, and subsequently becomes more uniform in temperature, producing near-isothermal conditions as a function of depth. For the first event, the water column becomes increasingly stratified until yd113 (April 23), after which vertical mixing occurs to 50 m, followed by a near-isothermal water column over the full range of observed depths (10–250 m) by April 28. Chlorophyll-*a* concentrations (Figure 3b) increase coincident with stratification of the upper ocean at April 17 down to 90 m, then declines as the upper 50 m become isothermal, with roughly constant levels (within $\pm 0.1 \,\mu$ g chlorophyll-*a* 1⁻¹) by April 28, from 10 to 150 m. Following this episode, chlorophyll-*a* at the shallowest three depths (10, 30, and 50 m) increases until the next time the water column mixes in mid-May.

It is likely that the increases in chlorophyll-*a* in the near-surface records (10, 30, and 50 m) are from phytoplankton growth. Certainly, estimates of the increase in chlorophyll-a, of about a doubling per day, are reasonable. Deeper than this the evidence is less clear. As the water column becomes isothermal, chlorophyll-a concentration at all depths declines except the two deepest depths (150 and 250 m), perhaps because concentrations at these depths increase as a result of mixing from above. Integrated over 10-250 m, however, chlorophyll-a declines by 30% from April 24 to 29 (data not shown). The increases shown for the 150 and 250 m depths are not enough to compensate for the losses shallower in the water column. The integrals may be inaccurate because of the limited depth resolution, because chlorophyll had been mixed deeper than our deepest sensor (250 m), or else because local currents (which were otherwise relatively weak during this period: Dickey et al., 1994) play a role in the variability. [Unfortunately, satellite altimetry data are unavailable for the period of our experiment, and satellite sea surface temperatures are not sufficiently resolved to identify mesoscale features. See Dickey et al. (1994).] The water column becomes isothermal over all depths by April 28 (yd118), and chlorophyll-a does as well. Nevertheless, temperature differences of less than a few tenths of a degree between adjacent instruments allow an increase chlorophyll-a concentrations by a factor of two during the first half of the record.

Daily PAR in the water column is shown in Figure 4. It is fairly constant at 20-30 mol photons m⁻² d⁻¹ until the wind event (May 18–May 20), and declines thereafter as the bloom develops. Daily-averaged net heat flux is also relatively constant over the course of the experiment [see Dickey *et al.* (1994)].

MLML91

The experiment in 1991 shows similar temperature variability, but very different biological behaviour than in 1989 (Figure 5). We had the benefit of extensive sampling from shipboard that we did not have in MLML89, and that allowed phytoplankton and zoo-plankton species to be identified.

Compared with 1989, the major chlorophyll-*a* increase over the water column occurred much earlier in 1991, and during the incipient stratification from yd125 to yd140 (May 5–20). The first stage of the bloom was interrupted by a storm (yd128–130, May 8–10), as recorded at the mooring's surface meteorological sensors (Plueddemann *et al.*, 1995). Shipboard observations during two ML–ML cruises, covering the period May 7–24 [see Marra *et al.* (1995)], identified the bloom occurring then as *Phaeocystis pouchetii*, an unusual occurrence south of Iceland. After a major storm on May 22 (yd142), with >70 knot (35 m s⁻¹) winds, the *Phaeocystis* bloom was no longer observed.



Figure 4. Daily PAR in the water column. $E(0)^{-}$ is calculated as the intercept from the linear regression of ln PAR (z).



Figure 5. Contour plots of (a) temperature (°C) and (b) chlorophyll-*a* (μ g l⁻¹) for the MLML91 spring data. There is more detail in the temperature plot because of the higher sampling resolution with depth. Depths for temperature sensors begin at the surface, then with ~20 m spacing until 310 m. Depths for chlorophyll-*a* sensors are 10, 30, 50, 70, and 90 m. Time is presented as calendar dates (mm/dd) in (a) and as yd in (b).

The water column quickly stratified under clear skies (total daily irradiance of 60 mol photons m⁻² d⁻¹: Marra *et al.*, 1995), and diatoms and copepods appeared in the surface layers (Cowles and Fessenden, 1995). Chlorophyll-*a* levels had declined by nearly an order of magnitude after the storm, and recovered only partially thereafter. At this time, nitrate concentrations in the upper water column ranged from 6 to 8 μ M (Marra *et al.*, 1995); therefore, nutrients were likely not a factor in the development of the bloom.

Forced Upper Ocean Dynamics Experiment, Arabian Sea, 1994 – 1995

The Arabian Sea mooring experiment extended an entire year, from October 1994 to 1995. The seasonal cycle is dominated by monsoons, with within-season effects from mesoscale eddies. The moored observations captured both the northeast (December 1994–February 1995) and southwest (June–August 1995) monsoons. The seasonal cycle in the vertical structure of temperature and areal chlorophyll-*a* (Figure 6) is reported in Kinkade *et al.* (2001), compiled from both mooring and shipboard data. This is the most complete description of the physical setting and biological response determined for the Arabian Sea. In the one-dimensional sense, convective cooling occurs during the northeast monsoon, as the winds from Asia blow over the northern Arabian Sea (Fischer *et al.*, 2002). The result is vertical, convective, mixing result-ing in deepening the mixed layer. In contrast, the mixing during the southwest monsoon is mechanical, and caused by windstress at the



Figure 6. (a) Contour plot of temperature overlain with areal chlorophyll-*a* (C_{tot} , mg m⁻²) from the mooring (open circles) and from shipboard hydrographic casts (filled circles), and (b) mixed layer depth. Mixed layer depths were estimated as a temperature difference of 0.1°C from the surface temperature.

surface. In neither case, however, does the mixing extend to great depth, never reaching >100 m, and perhaps never exceeding the euphotic zone (Barber *et al.*, 2001). The biological response to the southwest monsoon was greater than for the northeast monsoon, but for reasons that are not clear (Barber *et al.*, 2001).

Perhaps enhanced activity at the mesoscale, associated with the southwest monsoon, provides a source of nutrients (Keen et al., 1997) to support the greater productivity during the southwest monsoon. Fischer et al. (2002), using data from the array of five moorings and data from Sea Soar tows, show that cool and nutrient-rich waters are brought from the coastal upwelling regime out to the central mooring. In autumn of 1994, there is evidence of two mesoscale eddies at the mooring location (Figure 6a), one when the mooring was first deployed, and the second about a month later. In these cases, the increase in chlorophyll-a is associated with relatively shallow mixed layers, and the strong temperature contrast with depth suggests an enhanced nutrient supply that supports surface productivity. Over the year, there are four episodes of phytoplankton increases observed in the Arabian Sea, two occurring as a result of each of the monsoon periods, and two associated with the passage of mesoscale eddies in autumn of 1994.

Discussion

Sverdrup's (1953) critical depth hypothesis is a mathematical derivation of ideas presented earlier by Gran and Braarud (1935) and Riley (1942). These earlier authors recognized that since autotrophic respiration (R) was, perhaps, 20% of gross production (G), the phytoplankton cells could be mixed to five times the depth of the compensation irradiance (i.e. where G = R) without incurring a population decline [see Mills (1989)]. Conceptually, this is sound. The balance between net production by phytoplankton and the vertical mixing that they are subject to, should determine the fate of phytoplankton populations in a variety of environments. This is especially so in the late-winter North Atlantic where Sverdrup (1953) tested his ideas. The North Atlantic, unlike many other ocean regimes, convectively mixes during winter, producing mixed layers >600 m deep (Robinson *et al.*, 1979; Monterey and Levitus, 1997), and in effect, resetting the seasonal production cycle.

The critical depth hypothesis has achieved wide acceptance, becoming a core tenet of biological oceanography, but it has had few, if any, actual tests. Later, there were critiques. Smetacek and Passow (1990) note that actual critical depths may exceed winter mixing depths, anyway, and further that phytoplankton communities are capable of overwintering [see, e.g., Backhaus et al. (2003)]. They also remind that stratification occurs from the surface, and that there are difficulties in accounting for other losses (e.g. zooplankton grazing). They conclude that the critical depth hypothesis serves a little practical value. Behrenfeld (2010) takes a similar position, noting that there is significant biomass during winter in the boreal North Atlantic, and highlighting the balance between growth and grazing. This balance would be disrupted by seasonal restratification in favour of a spring bloom. Behrenfeld's (2010) evidence, however, comes from satellite ocean colour estimates of chlorophyll-a, which can be subject to error during winter at high latitudes, and carry no information on vertical structure.

While we do not have winter data, our records for the North Atlantic are from before the seasonal restratification of the water column, and indicate the initiation of the spring bloom. We cannot provide a direct test of the critical depth hypothesis; however, we can point to factors that are important for bloom initiation. For the Arabian Sea, we show how mixed layer dynamics affect chlorophyll-*a* for a situation where the mixed layer never exceeds the critical depth.

North Atlantic

For both the 1989 and 1991 programmes, the moorings provide a good realization of the temporal dynamics of bloom development for the Iceland Basin in the North Atlantic. Dickey *et al.* (1994) note that current velocities during the restratification period were weak and barotropic. For the 1991 experiment, Plueddemann *et al.* (1995) show that the spring evolution of the temperature structure in the upper water column could successfully be simulated by a one-dimensional mixed layer model. Thus, for 1989 and 1991, we conclude that we observed the temporal evolution of the spring bloom.

It is clear from the time-series observations of temperature and chlorophyll-a that stratification of the water column instigated the bloom. In 1989, there are two early, incipient episodes of stratification that elicit a chlorophyll-a response, followed by vertical mixing (isothermal periods). When the water column becomes persistently stratified, chlorophyll-a increases in the top 150 m. In both 1989 and 1991, there are periods of weak stratification interspersed with water column mixing, the result of wind events (1989) or major storms (1991), with the stratified periods associated with strong increases in chlorophyll-a. The timing of the blooms in 1989 and 1991 are within two weeks of each other. The seasonal restratification (Figures 2 and 5) begins at yd135-140 (May 15-20) in 1989, and yd140-143 (May 20-23) in 1991. Stramska and Dickey (1993) have pointed out that chlorophyll-a is very sensitive to water column stratification. A vertical difference of a few tenths of a degree celsius within the top layers is enough to stabilize the surface layers and thereby allow increases in chlorophyll-a. Similarly, mixing those top layers disperses the chlorophyll-a.

We can try to interpret our data using the critical depth idea, to make an inference as to what happens earlier in the season (before our observations), and whether it is a useful guide for the initiation of the bloom. We use a simplification of Sverdrup's (1953) equation, presented in Lalli and Parsons (1993), whereby

$$Zcr = \frac{E(0)}{(k \cdot Ec)}$$

Here, Zcr is the critical depth, E(0) is the solar irradiance penetrating the surface, k is the vertical diffuse attenuation coefficient for PAR, and Ec the compensation irradiance. The 1989 observations show that E(0) is $\sim 20-30$ mol photons m⁻² d⁻¹ (Figure 4), with a vertical diffuse attenuation coefficient of 0.06 m⁻¹. Marra (2004) has estimated that Ec for the data from 1989 is 0.1-0.3 mol photons $m^{-2} d^{-1}$ based on the time and depth changes in chlorophyll-a at the height of the bloom. If we assume a surface irradiance of 10 mol photons $m^{-2} d^{-1}$ to represent times earlier in the year than our observations, then the critical depth will have a calculated range from 600 to 1600 m. This depth range is large, but comparable to, or greater than, prior estimates of the late-winter mixed layer depths (Monterey and Levitus, 1997; see also Smetacek and Passow, 1990). The depth range also suggests that the critical depth will be greater than the mixed layer depth for the observations in MLML89 and MLML91. As the season progresses, and E(0)increases, the critical depth will increase accordingly. We do not have data for the late-winter population of phytoplankton; however, it is unlikely that the balance between photosynthesis and respiration, as suggested by Sverdrup (1953), is a primary factor to the initiation of the bloom.

Thus, we conclude that seasonal restratification of the water column drives the change in chlorophyll-a concentration in surface waters from midwinter lows to spring highs. The change in stratification may be episodic, and the spring bloom may therefore proceed episodically, and be spatially heterogeneous. We recognize that there are other processes at work that we cannot account for with our dataset. For example, perhaps there is advection of more stratified water past the mooring. However, 1D models (Stramska and Dickey, 1994; Plueddemann et al., 1995; Stramska et al., 1995) support the notion that air-sea interaction processes could explain the change in water stratification that we observe. Recently, Mahadevan et al. (2012) suggest that mixed layer "slumping" produces stratification that can affect the timing of spring bloom. Our data do not contradict that assessment. Our data support the view that it is a decrease in mixing intensity followed by the development of water column stratification that is the driver for the changes in chlorophyll-a concentration observed.

Another control on biomass (although not on physiology) is grazing. Sverdrup (1953) considered this as a significant loss term in his analysis of spring bloom, and it has been considered so in subsequent treatments (e.g. Platt et al., 1991; Behrenfeld, 2010). Behrenfeld (2010) regards grazing as a strong control of overwintering phytoplankton populations in the North Atlantic. Although we do not have the appropriate measurements to assess the impact of grazing for the 1989 dataset, there are shipboard observations for the MLML91 experiment, for the period of May 17-24 (yd137-144). During the Phaeocystis bloom, there are few mesozooplankton, but they become abundant after the seasonal stratification, after May 23 (Cowles and Fessenden, 1995). Despite that abundance, these authors calculate that the grazing impact by copepods after 23 May is \sim 5% of primary production. The impact of grazing by microzooplankton is higher, but as well, only after the onset of persistent stratification (Gifford et al., 1995). To be sure, there are no data earlier in the season than this, but the sequence suggests that grazing only becomes important after the bloom is established, and plays little role in the initial stages. Finally, incubation estimates of primary production (¹⁴C assimilation and ΔO_2) are roughly comparable to changes in in situ biomass, calculated from diurnal changes in beam attenuation (Marra et al., 1995). This is further evidence that grazing is not a large loss process during the spring bloom in the North Atlantic.

Arabian Sea

In the Arabian Sea, unlike in the North Atlantic, there is not a dominant annual cycle. Incoming shortwave radiation, expressed as PAR, averages $\sim 30 \pm 5$ mol photons m⁻² d⁻¹ over the year, with summertime values dropping significantly below that because of cloudiness (Marra et al., 1998; Weller et al., 1998). Sea surface temperature lacks a summer peak, instead showing cooling during both summer and winter (Weller et al., 1998) from the effects of the two monsoons. The Arabian Sea, like most other ocean areas, also has mesoscale variability and advective transports that are at times significant contributors to local water column properties. Like many tropical areas (e.g. Lukas and Lindstrom, 1991), vertical mixing in the Arabian Sea does not extend deeper than 100 m (Dickey et al., 1998; Weller et al., 2002). Because of these attributes, we can expect that biological interactions, most prominently zooplankton grazing on phytoplankton, will be relevant to the dynamics in the Arabian Sea.

One way to ascertain the importance of grazing is to compare photosynthetic carbon assimilation in incubations (Barber et al., 2001) with the variability of chlorophyll-a from the moored fluorometers (Figure 6a). The largest change in in situ chlorophyll-a occurs with the southwest monsoon. The data are scattered towards the end of the monsoon period, but the realized increase in chlorophyll-a from July to September (~90 d) is 0.3- $0.5 \text{ mg m}^{-2} \text{ d}^{-1}$. Assuming a (high) carbon : chlorophyll-a ratio of 100, this daily increase amounts to $30-50 \text{ mg C m}^{-2} \text{ d}^{-1}$, about a factor of 20 smaller than the daily photosynthetic carbon assimilation measured during the southwest monsoon (Barber et al., 2001). Still, zooplankton grazing does not completely regulate phytoplankton biomass in the Arabian Sea; biomass variations are observed. The argument made by Marra and Barber (2005) and also by Marra and Moore (2009) is that the monsoons affect more strongly micrograzer populations than the phytoplankton, since the phytoplankton are not mixed to depths greater than their capacity for positive production. Thus, in the Arabian Sea, we have a situation where vertical mixing may apply more to heterotrophs than autotrophs.

In conclusion, our observations from moorings in the Iceland Basin (1989 and 1991) support the idea that water column stratification is the trigger for the spring phytoplankton bloom in the North Atlantic. Before the observed spring increase, calculations of the critical depth suggest that the phytoplanktons are capable of maintaining themselves through winter, with perhaps small episodic increases of biomass with transient stratification events. The Arabian Sea serves as a useful contrast to the North Atlantic, in that vertical mixing does not extend beneath the euphotic zone (and certainly not to a critical depth). Thus, for the Arabian Sea, vertical mixing affects grazer populations to a greater extent than the phytoplankton.

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