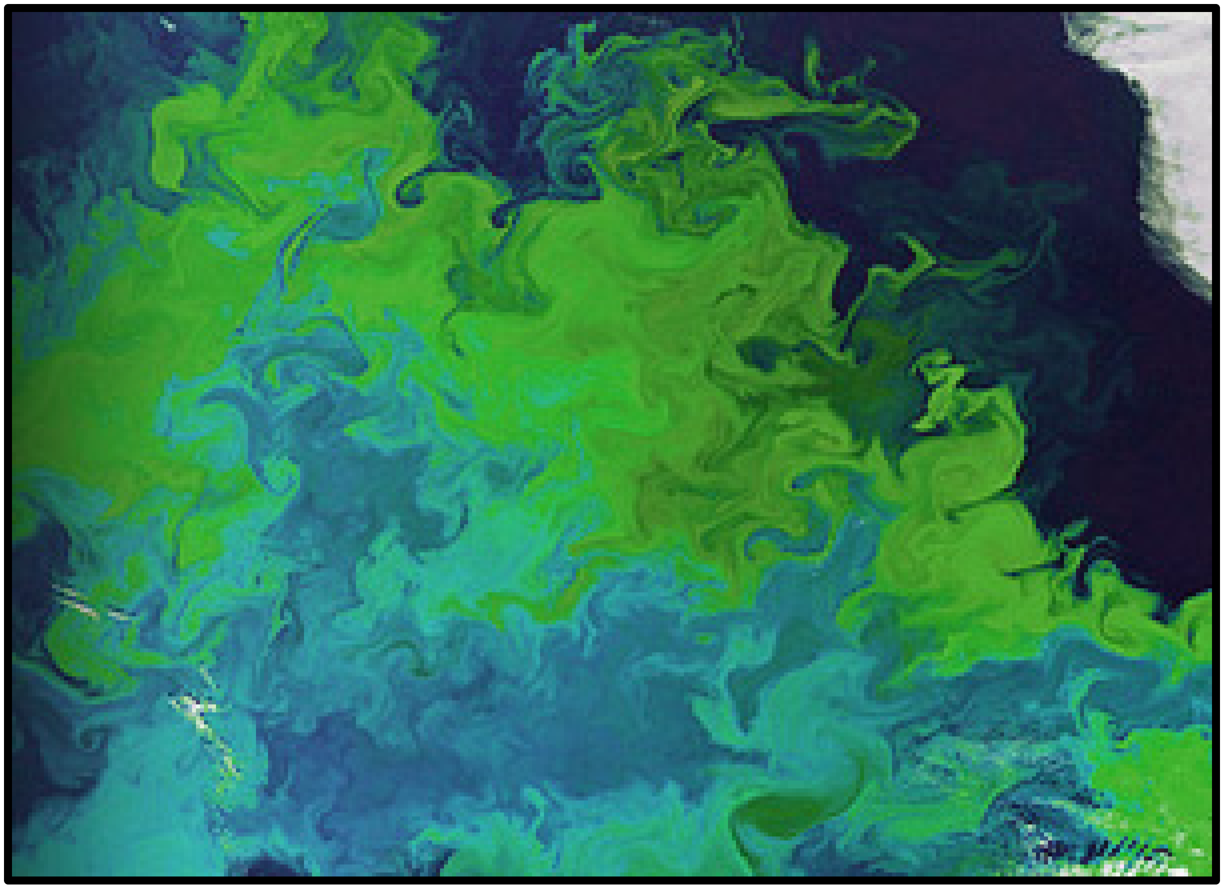
This work has been supported by NASA's
Ocean Biology and Biogeochemistry Program

"Overview of Blooms: Properties and mechanisms"



Michael Behrenfeld
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Oregon State University

Some interesting questions

- What is a bloom and what causes it?
- Under what conditions can the state of ‘blooming’ be initiated?
- What sustains a bloom from initiation to climax?
- With what basic conceptual framework should we think about blooms
- Blooms are diverse. Are there fundamental ‘rules to the game’ ?
- How do trophic interactions, taxonomic composition, and successional dominance influence blooming and the characteristics of a bloom?

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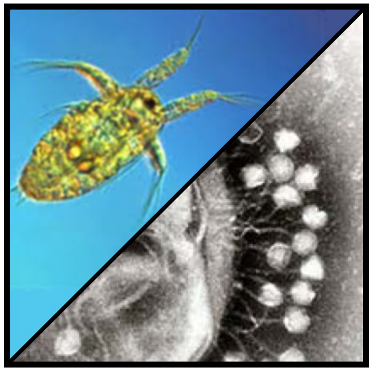
not a prayer in h@##

What is a phytoplankton bloom?

A *bloom* is the condition of elevated phytoplankton concentration.

What causes a phytoplankton bloom?

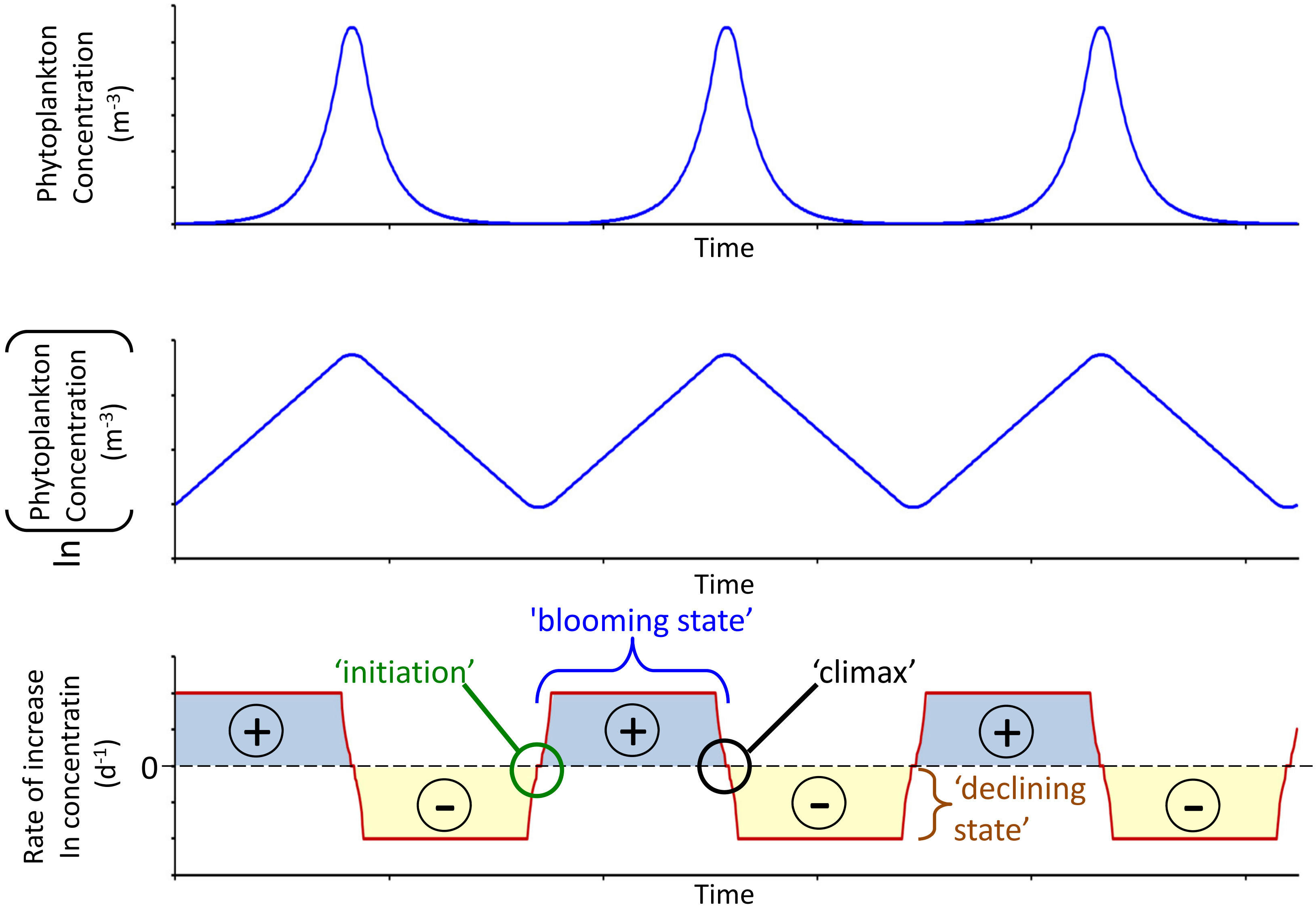


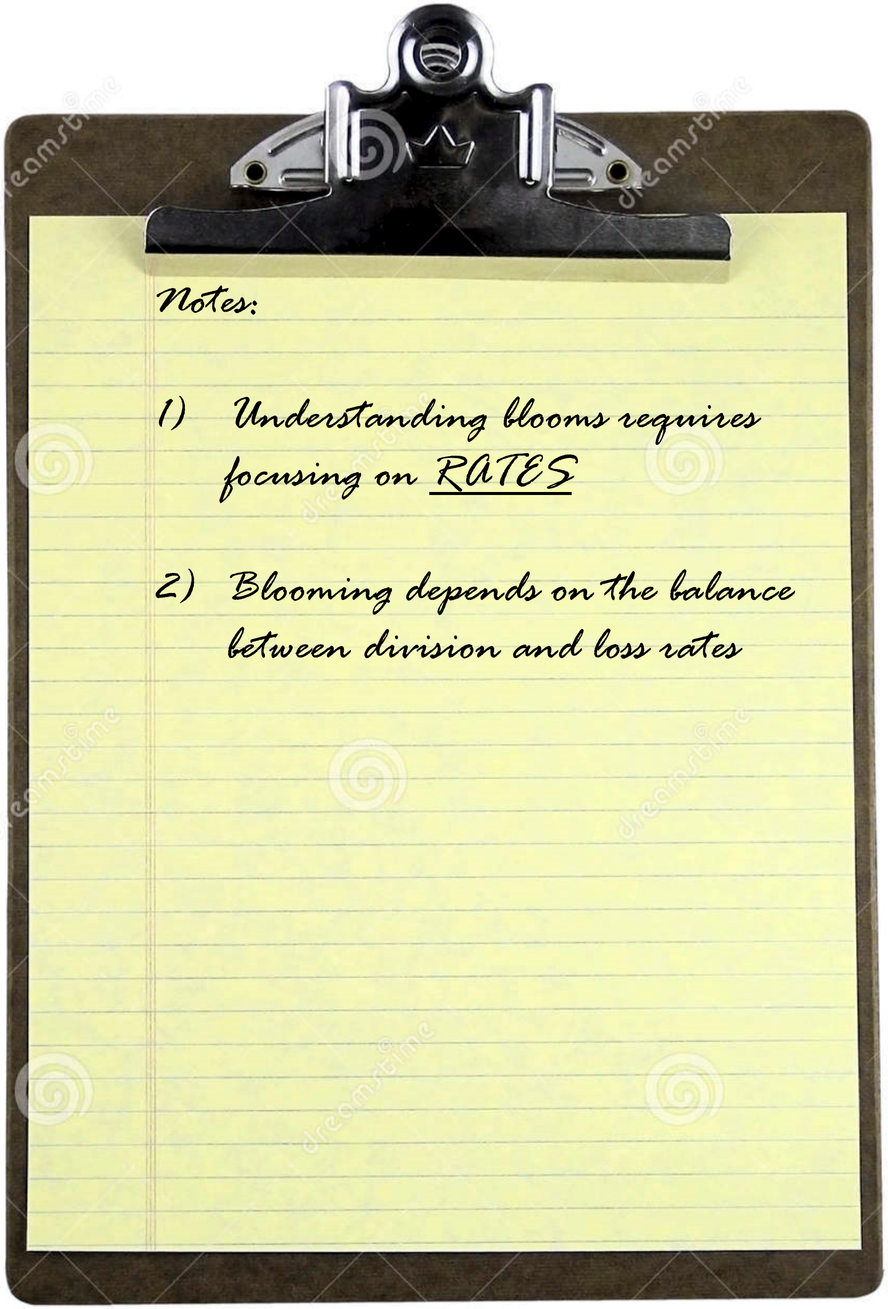
[simple answer] A bloom is caused by the rate of phytoplankton division (μ) exceeding the rate of phytoplankton loss (l)

When $\mu > l$, the rate of accumulation (r) is positive and biomass increases (i.e. 'blooming').

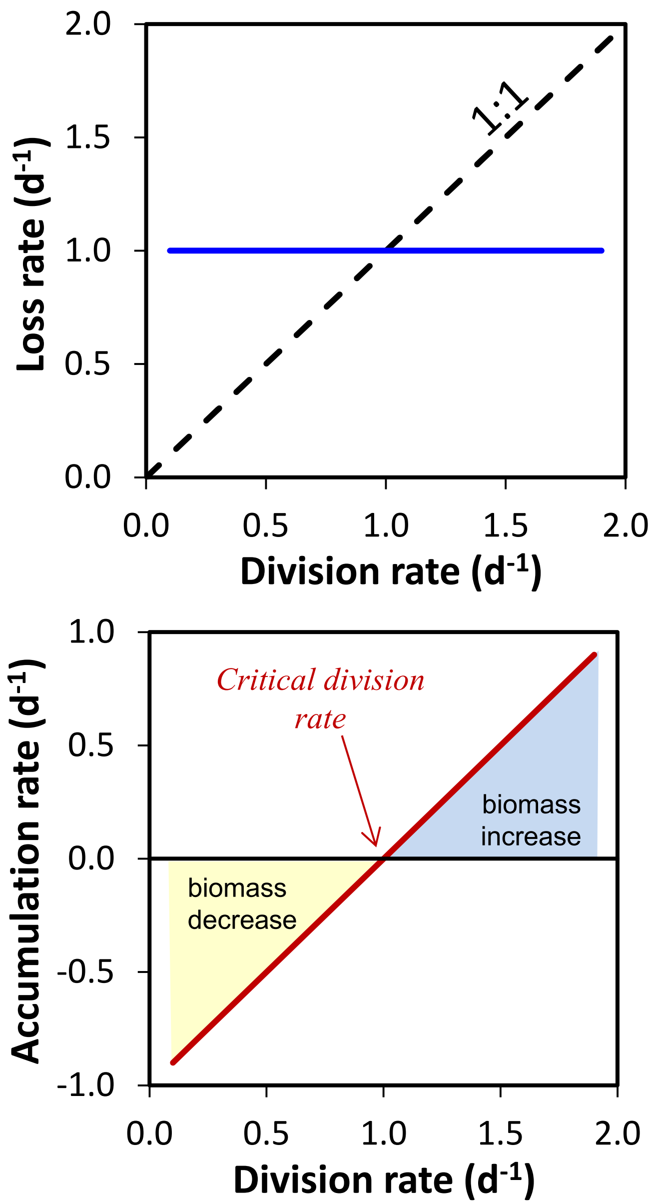
To understand blooms, it is essential to evaluate ***RATES***

Evaluating Blooms




Notes:
1) Understanding blooms requires focusing on RATES
2) Blooming depends on the balance between division and loss rates

Conceptual framework



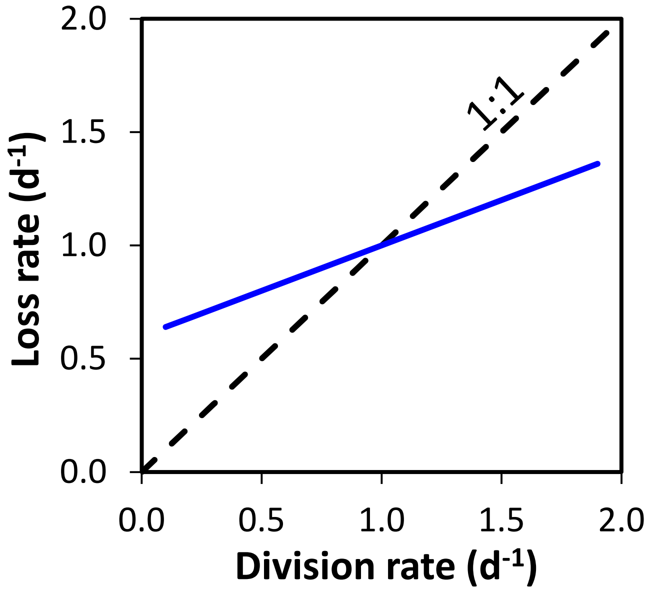
Threshold framework

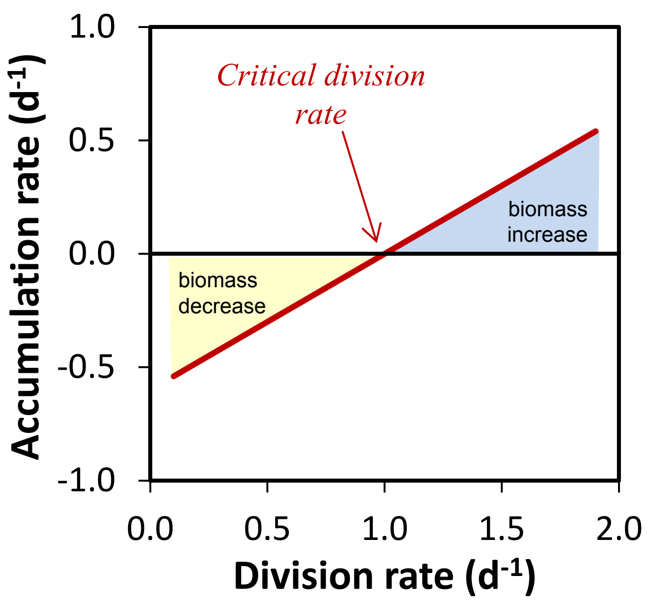
[classic 'critical depth' formulation]

- Loss rate treated as constant
- Threshold (i.e., critical) rate at which division = losses
- Rate of accumulation in biomass is directly proportional to division rate

The 'critical depth hypothesis' is better taught as the 'critical division rate hypothesis'

Conceptual framework

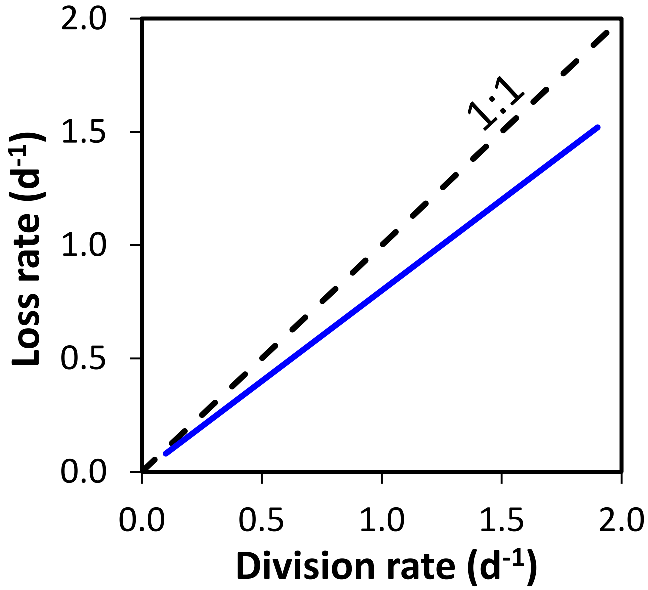


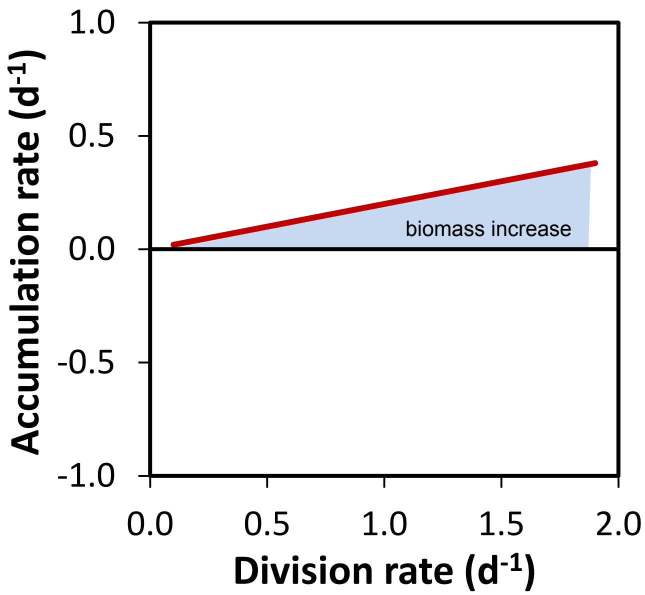


Modified threshold framework

- Loss rate allowed to vary
- Threshold (i.e., critical) rate at which division = losses
- Rate of accumulation in biomass is proportional to division rate

Conceptual framework

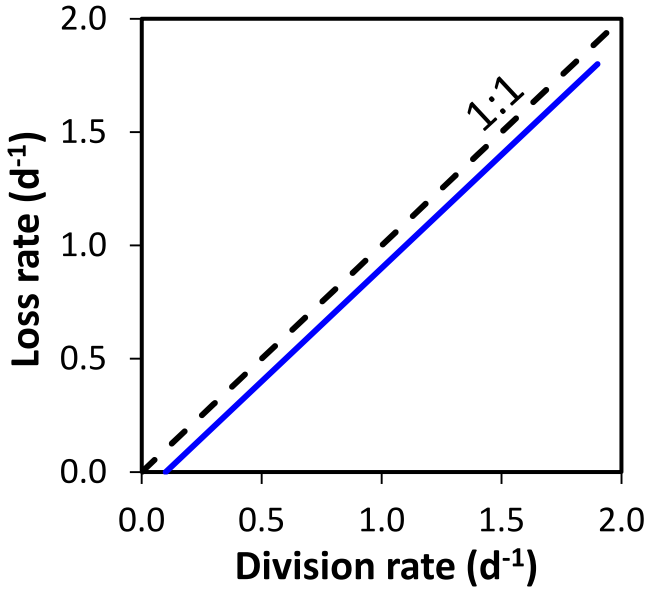


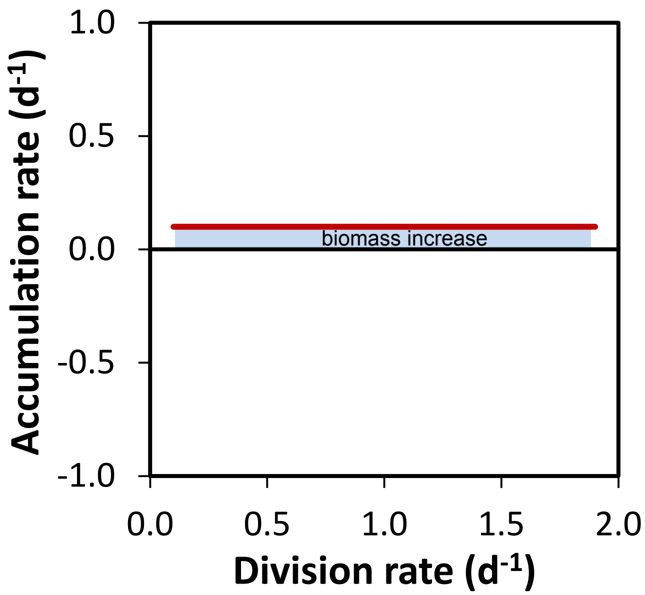


Fractional loss framework

- Loss rate allowed to vary
- Biomass accumulates at all division rates > 0 d^{-1} (i.e., no critical threshold)
- Rate of accumulation in biomass is proportional to division rate

Conceptual framework





'Quasi-equilibrium' framework

- Loss rate parallels division rate
- Biomass accumulates in proportion to division-loss disequilibrium
- Rate of accumulation in biomass is independent of division rate

Summary

Three basic frameworks with testable hypotheses

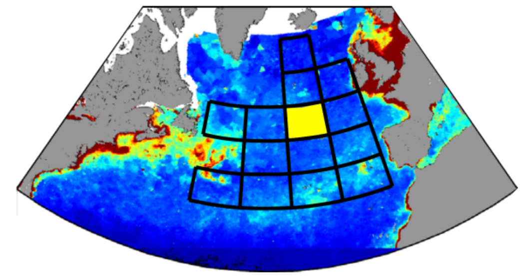
(A) Threshold

(B) Fractional loss

(C) Quasi-equilibrium

Hypothesis	*Null Hypothesis*
A threshold division rate exists for blooming ($\mu > l$) to occur (A)	Blooming can occur at any division rate > 0 d^{-1} (B, C)
Biomass accumulation rate (i.e., blooming rate) is proportional to division rate (A, B)	Biomass accumulation rate is independent of division rate (C)

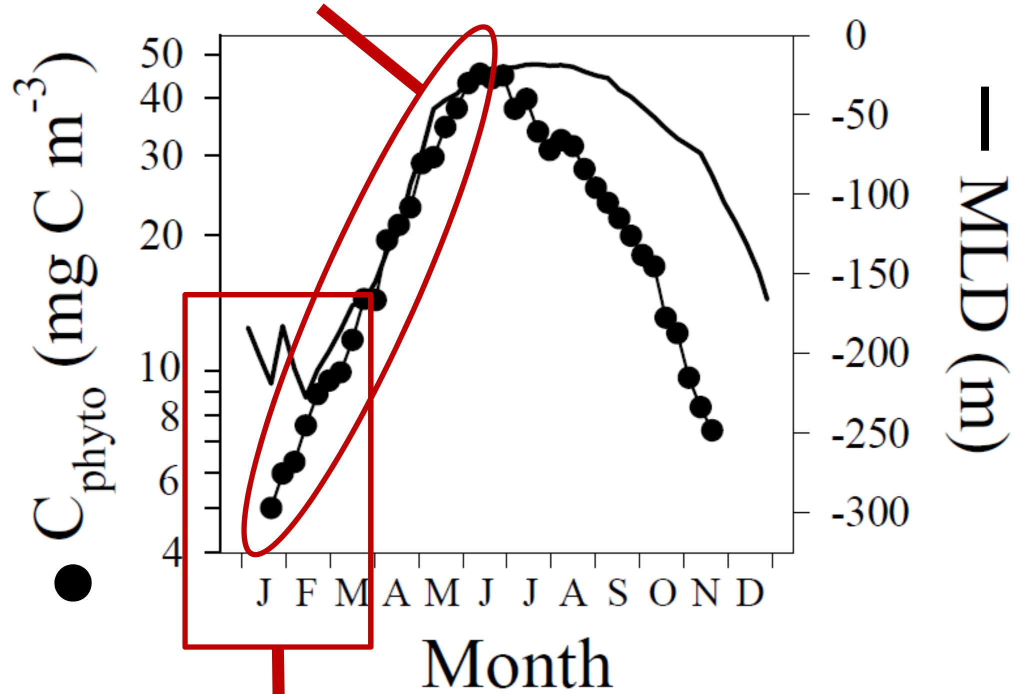
North Atlantic data



Relationship between division & accumulation rates?

A conserved slope = conserved rate

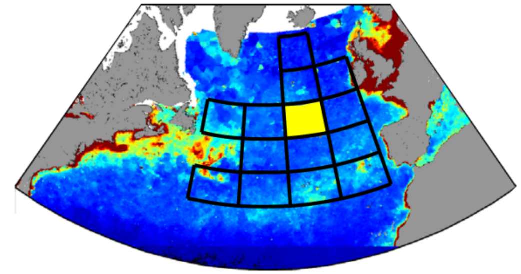
Log Scale →



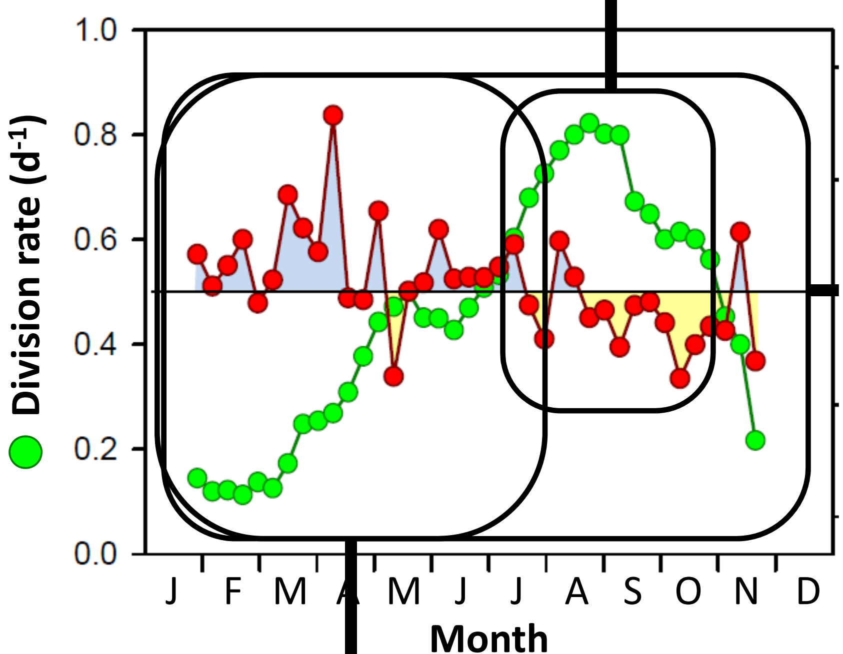
Concentrations begin to increase when the mixed layer stops deepening

Behrenfeld 2010 *Ecology* 91(4): 977-989

North Atlantic data



Bloom can end when division rates are still high

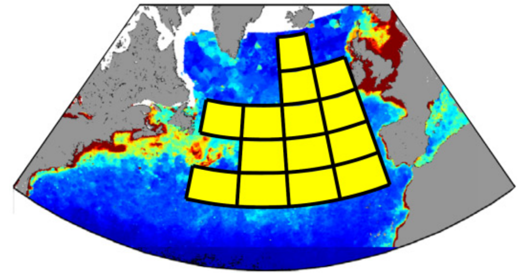


Winter-to-Summer rise in division rate is not reflected by a similar pattern in accumulation rate

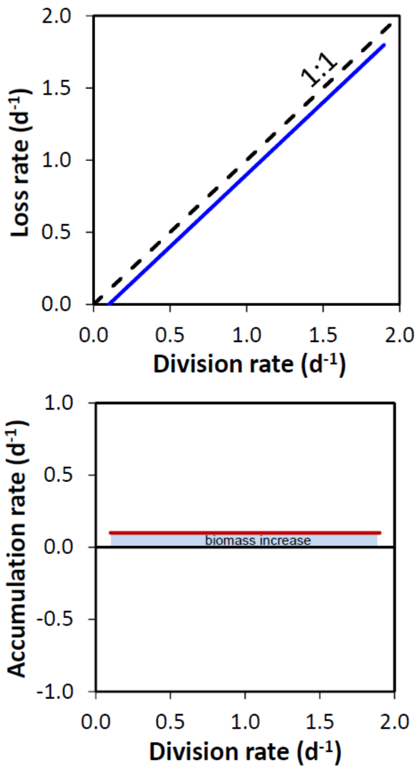
- Overall, division and accumulation rates are uncorrleated

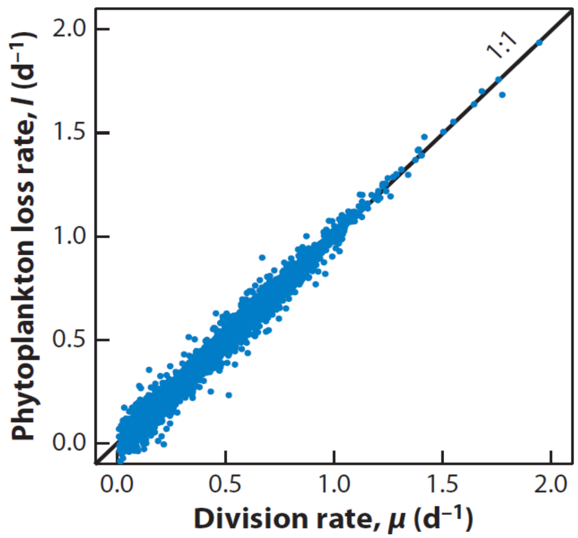
Behrenfeld 2014 Nature Climate Change, doi:10.1038/NCLIMATE2349

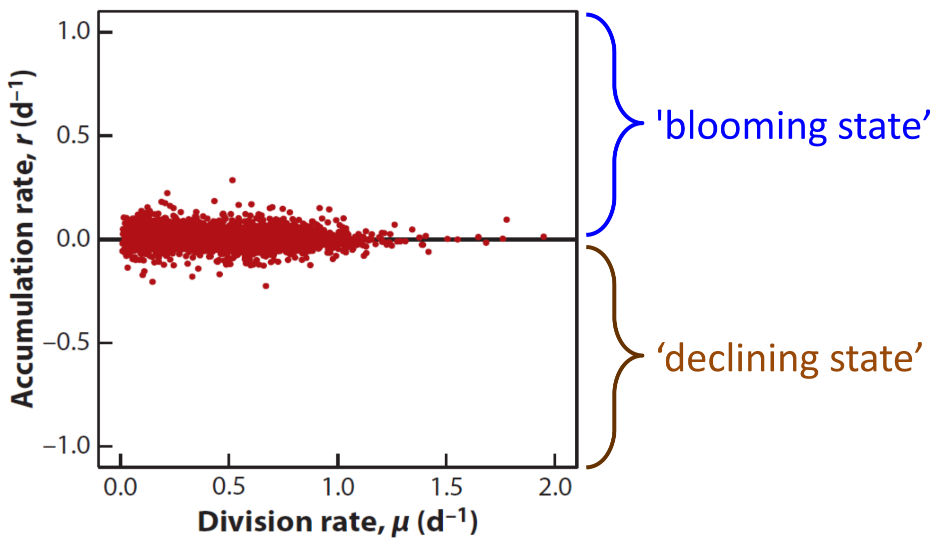
North Atlantic data



‘Quasi-equilibrium’ framework







- Ten years of SeaWiFS
- 8-day resolution
- All NA bins

Behrenfeld & Boss 2014 Annu. Rev. Mar. Sci. 6:167-194

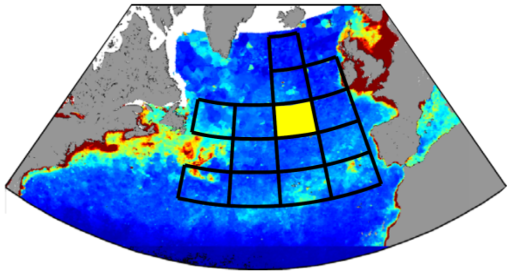
Notes:

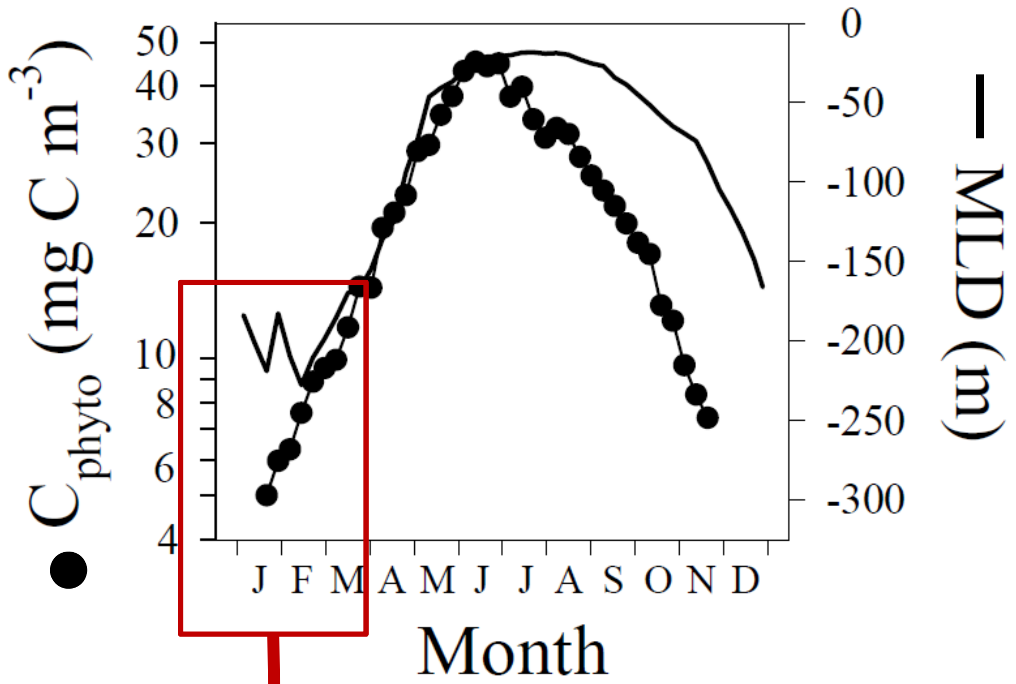
1) Understanding blooms requires focusing on RATES

2) Blooming depends on the balance between division and loss rates

3) The rate at which biomass increases during a bloom appears independent of division rate (consistent with 'quasi-equilibrium view)

North Atlantic data

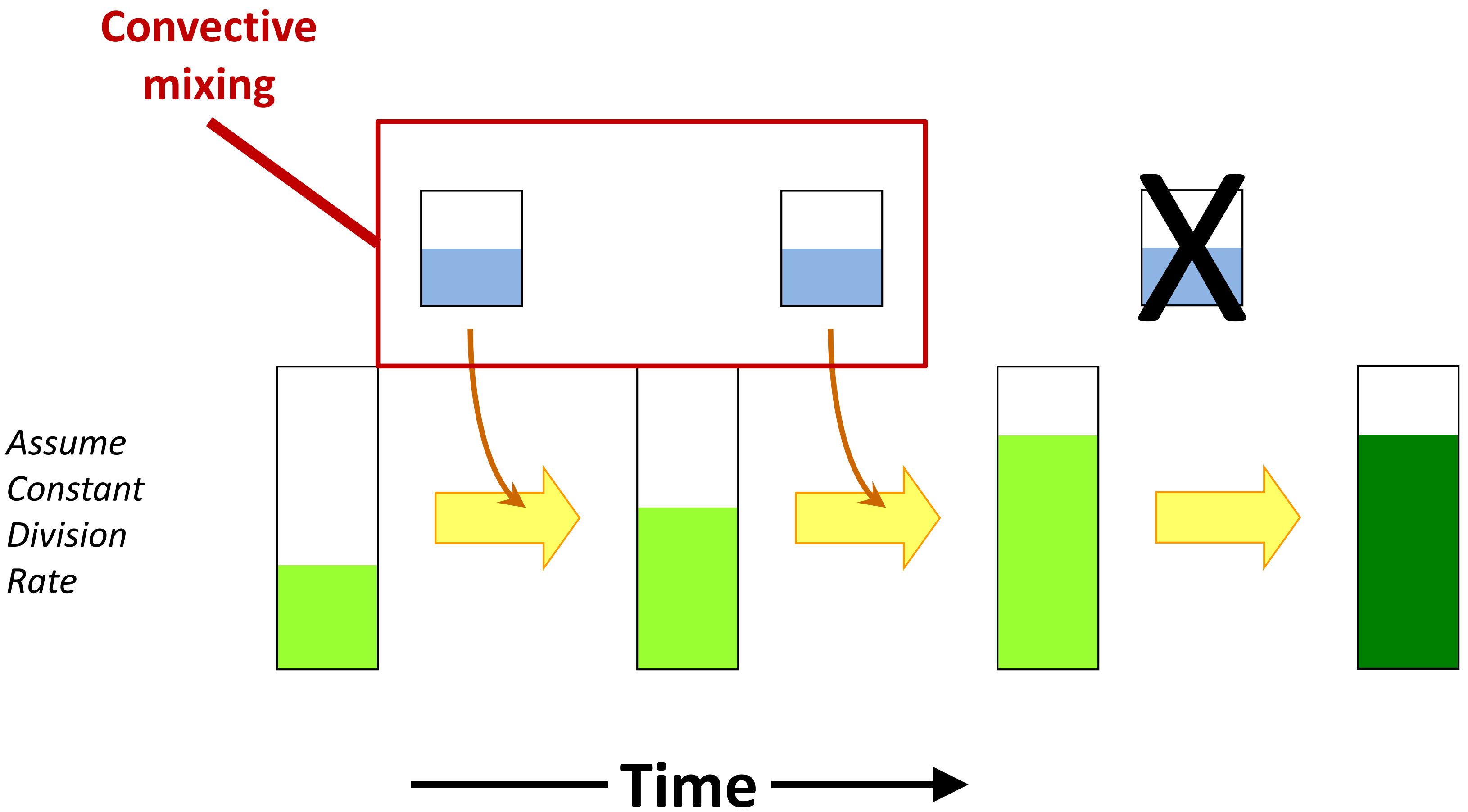




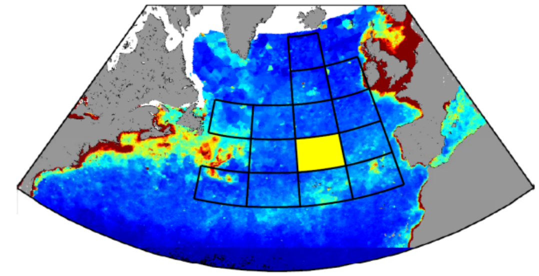
Why do concentrations begin increasing when convection stops deepening the mixed layer?

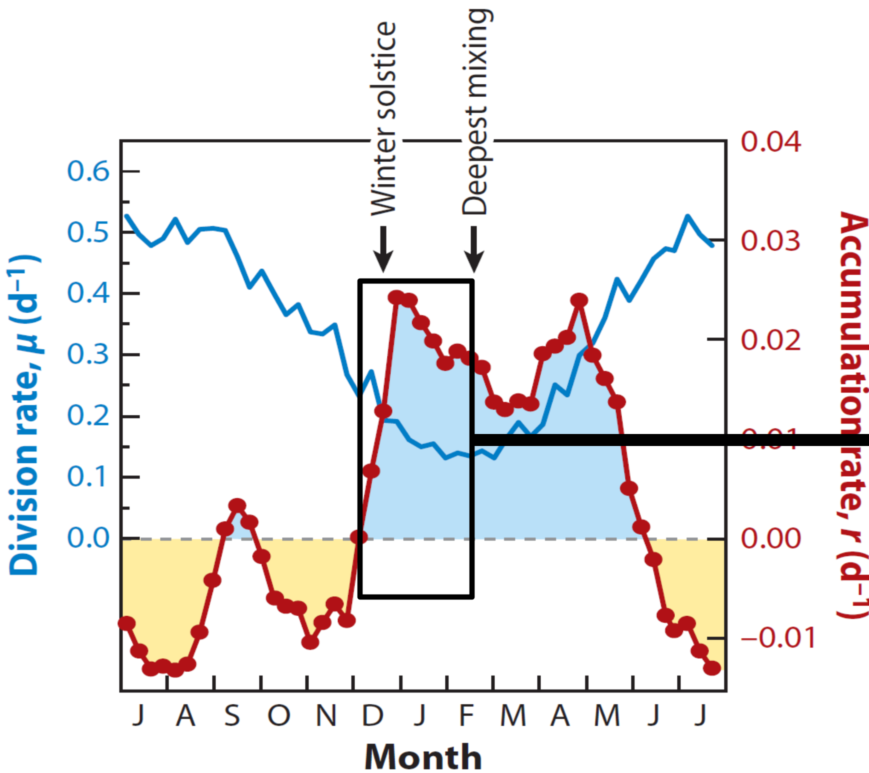
Behrenfeld 2010 *Ecology* 91(4): 977-989

Thought experiment



North Atlantic data

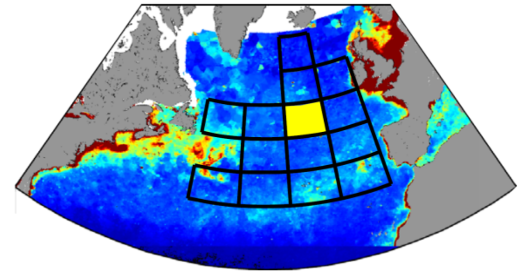


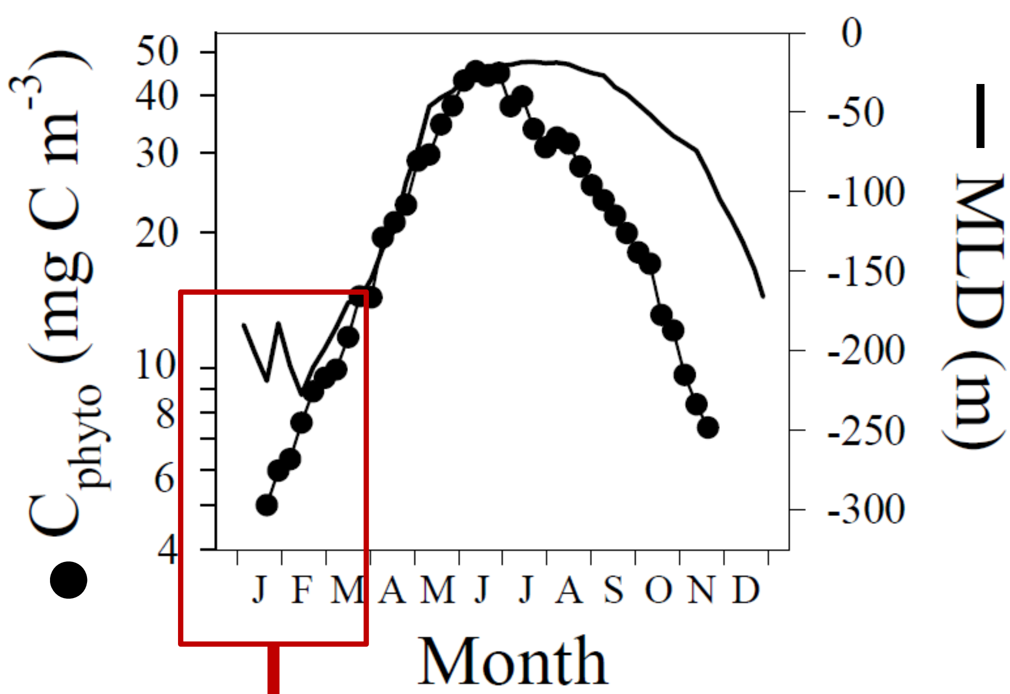


Mixed layer biomass increases ($\mu > l$) prior to the end of convective mixed layer deepening, but this increase is diluted over a growing volume of water so it is not reflected by a change in concentration

Behrenfeld & Boss 2014 Annu. Rev. Mar. Sci. 6:167-194

North Atlantic data



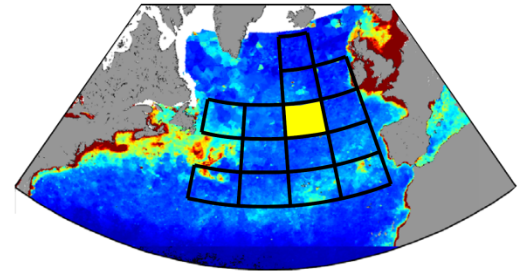


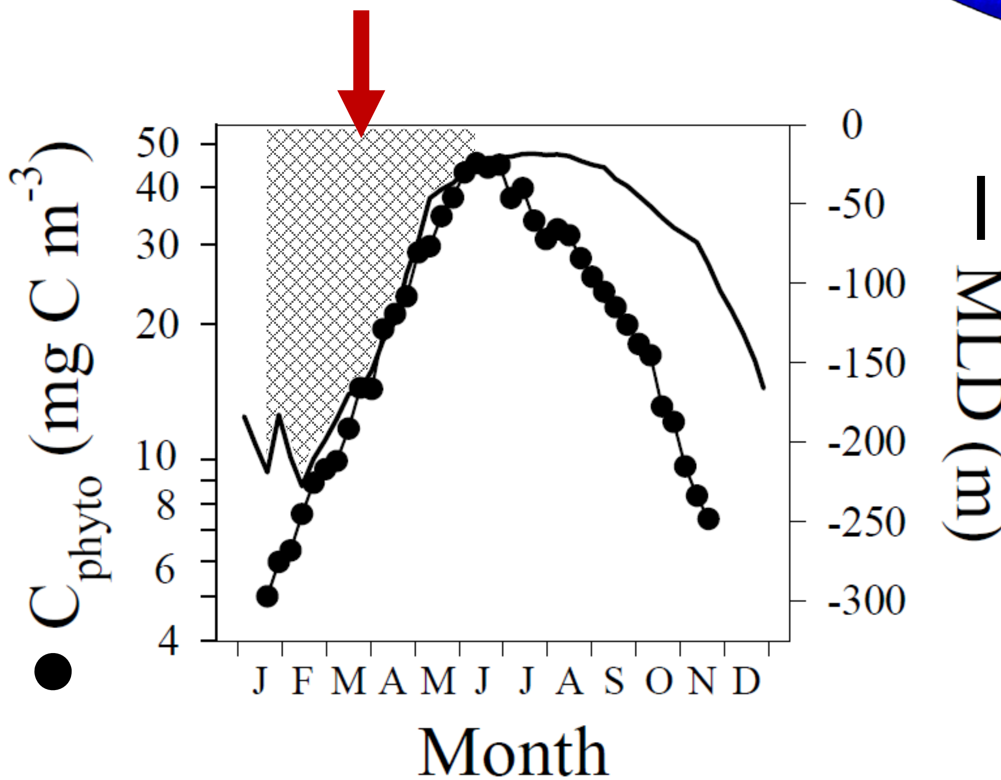
Why do concentrations begin increasing when convection stops?

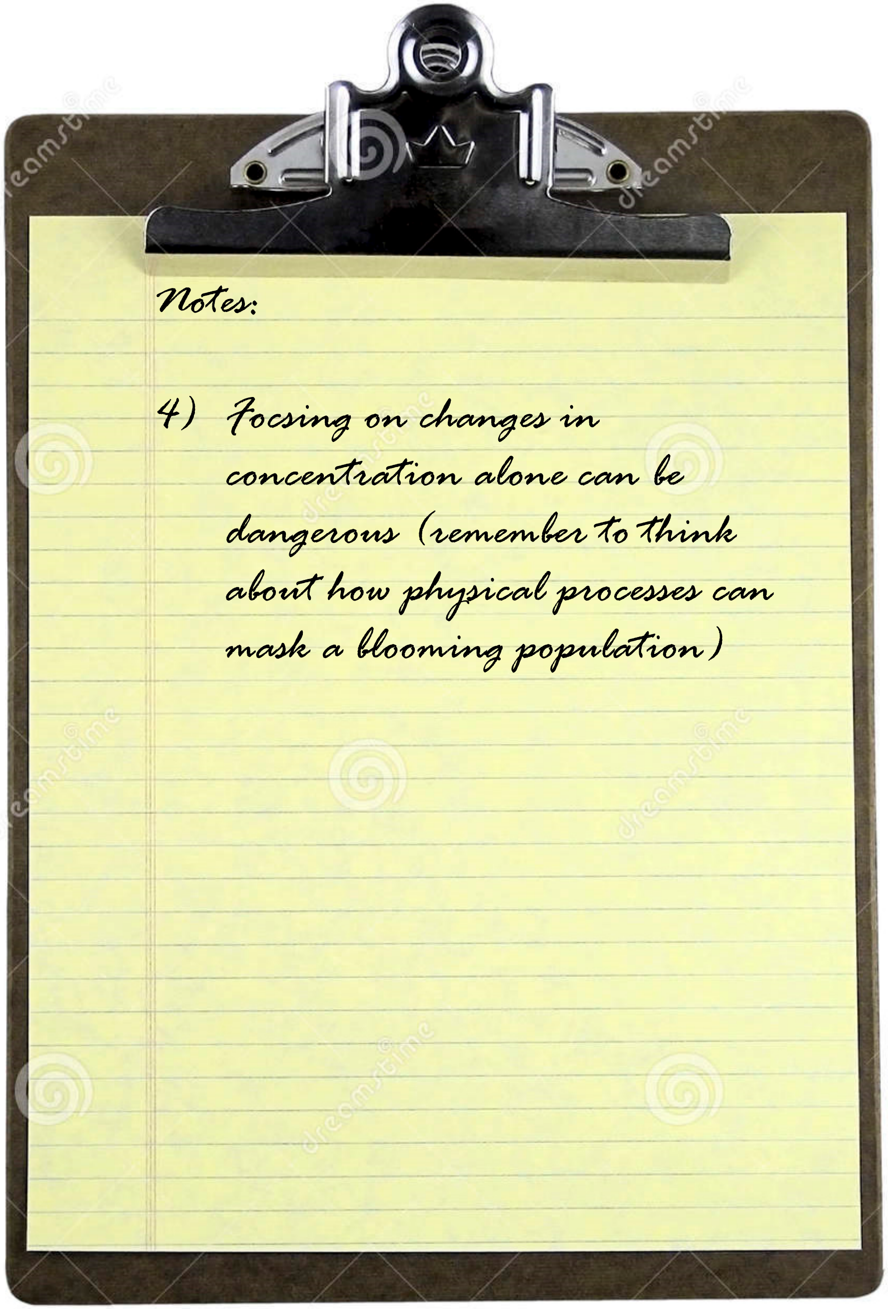
Because the population is no longer being diluted, so the excess of division over loss starts being expressed as an increase in phytoplankton concentration (m^{-3})

Behrenfeld 2010 *Ecology* 91(4): 977-989

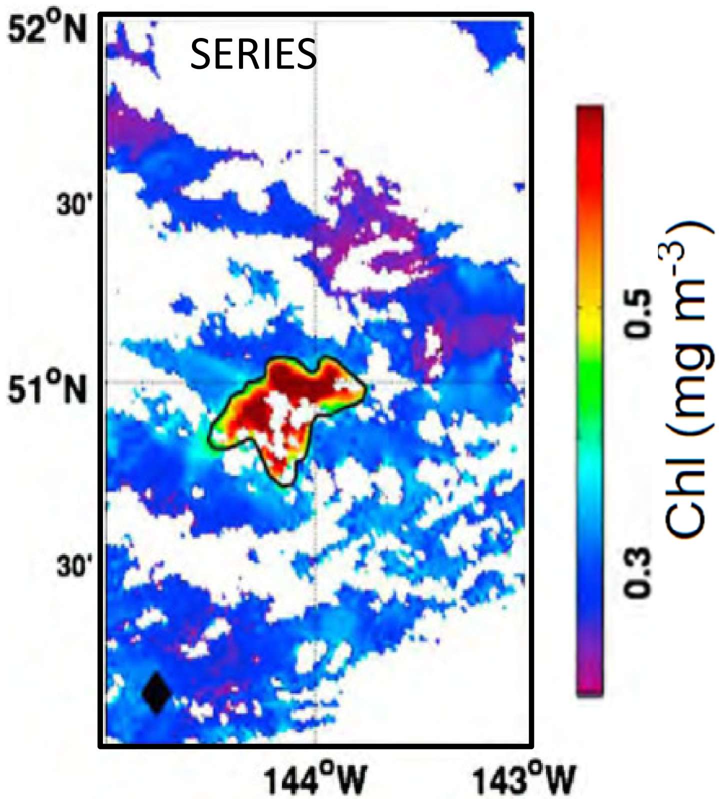
Mixing vs Mixed Layer






Notes:
4) Focsing on changes in concentration alone can be dangerous (remember to think about how physical processes can mask a blooming population)

Blooms are diverse. Are there any common rules?

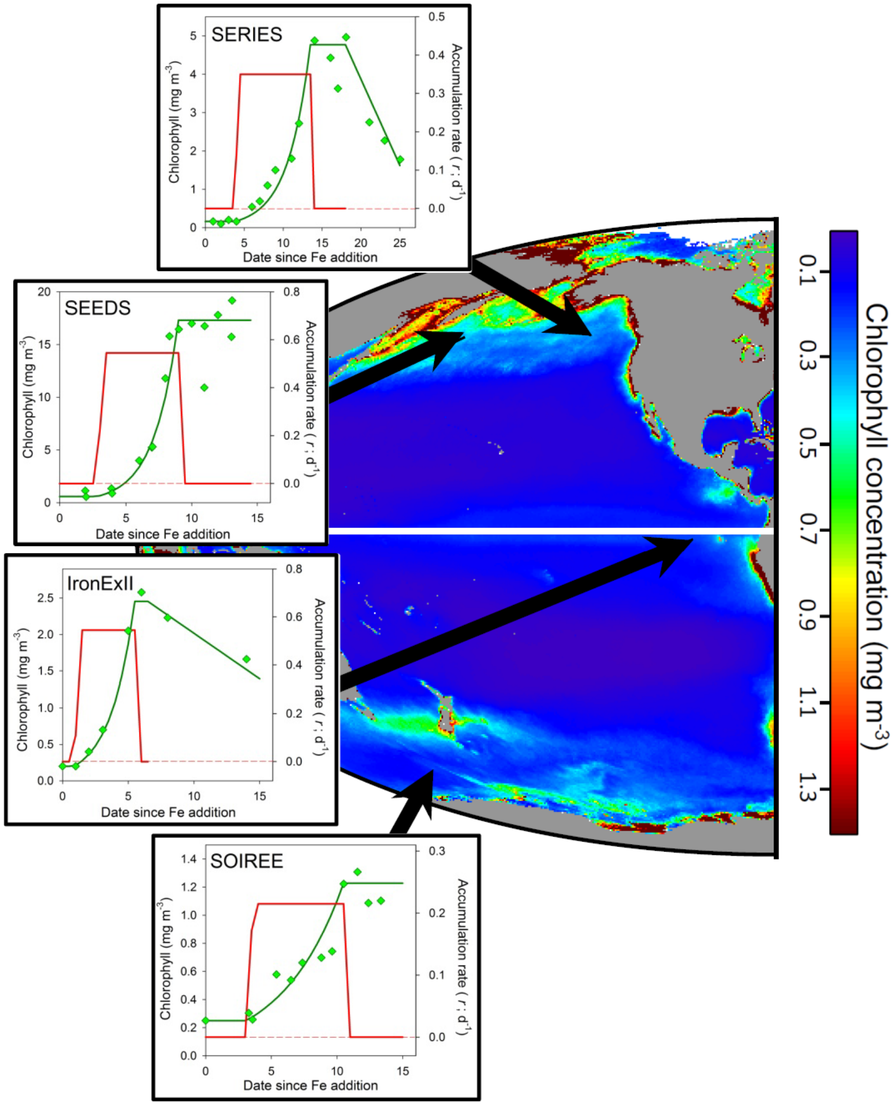


- In the subarctic Atlantic, the blooming season can begin from a physical disturbance of division-loss balance (while division rates are still declining)

- What about an iron-enrichment bloom?

  - clearly a poster child example of a 'bottom up' generated bloom…

Iron-induced blooms



… the figure …

Behrenfeld & Boss 2014 Annu. Rev. Mar. Sci. 6:167-194

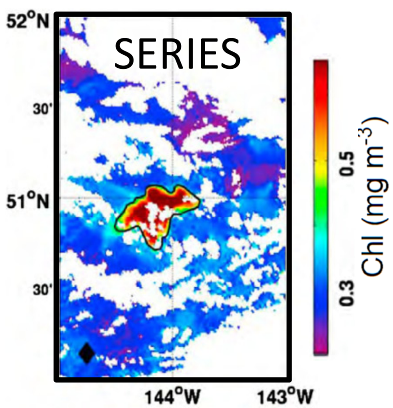
Notes:

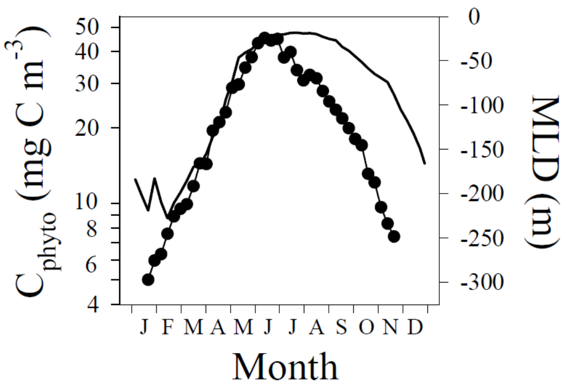
4. Focsing on changes in concentration alone can be dangerous (remember to think about how physical processes can mask a blooming population)

5. Disturbance initiates blooms, but can take different forms

6. Plankton ecosystems have a strong propensity to re-equilibrate following a disturbance

Fly in the ointment





[Question] If loss rates can catch up within a week or so following the major increase in division rate associated with iron addition….

…. then what allows a natural bloom, such as in the subarctic Atlantic, to keep going for months?

Behrenfeld & Boss 2014 Annu. Rev. Mar. Sci. 6:167-194

CHANGE: One of the 'common rules' ?

- [Idea] During blooming, phytoplankton *concentrations* can continue increasing so long as the rate of division continues to *increase*

- North Atlantic

  step 1: early winter conditions decouple division and loss (disturbance), mixed layer biomass increases but concentrations do not (no response of loss rates)

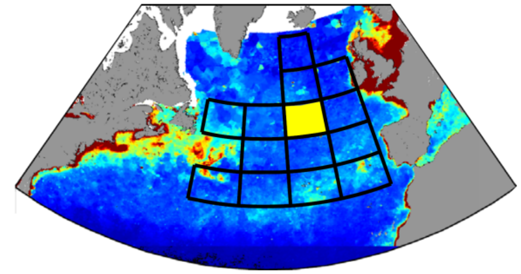
  step 2: convective mixing ends, concentrations increase, grazing/other losses respond

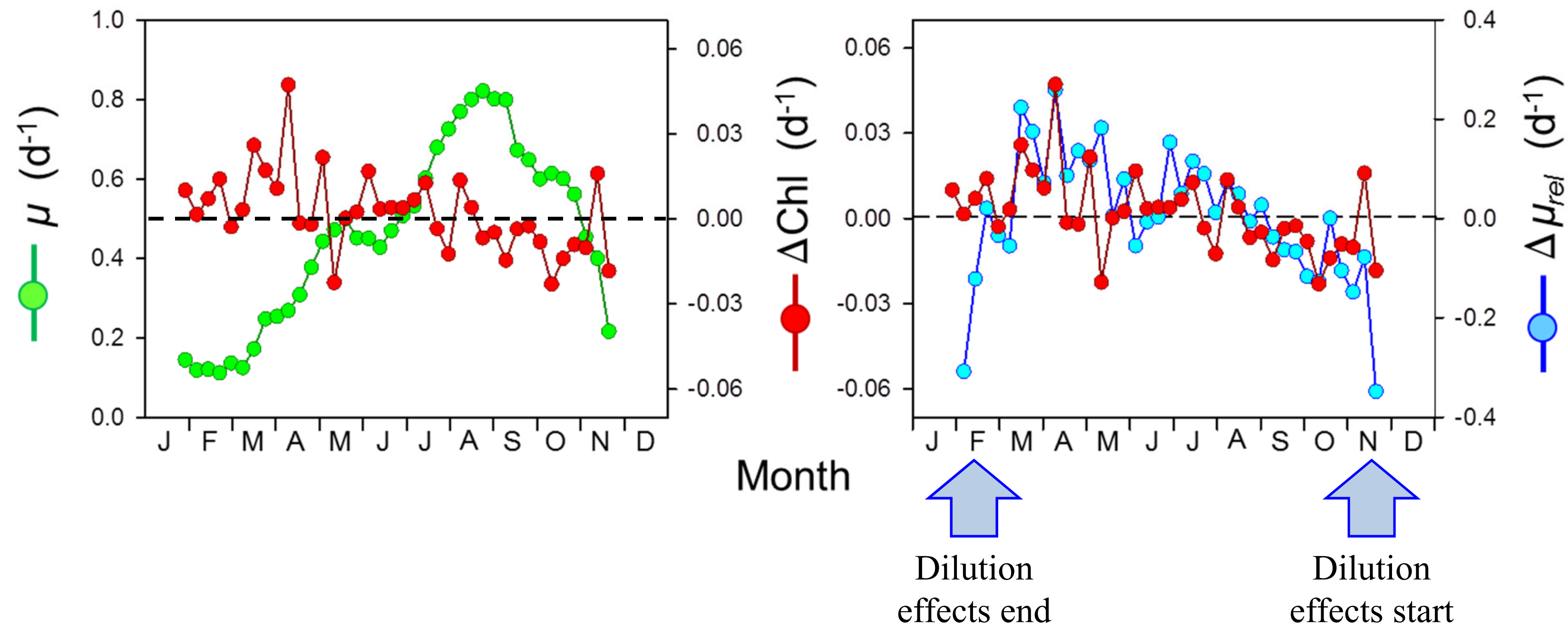
  step 3: (unlike Fe+) division rates continue to accelerate, decoupling sustained despite rising loss rates

  step 4: blooming phase continues until division rates reach maximum or become resource limited, losses catch up, bloom reaches climax and terminates

Prediction: Post-convective mixing, phytoplankton concentration changes reflect relative accelerations and decelerations (i.e., changes) in division rate

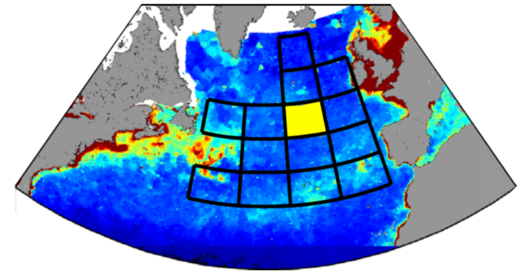
North Atlantic data

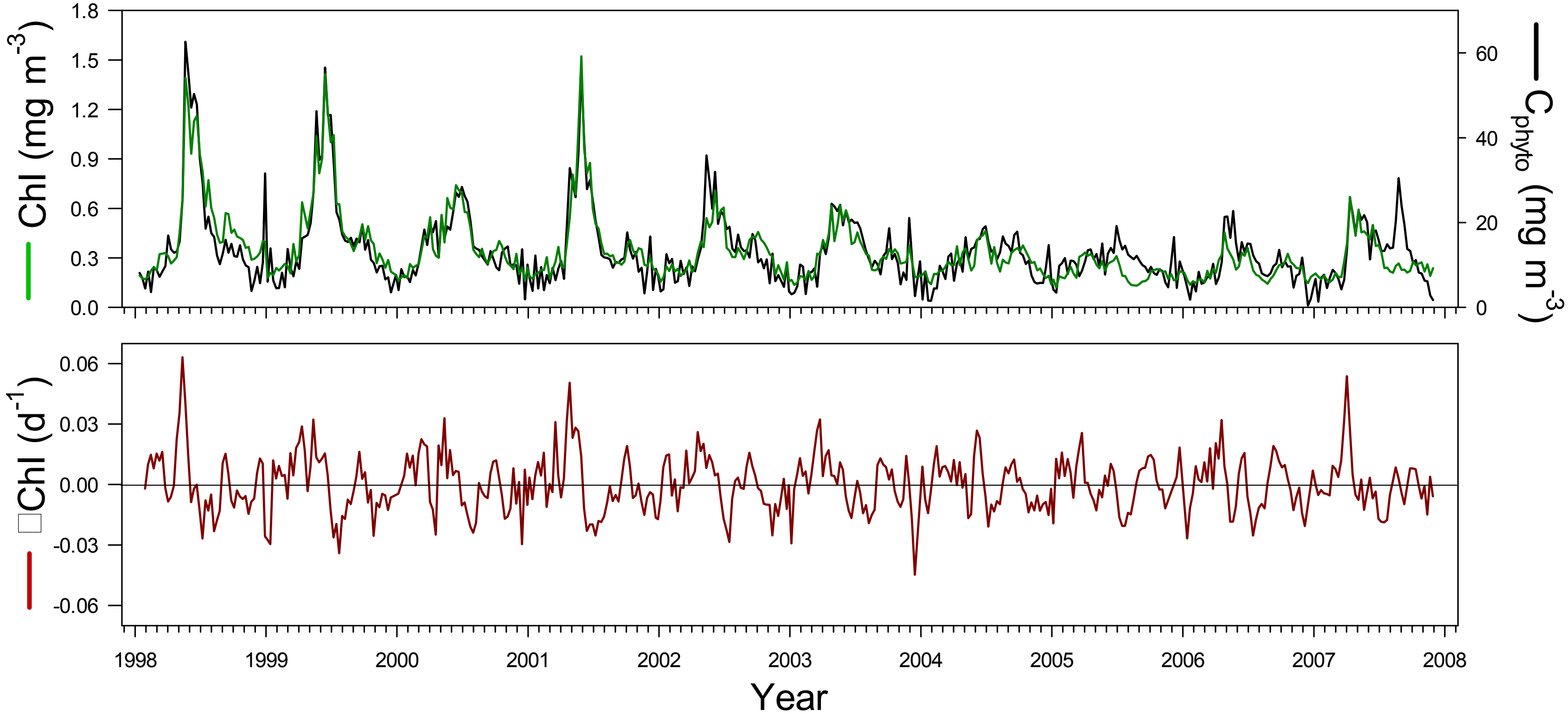




Behrenfeld 2014 Nature Climate Change, doi:10.1038/NCLIMATE2349

North Atlantic data





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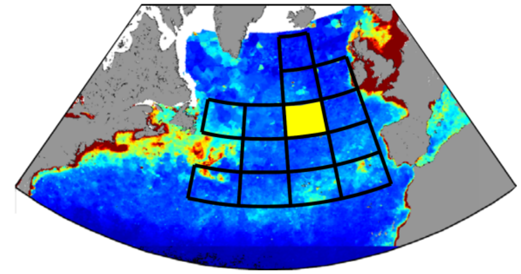
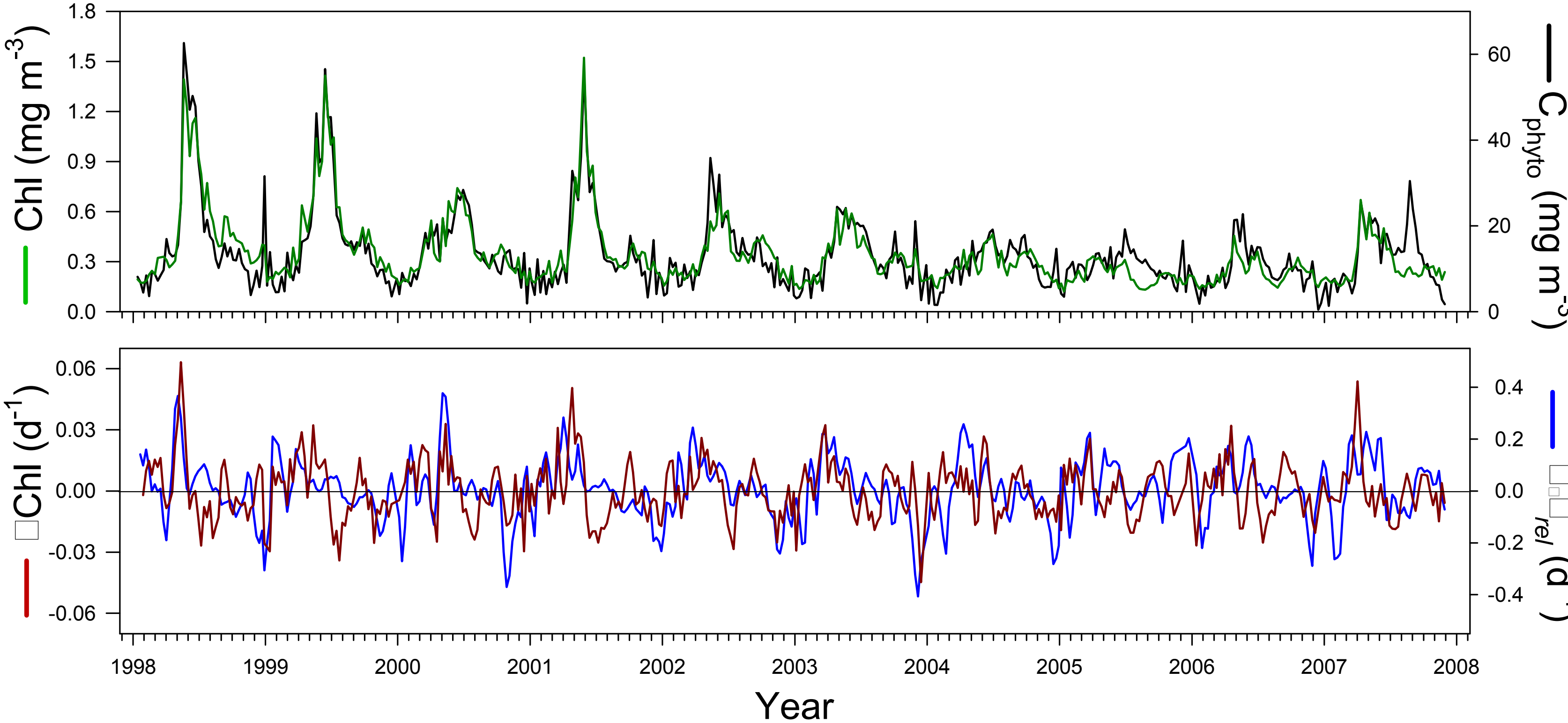


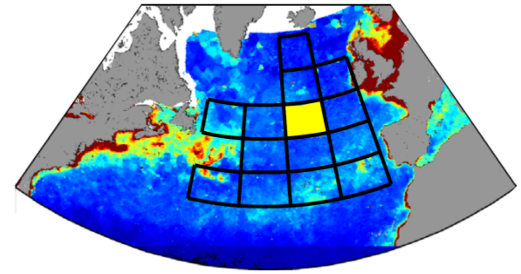


Behrenfeld 2014 Nature Climate Change, doi:10.1038/NCLIMATE2349

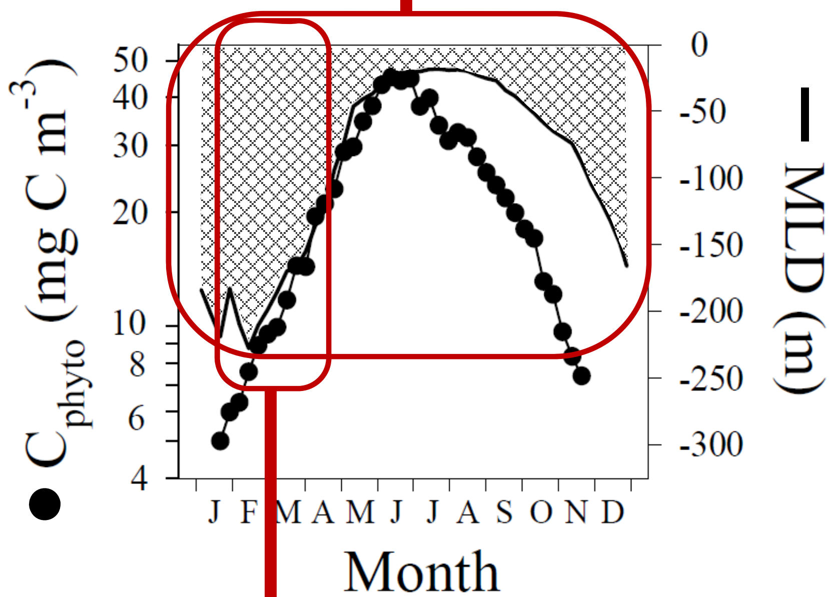
Notes:

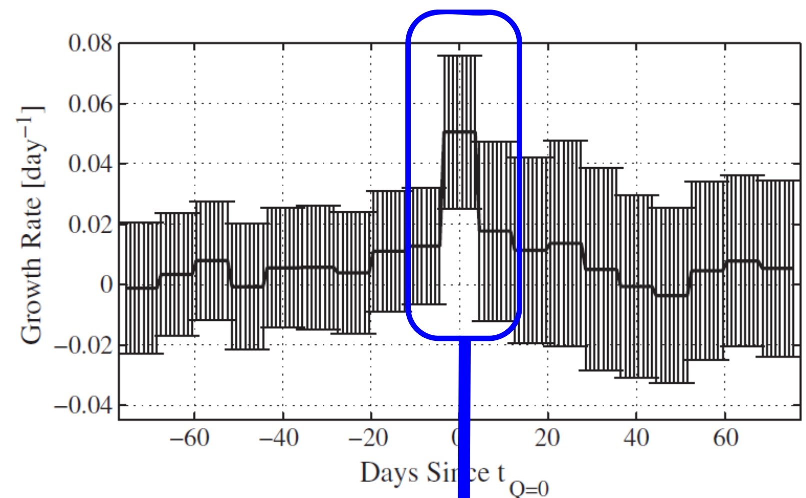
7. Phytoplankton concentrations change in response to accelerations and decelerations in division rate

Mixing vs Mixed Layer



Uncertainty in mixing depth introduces uncertainty in division rate changes



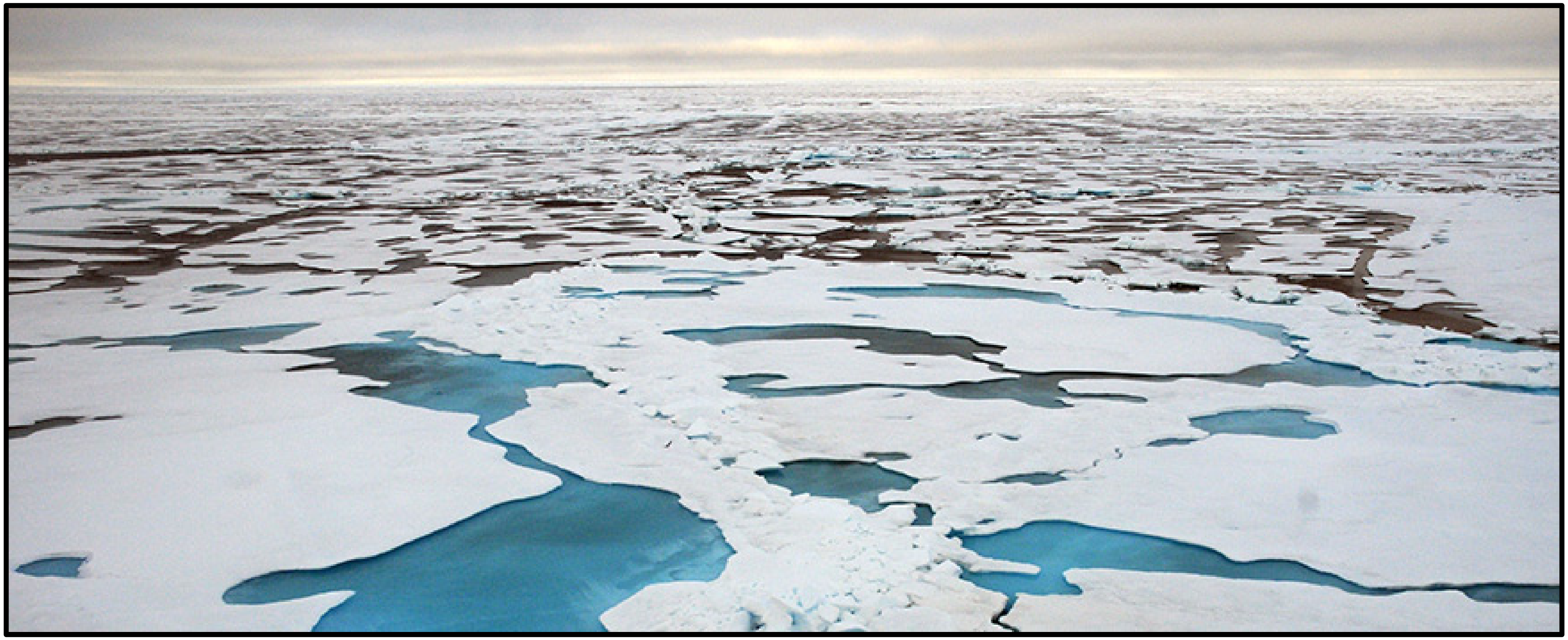


Rapid change in mixing =
Rapid change in division =
Enhance rate of change in accumulation

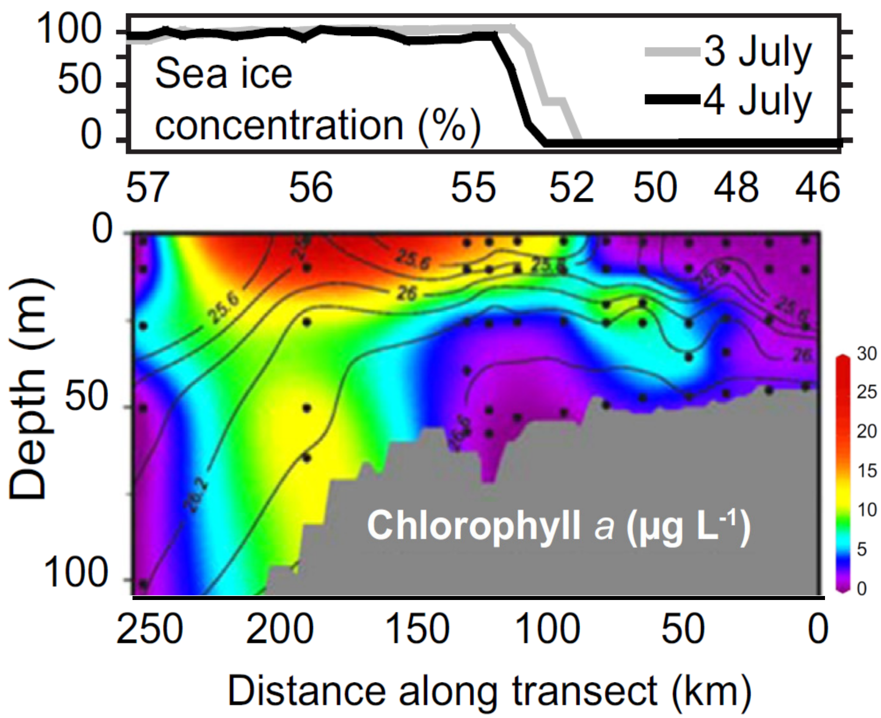
Potential errors are particularly large shortly after convective mixing ends

R. Ferrari et al. / Journal of Marine Systems 147 (2015) 116–122

What about other types of blooms?



Under-ice blooms



- ICESCAPE, Chukchi Sea
- Division rate @ sea-ice interface ~0.9 d^{-1}
- [Chl] ~ 20 - 30 ug L^{-1}
- Euphotic depth ~ 10 m
- Mixing depth ~ 10 m

Mixed layer population doubling time: once every ~ 4+ days

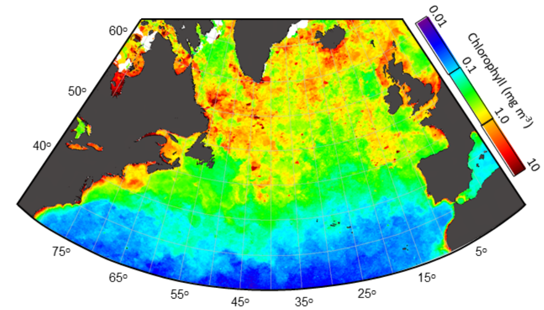
- Is this an example of a bloom where increases in concentration were sustained despite decreasing division rates?
- Light history?
- Grazers simply couldn't respond?

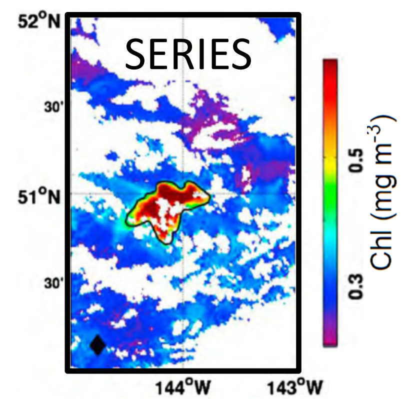
K.R. Arrigo et al. / Deep-Sea Research II 105 (2014) 1–16

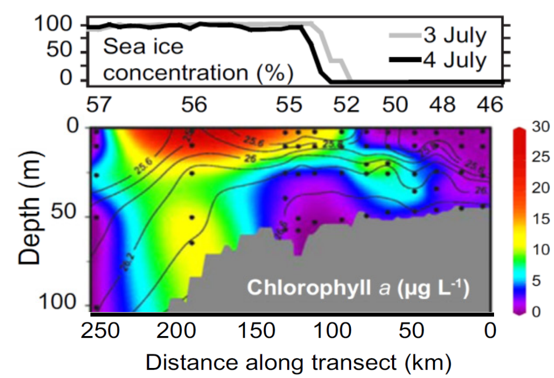
Rules to the Game

- Blooms differ in their form, composition, duration, and cause of initiation
- Blooms appear to start in response to disturbances in predator-prey relationships,

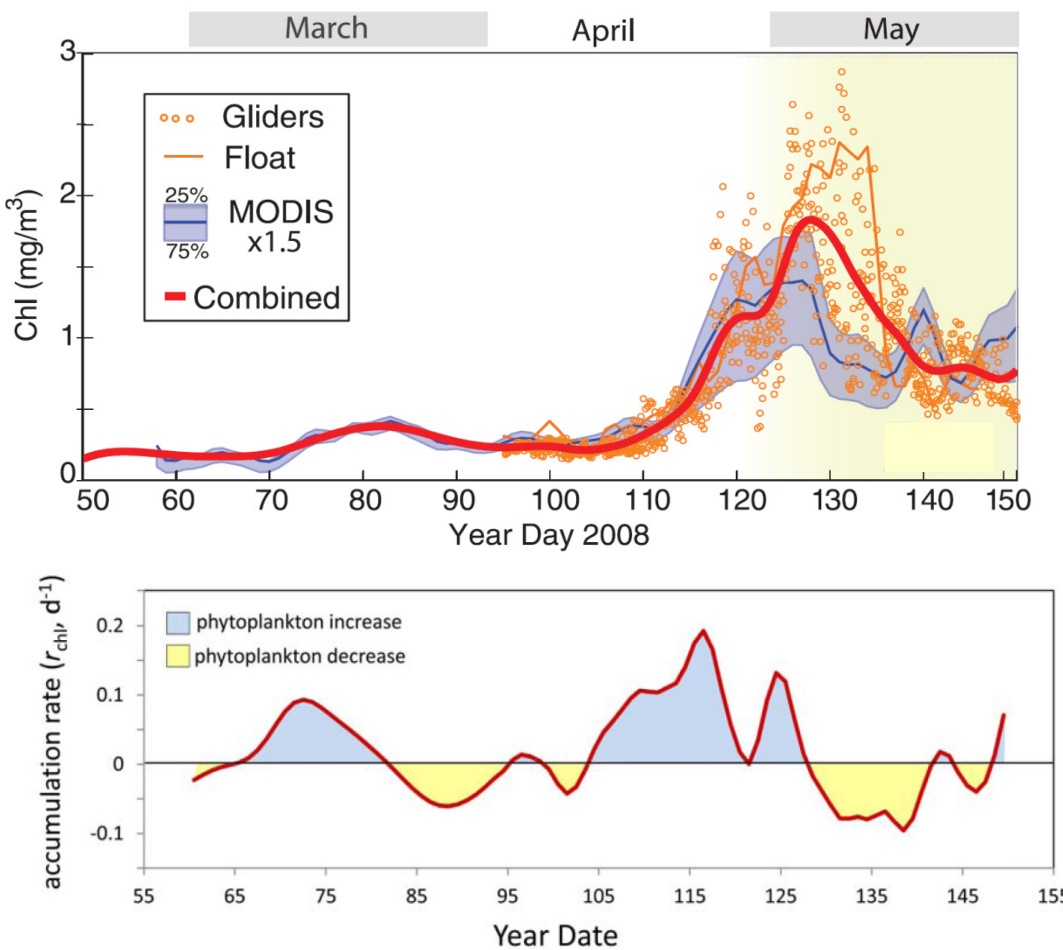
  e.g., population dilution (e.g., N. Atlantic), a change in division rate (e.g., iron addition), growth opportunities out of phase with loss processes (melt ponds and low temp), rapid loss of grazers (e.g., carn. zoop. swarm?)
- Blooming persists so long as division rates accelerate (??), but the fraction escaping losses declines
- Blooming ends when division rates remain constant or decline, allowing losses to catch up
- Blooms do not require rapid division rates
- Models should be evaluated against **rates**…







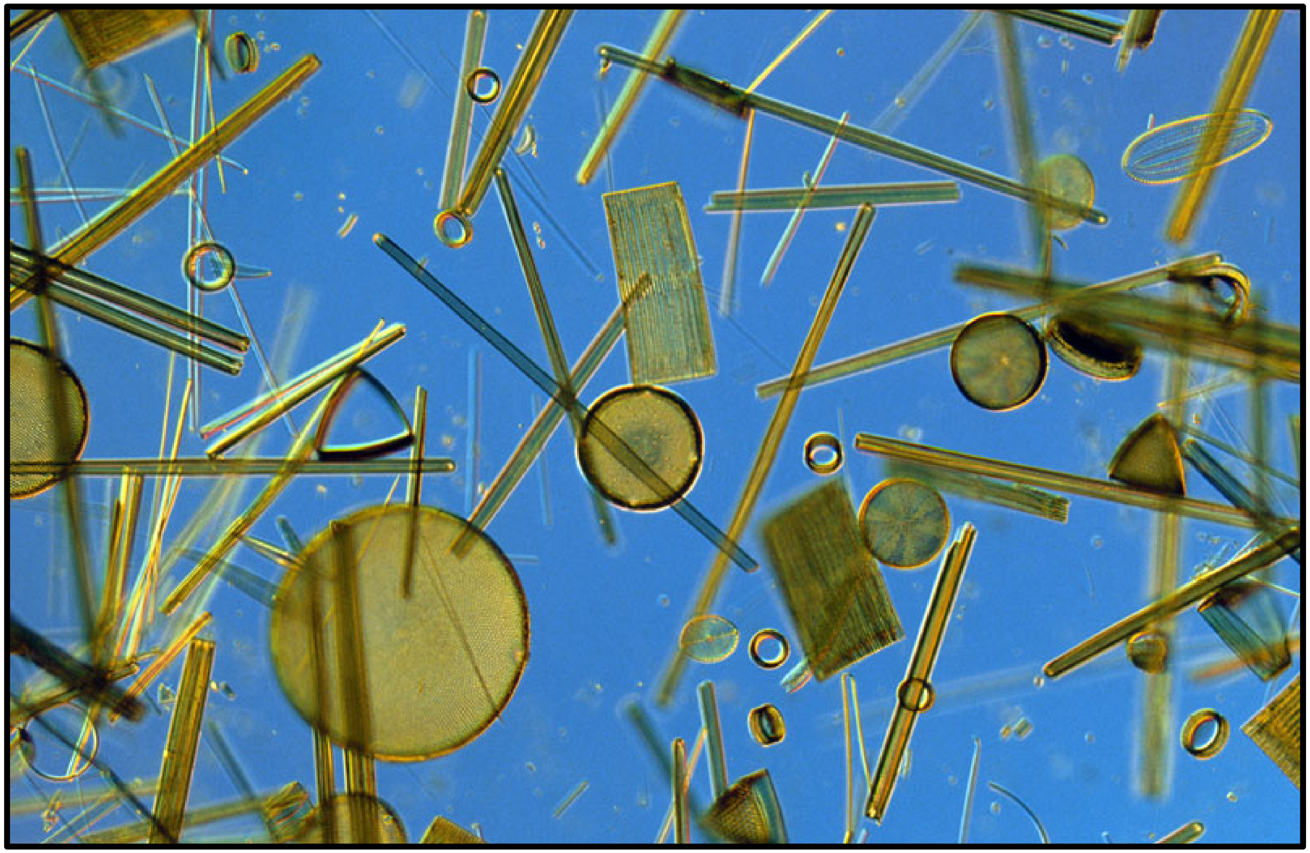
Random thoughts: If the subarctic Atlantic blooming phase lasts for many months, why is the climax in the spring/summer?



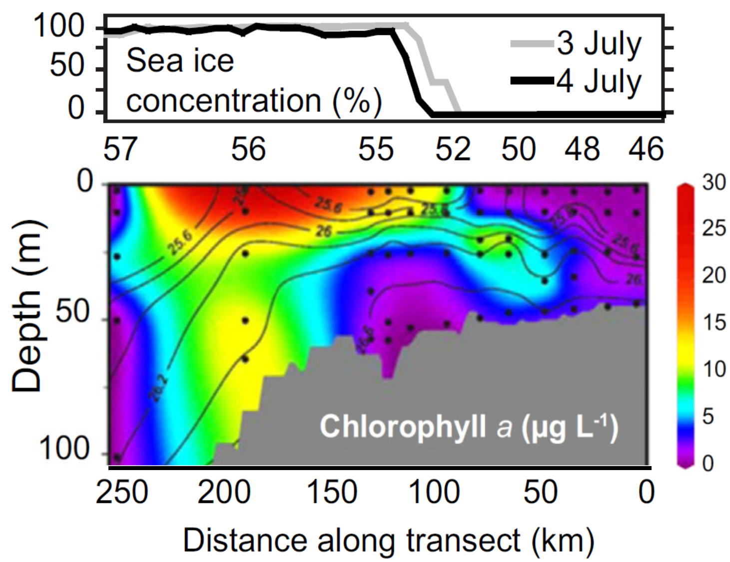
Mahadevan et al. 2012 Science 337: 54-58

Behrenfeld & Boss 2014 Annu. Rev. Mar. Sci. 6:167-194

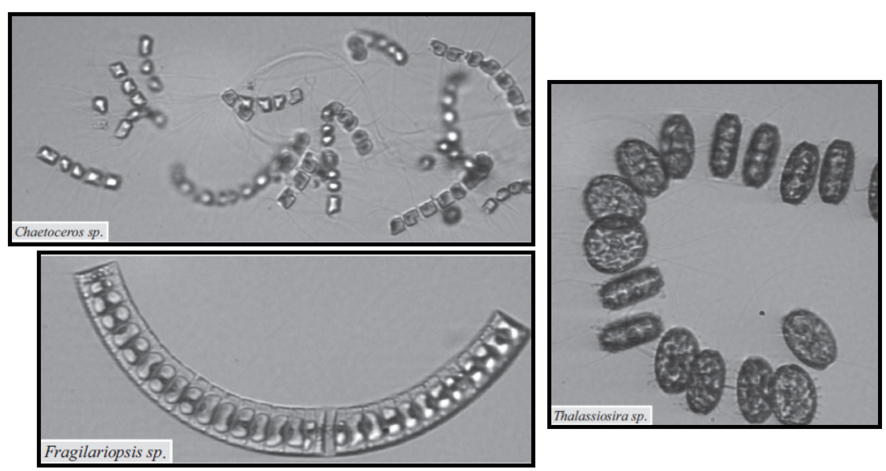
Random thoughts: Why do diatoms often dominate the climax community?



Random thoughts: Why do diatoms often dominate?



- Three diatoms dominated
- Temperature < $0^{o}C$
- Average ML division rate ~ $0.15\ d^{-1}$
- $P^{b}_{max} = 1.35$ mg C $(mg\ Chl\ h)^{-1}$
- E_k ~ 65 µmol photons $m^{-2}\ s^{-1}$



S.R. Laney, H.M. Sosik / Deep-Sea Research II 105 (2014) 30–41

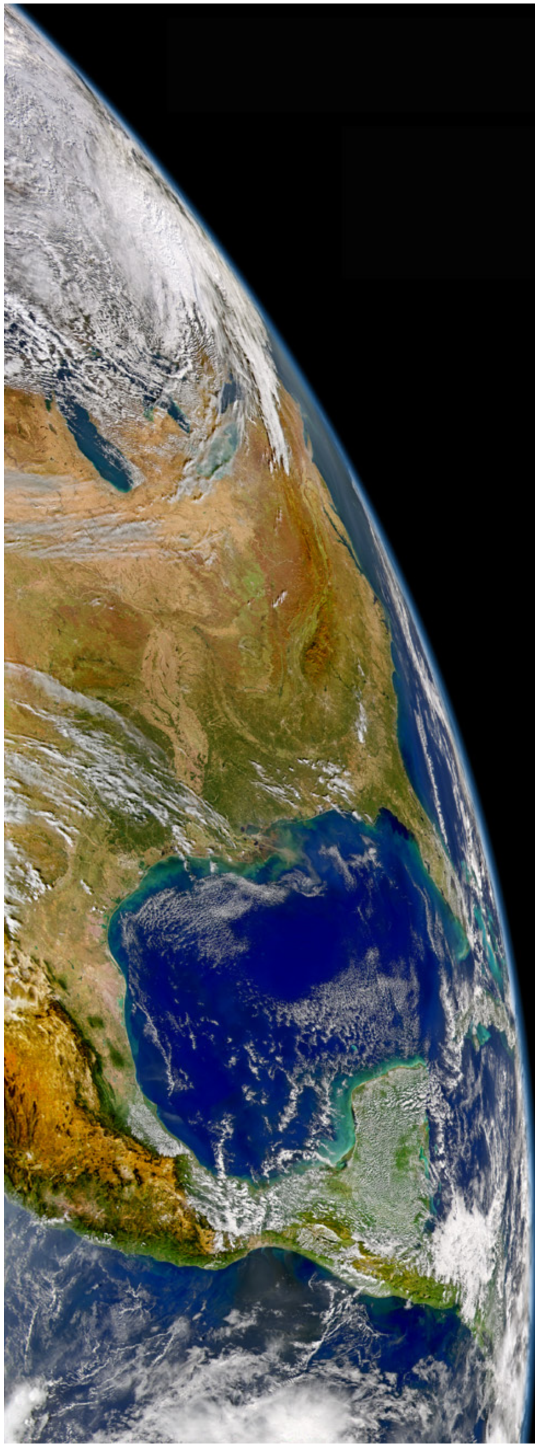
K.R. Arrigo et al. / Deep-Sea Research II 105 (2014) 1–16

Random thoughts

- Martha's Vineyard record (Heidi Sosik): Monotonic increase in chlorophyll, rapid succession of dominance
- Extremely selective losses: Grazers + Viruses?
- To become uncommonly abundant, do you first need to be uncommonly rare?
- Do diatoms have an advantage during prolonged blooming conditions because of their ability to continue accelerating?
- What if winter mixing is dampened in the future?

Summary

… RATES …



This work has been supported by NASA's Ocean Biology and Biogeochemistry Program

THANK YOU

Backup Slides

- NAAMES
- r:mu ratio
- NA float data
- a gambling man
- r is really small