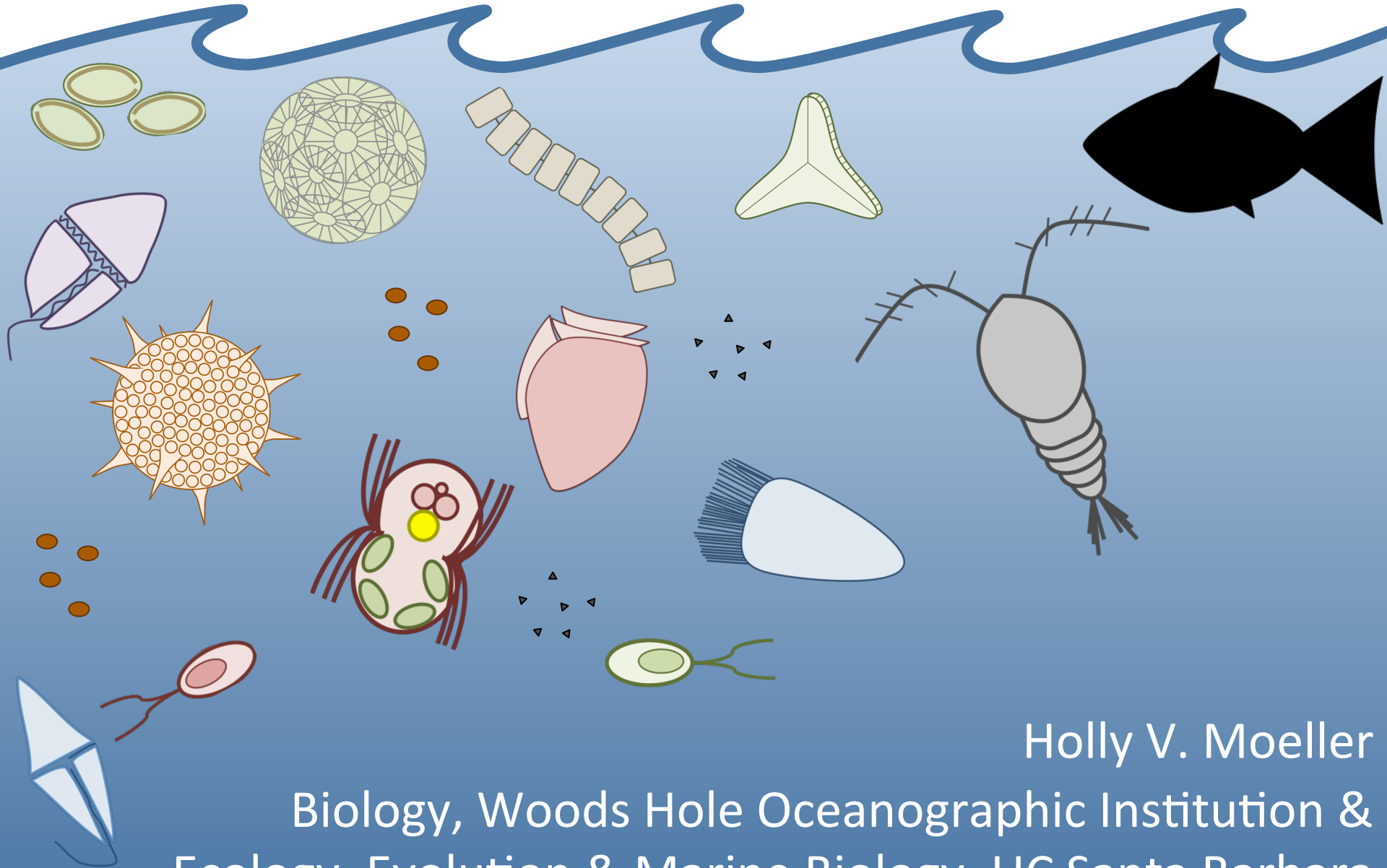
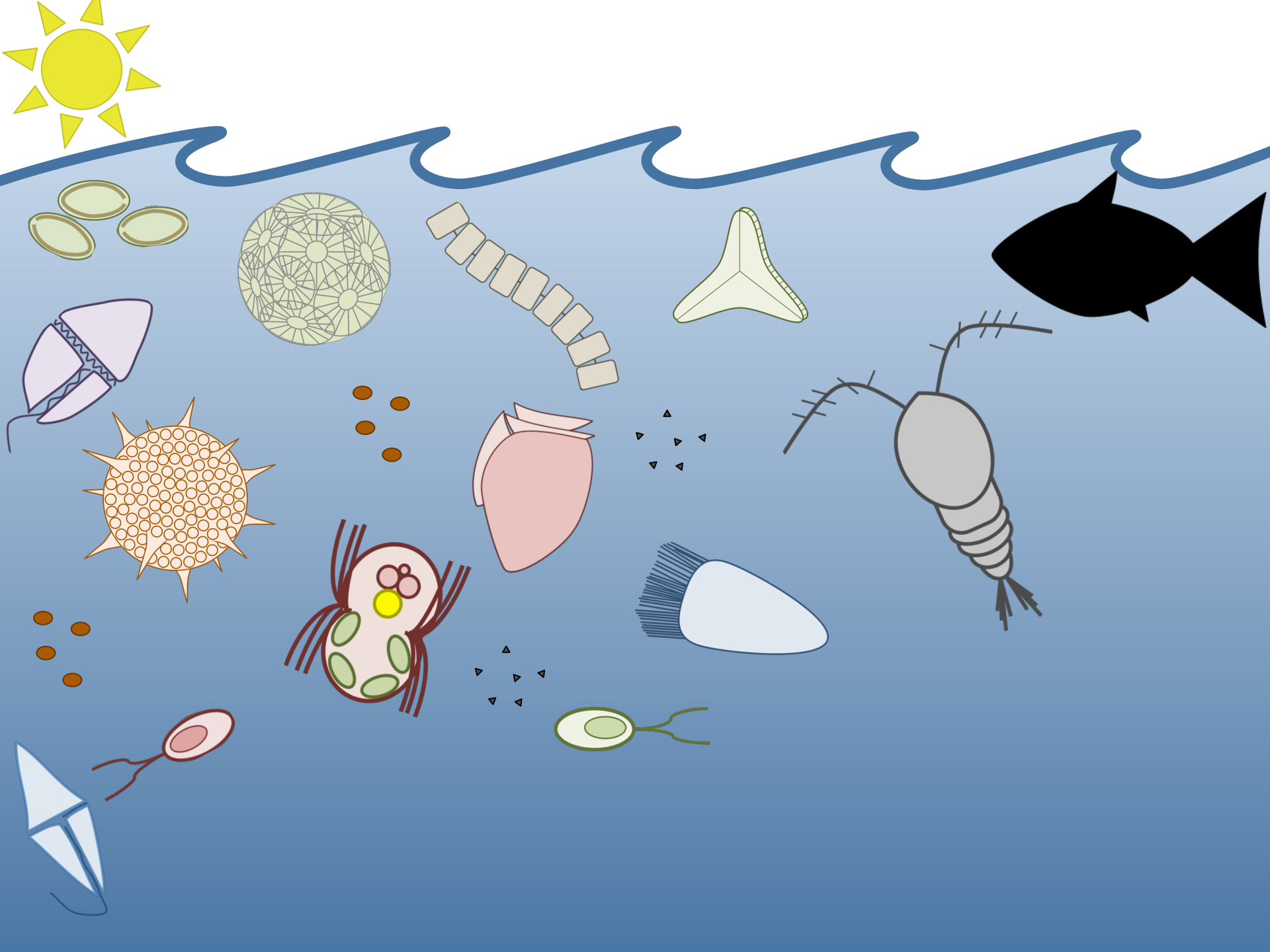


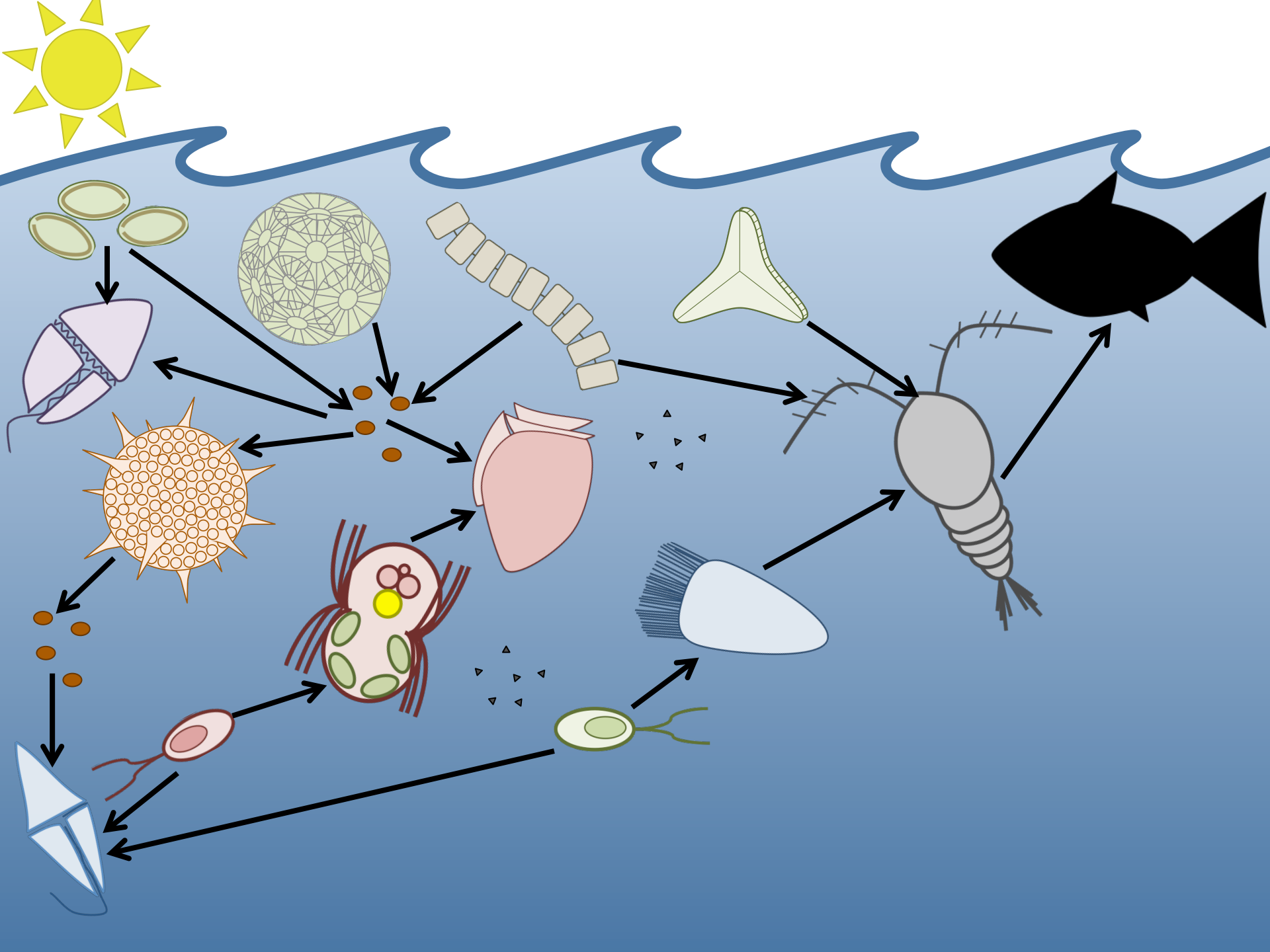
# Mixotrophic Modulators of the Biological Pump

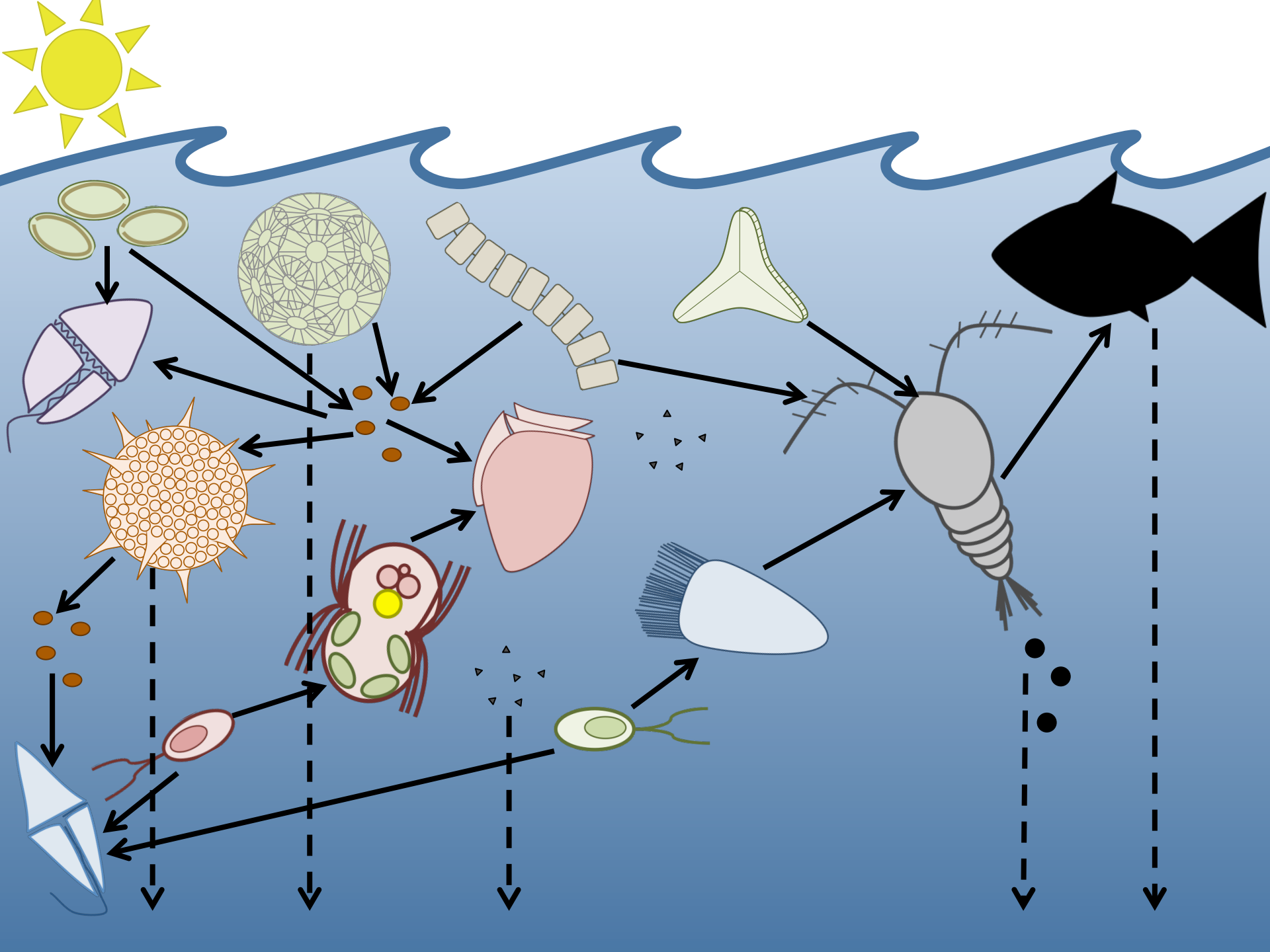


Holly V. Moeller

Biology, Woods Hole Oceanographic Institution &  
Ecology, Evolution & Marine Biology, UC Santa Barbara

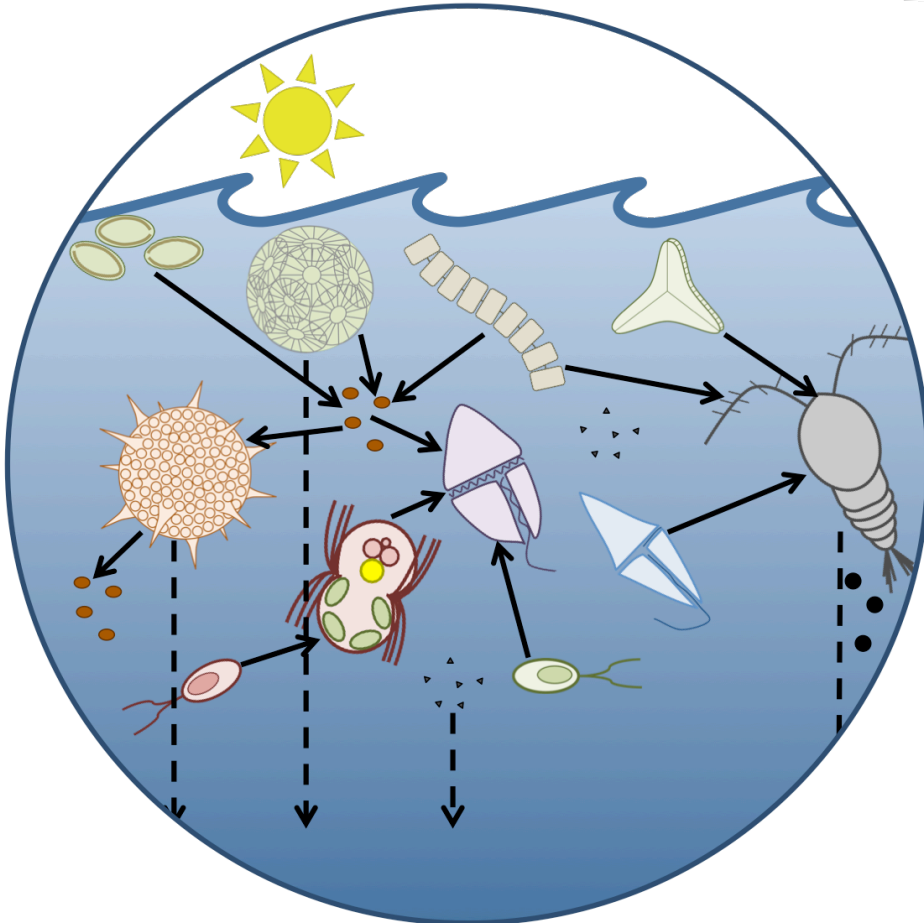




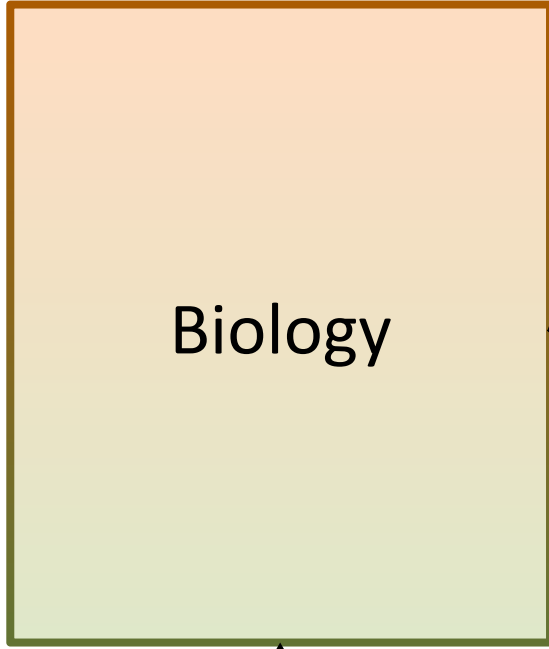




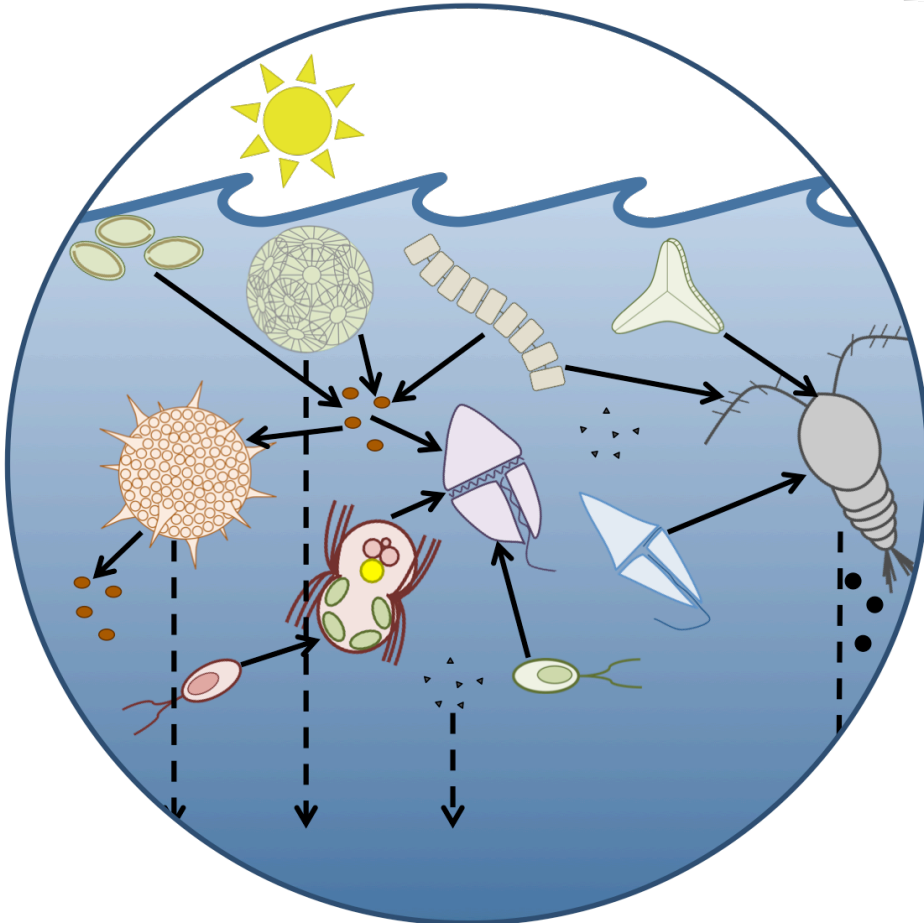
# How complicated should we get?



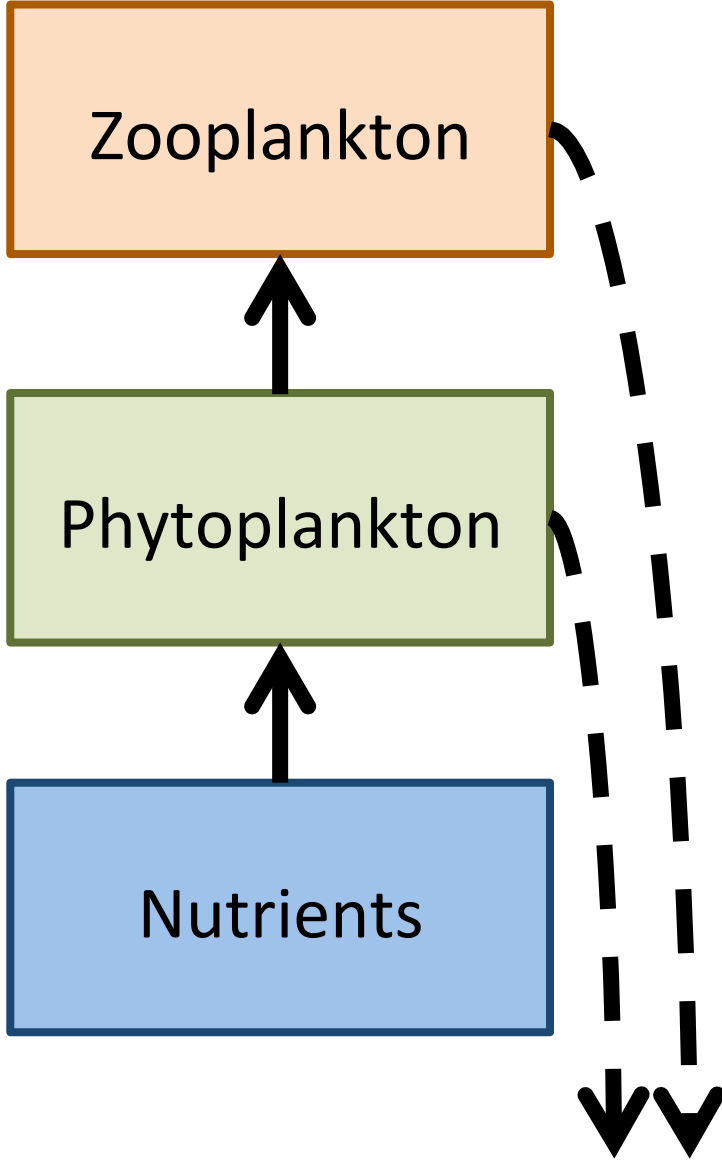
**vs.**



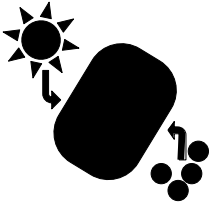
# How complicated should we get?



vs.

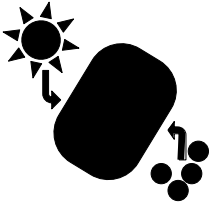


# Mixotrophic Modulators of the Biological Pump



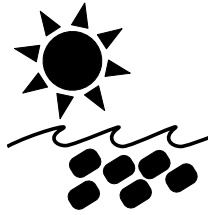
What is a mixotroph?

# Mixotrophic Modulators of the Biological Pump



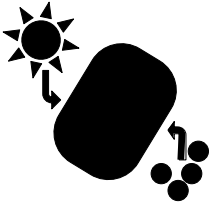
What is a mixotroph?

Impacts on the  
Biological Pump



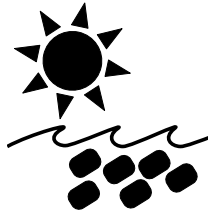
How mixotrophs modulate  
primary productivity

# Mixotrophic Modulators of the Biological Pump

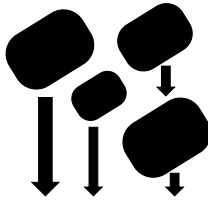


What is a mixotroph?

Impacts on the  
Biological Pump

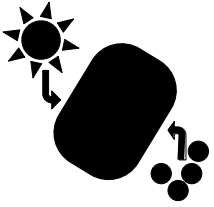


How mixotrophs modulate  
primary productivity



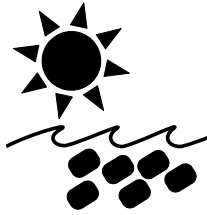
How mixotrophs modulate  
particle flux

# Mixotrophic Modulators of the Biological Pump

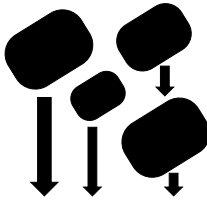


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity

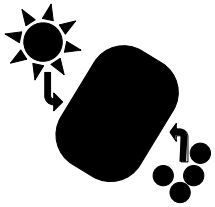


How mixotrophs modulate  
particle flux



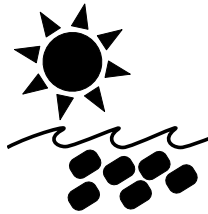
How mixotrophs modulate  
reminereralization rates

# Mixotrophic Modulators of the Biological Pump

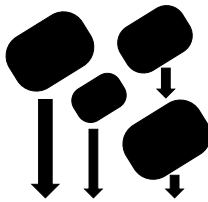


What is a mixotroph?

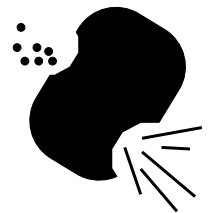
Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



How mixotrophs modulate  
particle flux



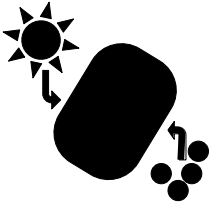
How mixotrophs modulate  
reminereralization rates



Where and when should mixotrophs matter?

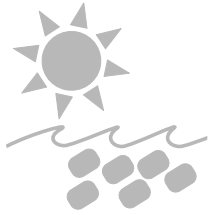


# Mixotrophic Modulators of the Biological Pump

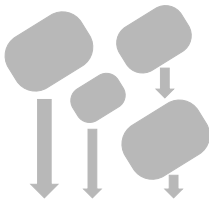


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



How mixotrophs modulate  
particle flux

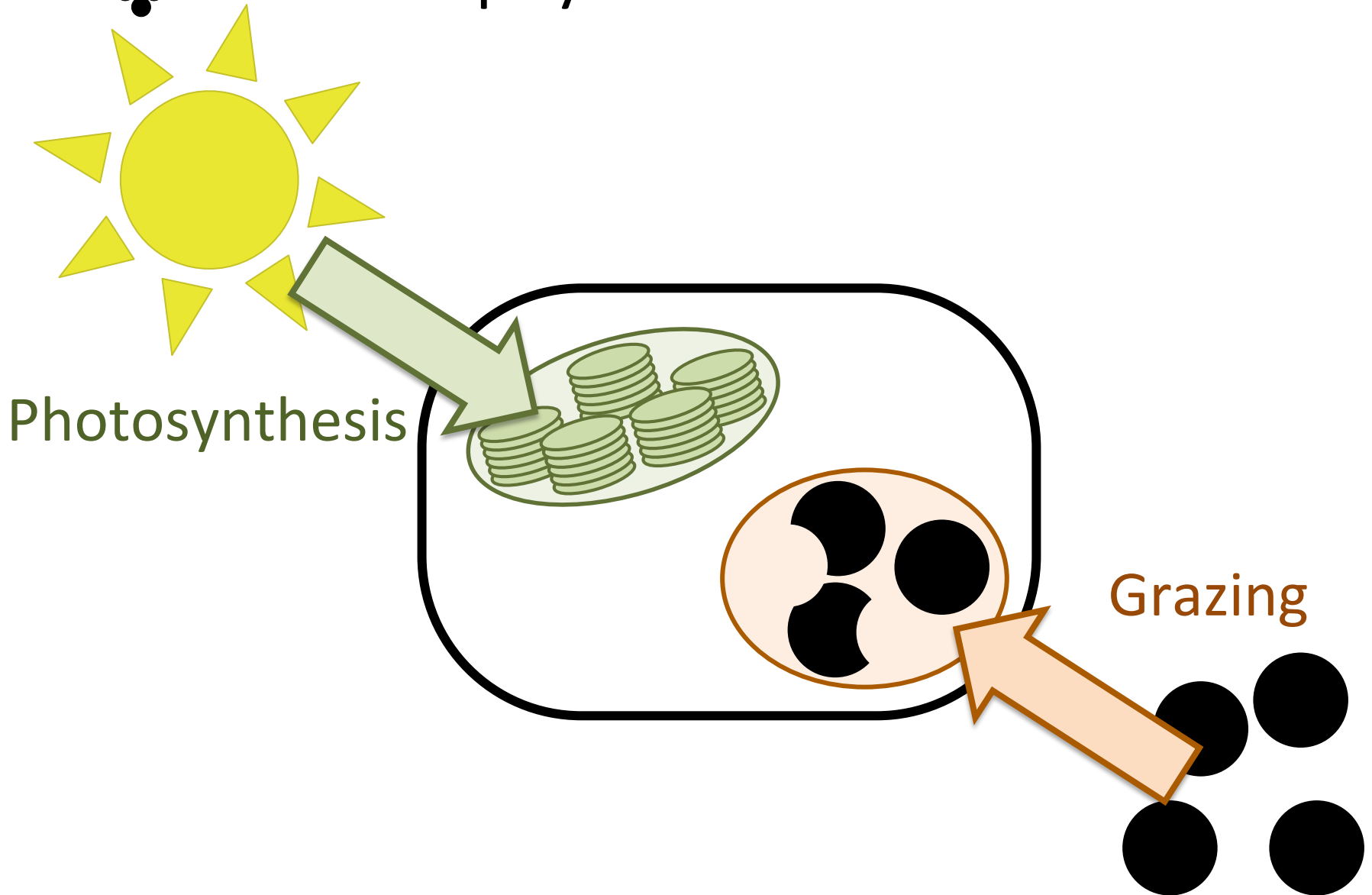


How mixotrophs modulate  
remineralization rates

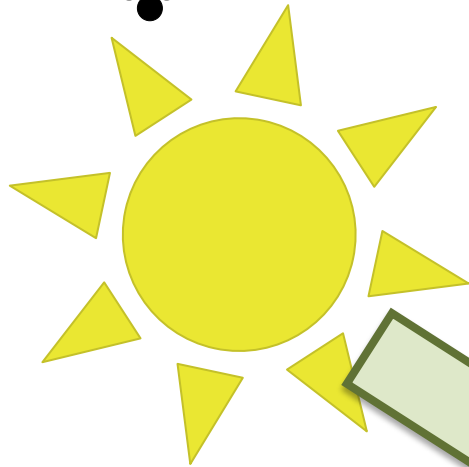
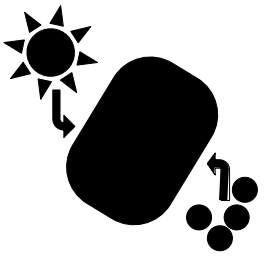


Where and when should mixotrophs matter?

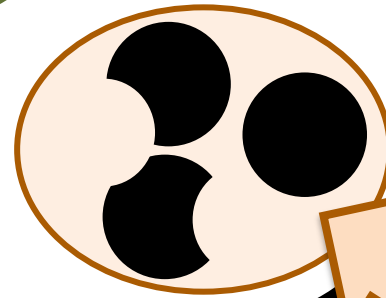
  Mixotrophs “mix” phototrophy and heterotrophy



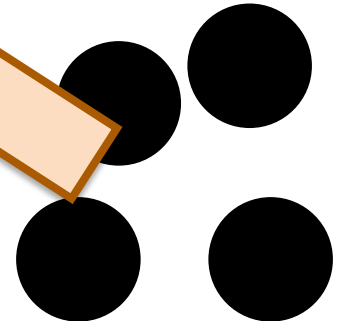
# Mixotrophs are “jacks of all trades”



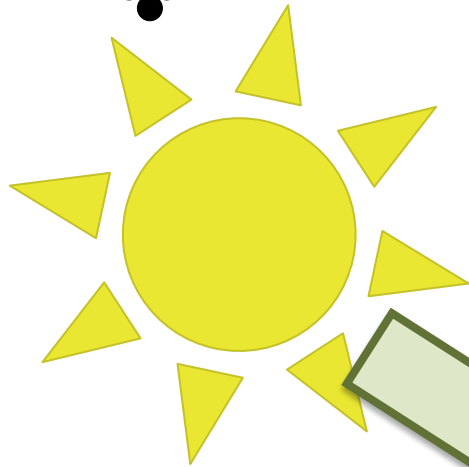
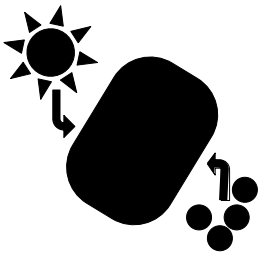
Photosynthesis



Grazing

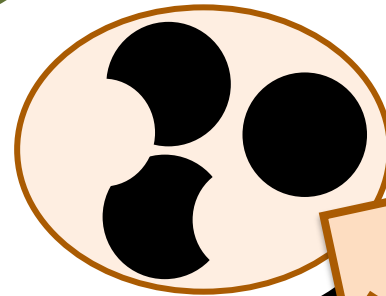


# Mixotrophs are “jacks of all trades”

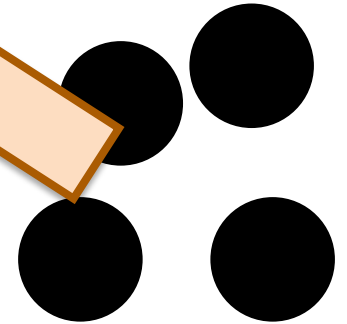


Photosynthesis

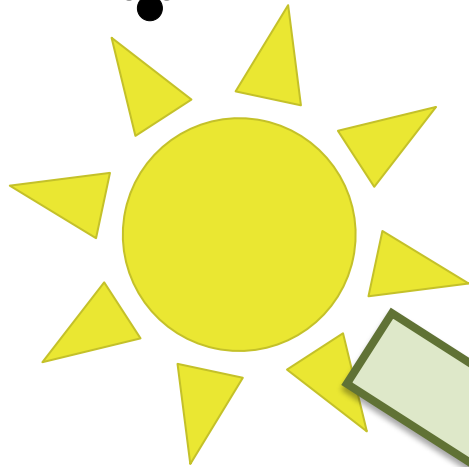
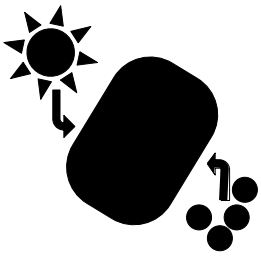
Carbon source  
when prey is  
limiting



Grazing

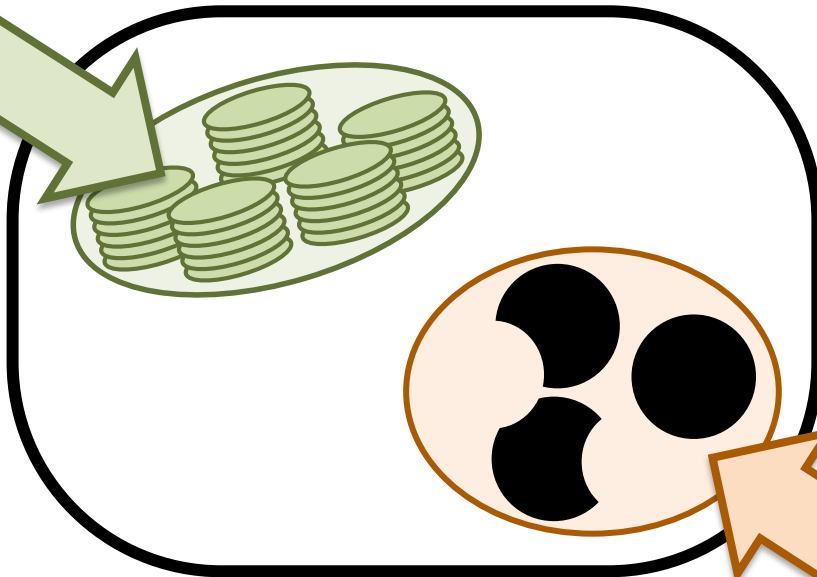


# Mixotrophs are “jacks of all trades”



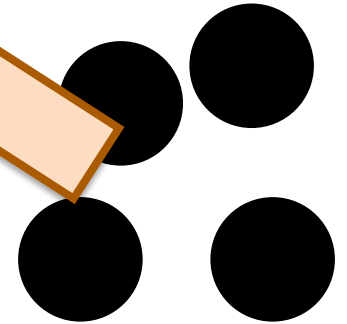
Photosynthesis

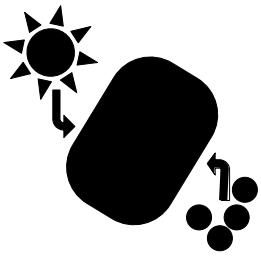
Carbon source  
when prey is  
limiting



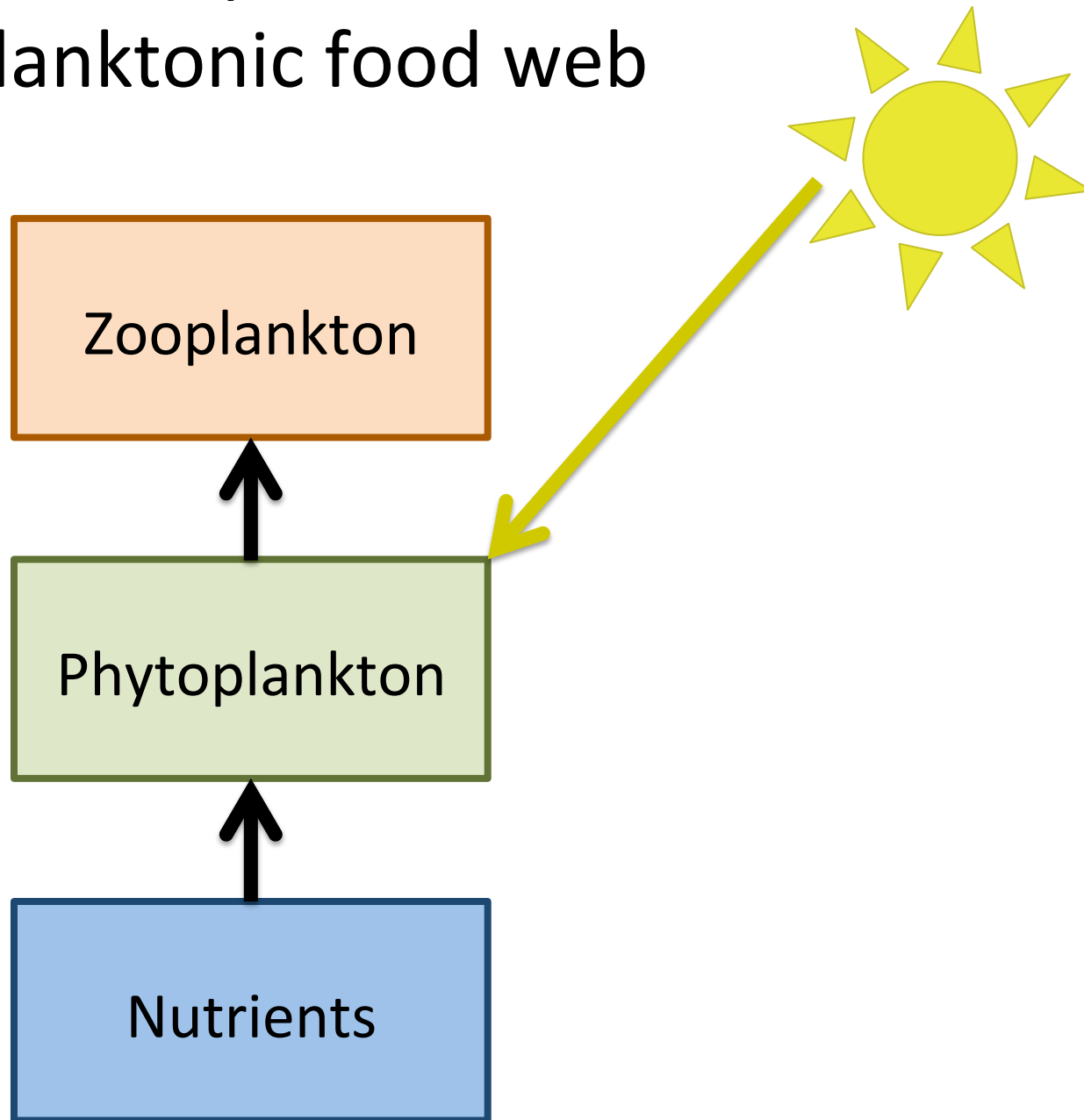
Nutrient source  
when nutrients  
are limiting

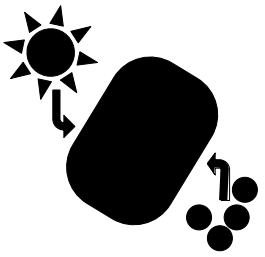
Grazing



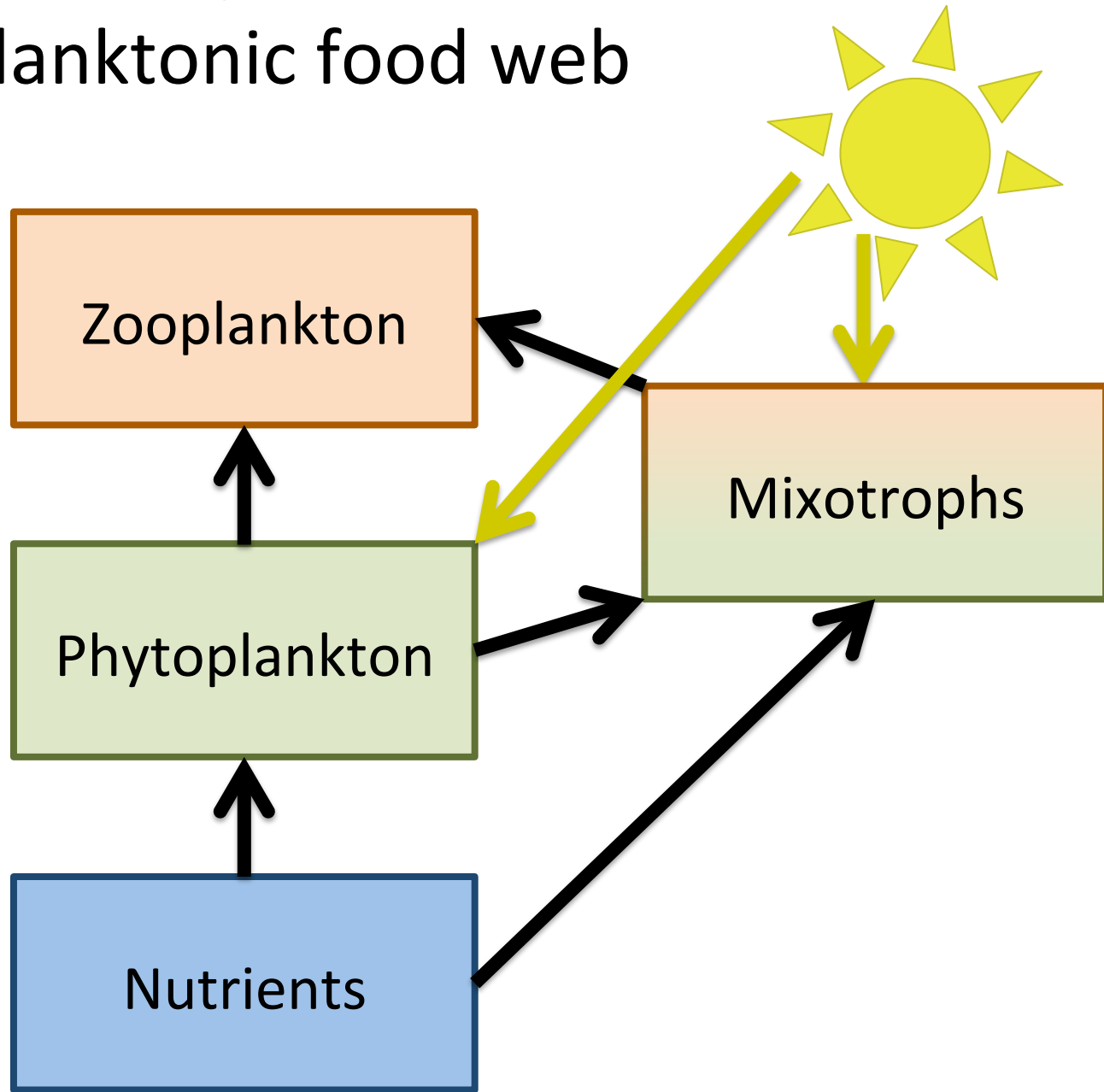


# Mixotrophs can “short-circuit” the planktonic food web

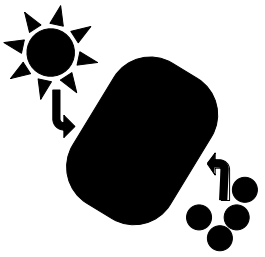




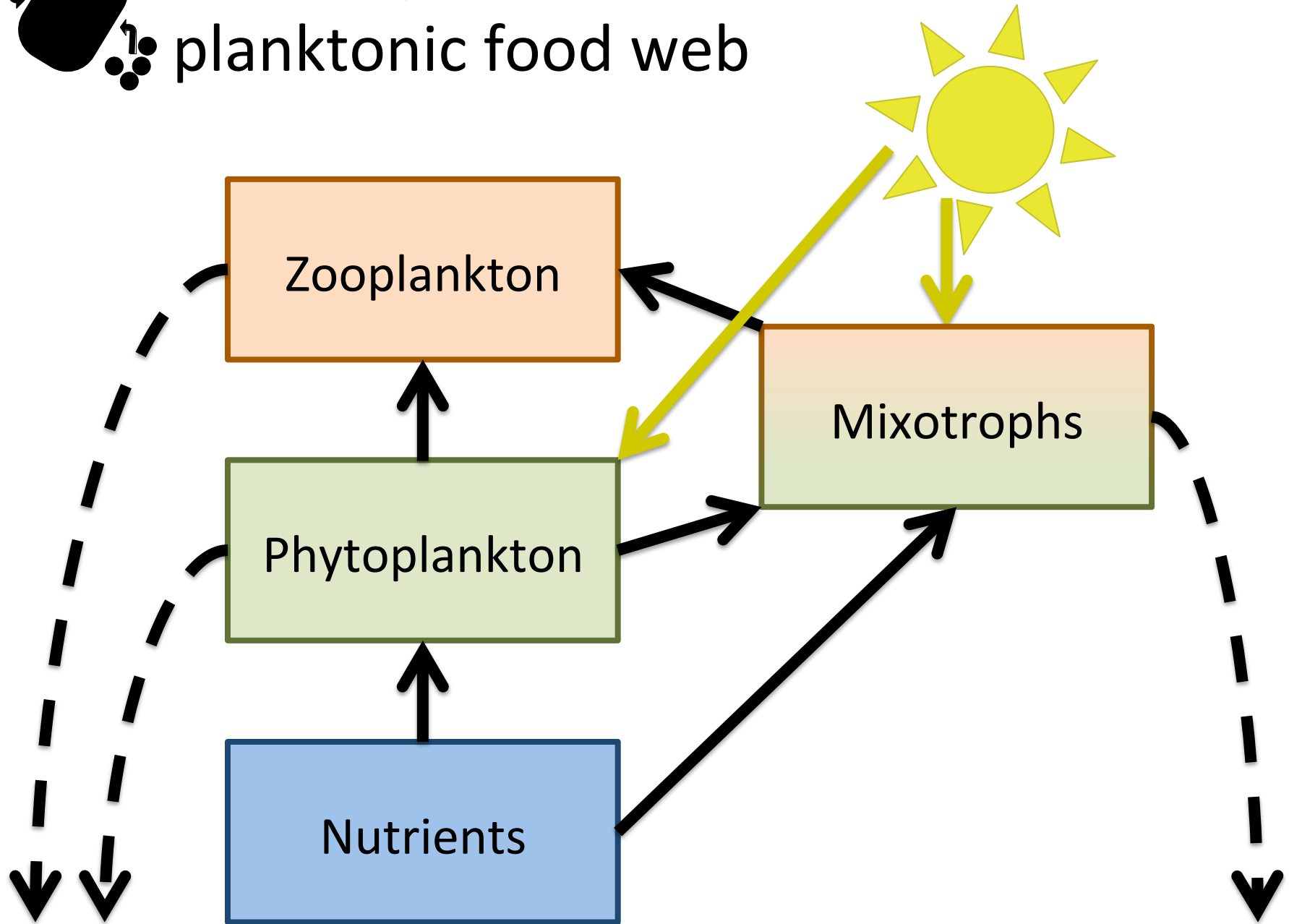
# Mixotrophs can “short-circuit” the planktonic food web



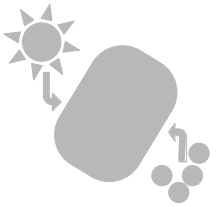




# Mixotrophs can “short-circuit” the planktonic food web

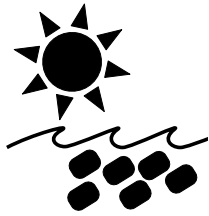


# Mixotrophic Modulators of the Biological Pump

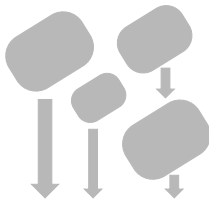


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



How mixotrophs modulate  
particle flux

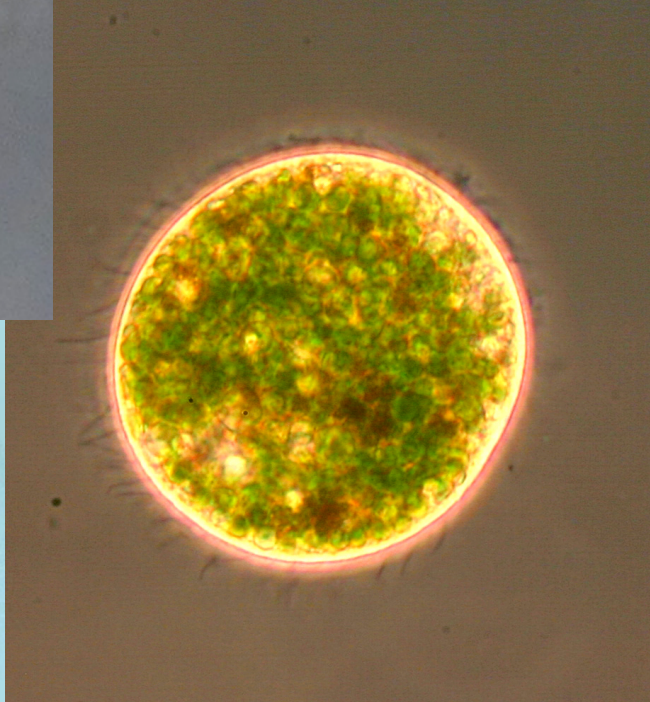
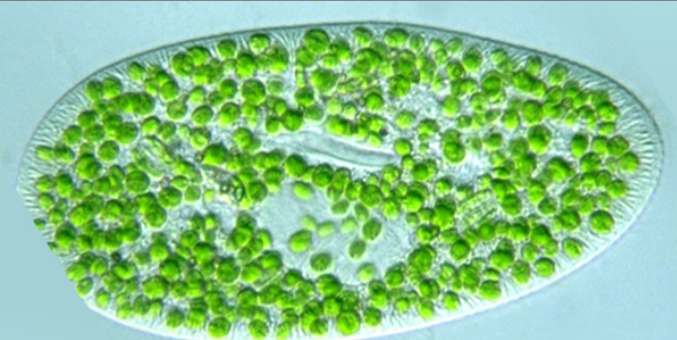
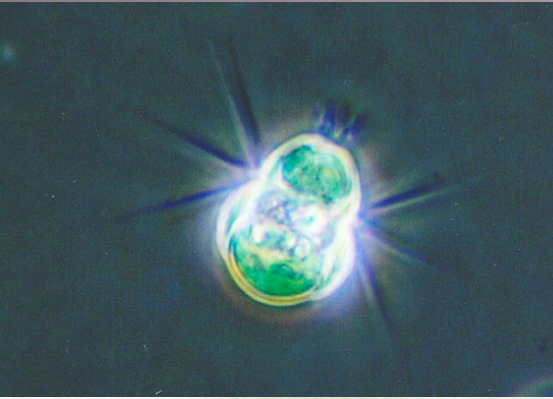
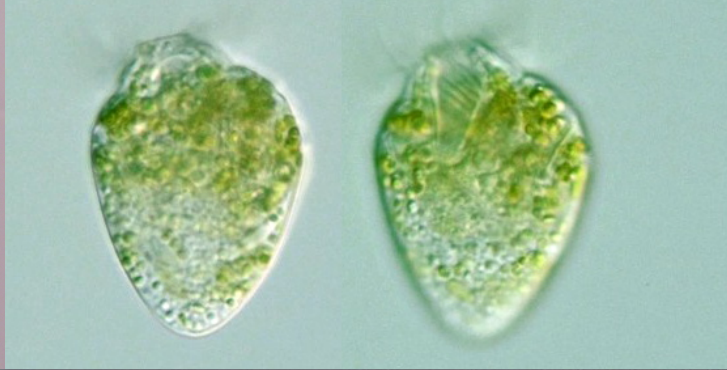
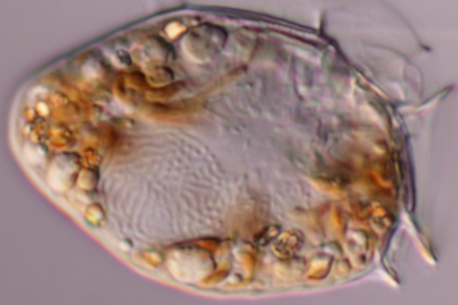


How mixotrophs modulate  
reminereralization rates



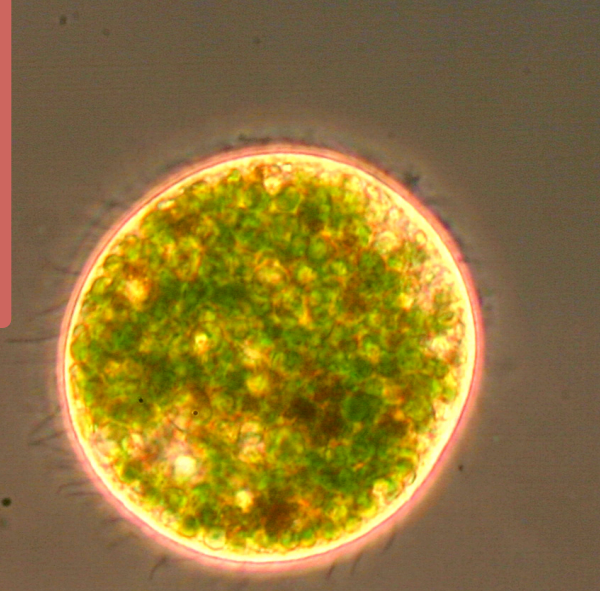
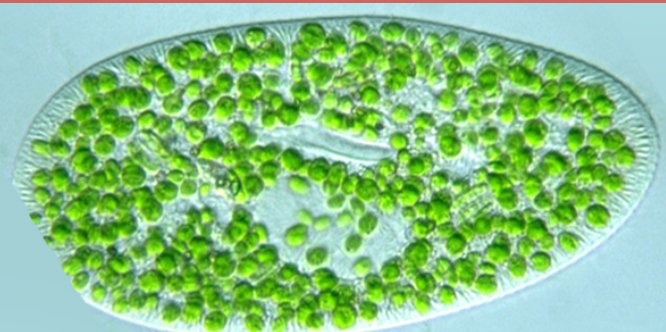
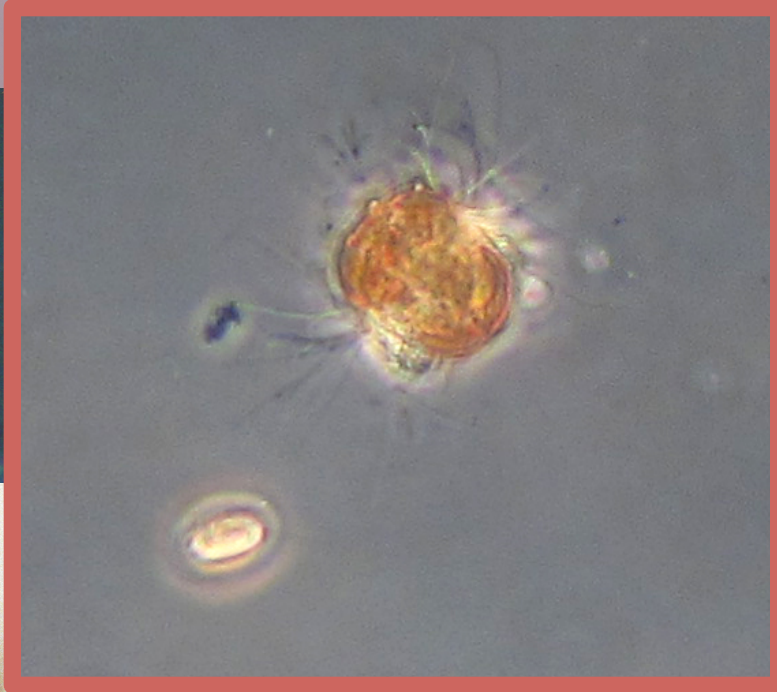
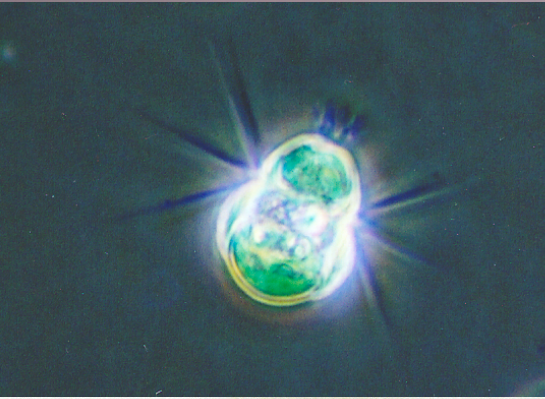
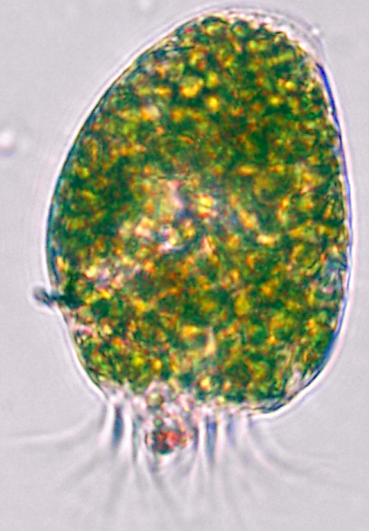
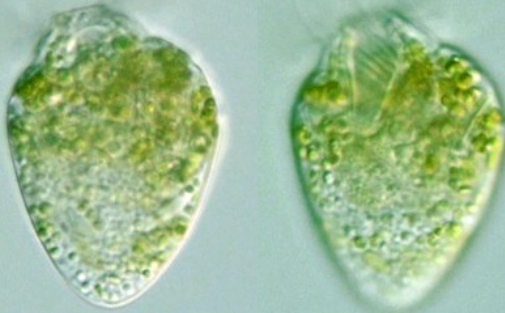
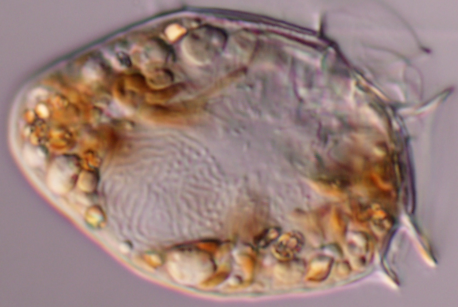
Where and when should mixotrophs matter?





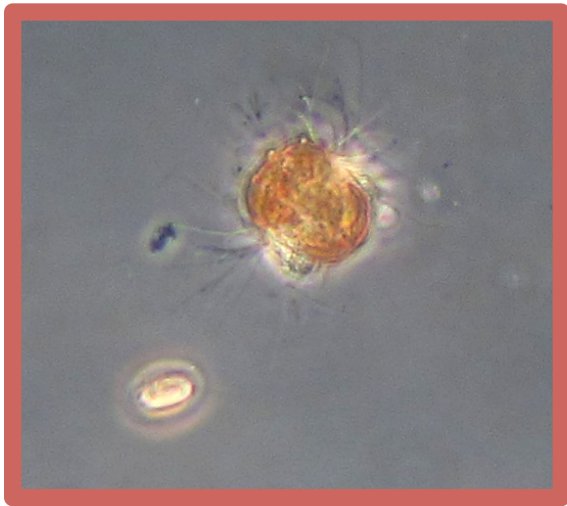
Images courtesy of:  
PJ Hansen, MD Johnson, T Lindholm, G McManus, and L Nielsen





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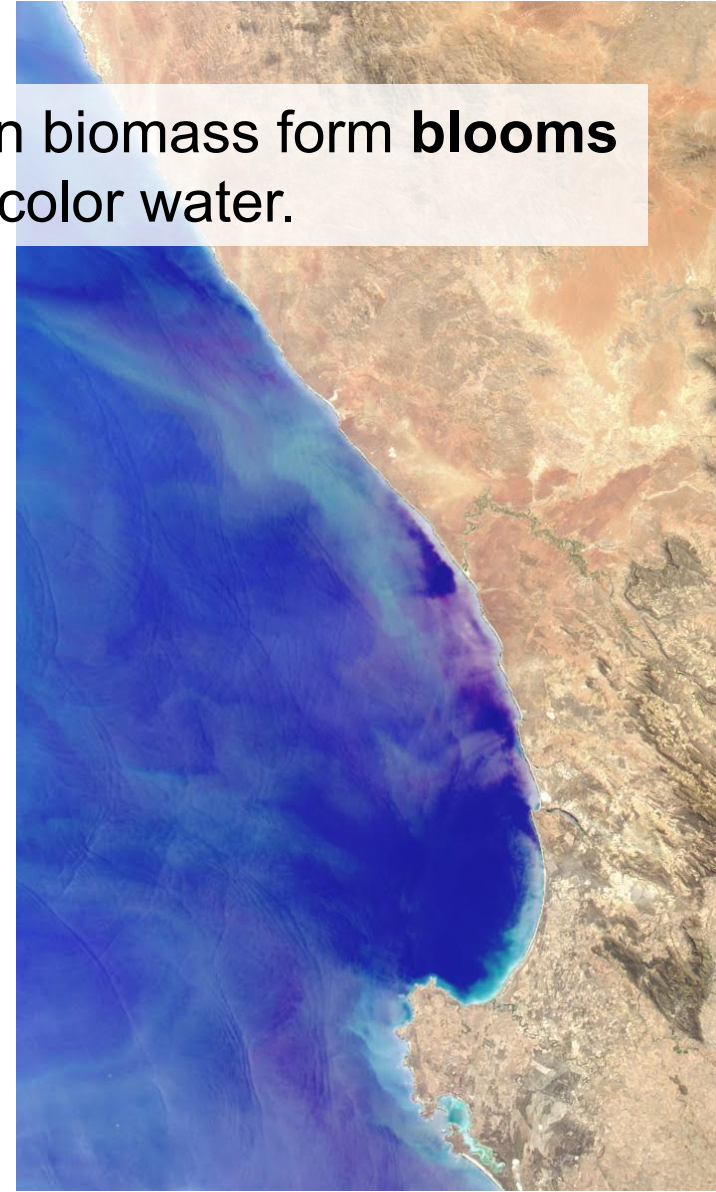




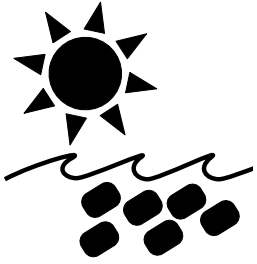
Rapid increases in biomass form **blooms** dense enough to color water.



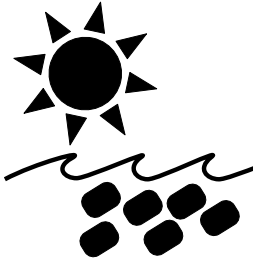
APL-UW



NASA MODIS



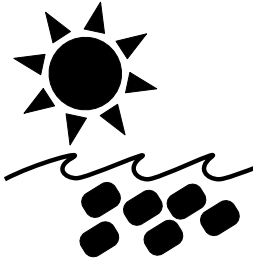
# A model of acquired phototrophy



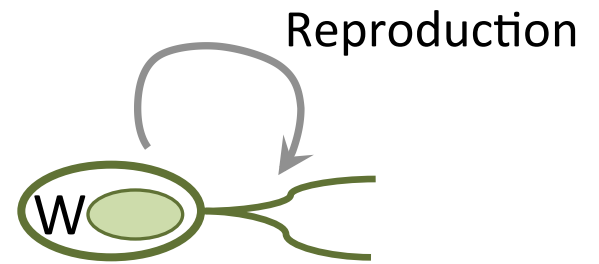
# A model of acquired phototrophy

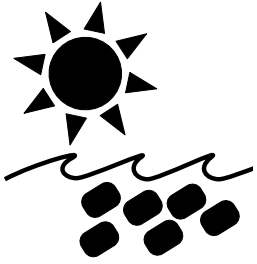




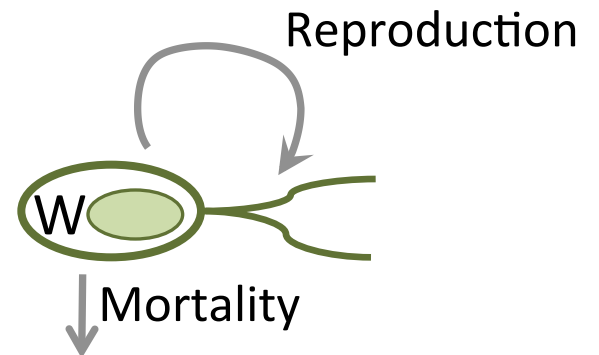


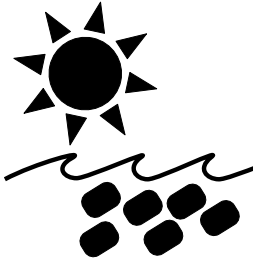
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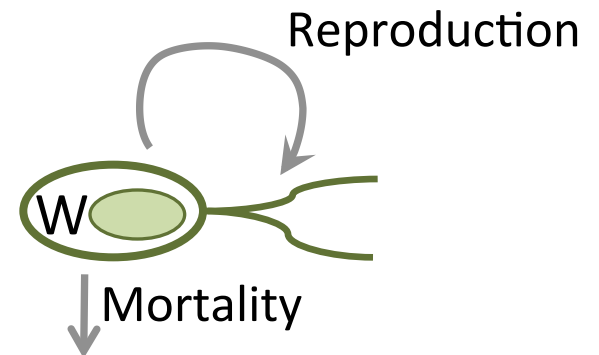
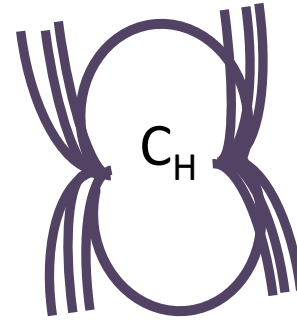


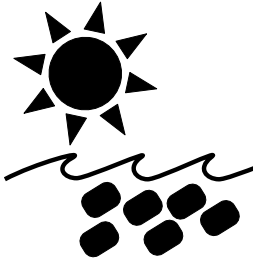
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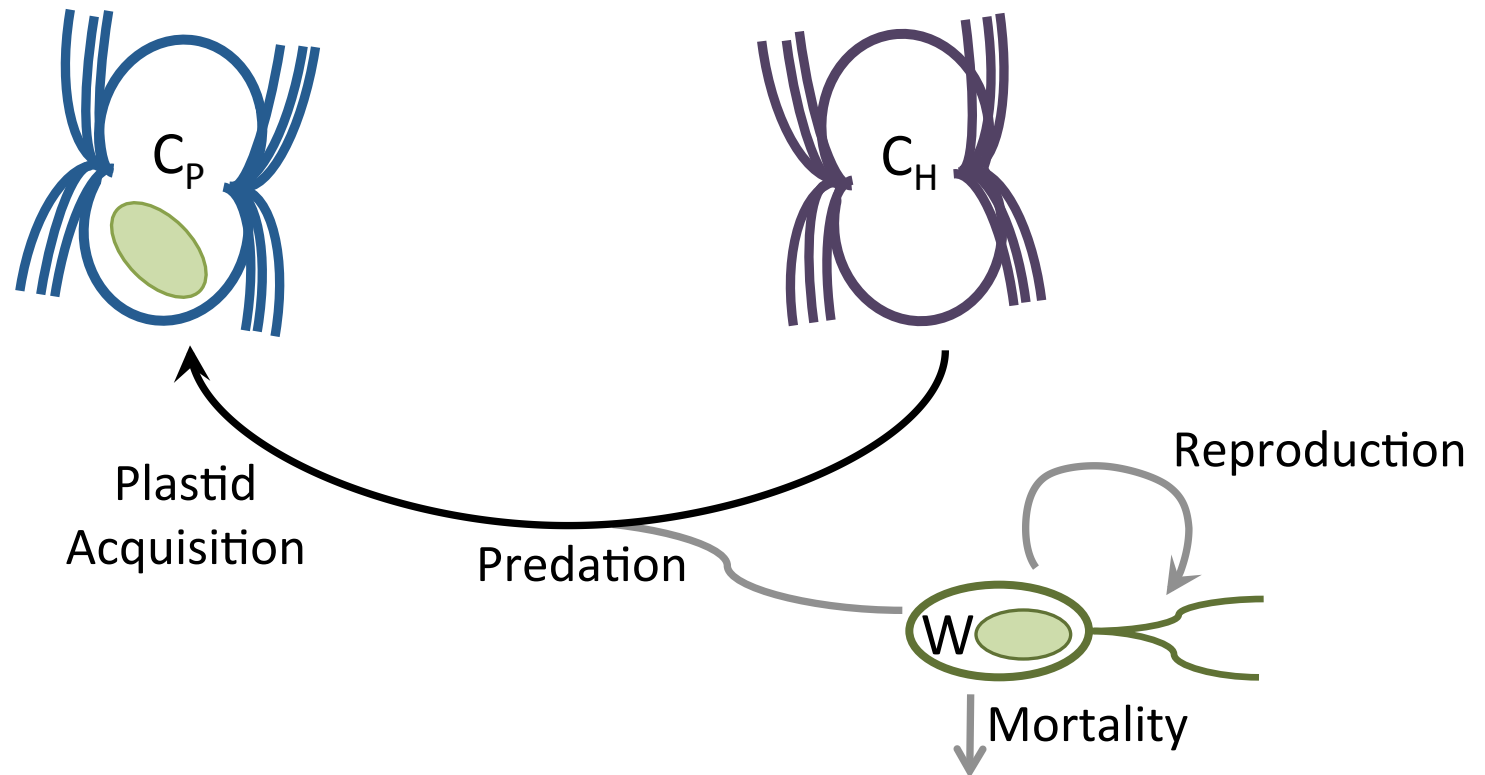


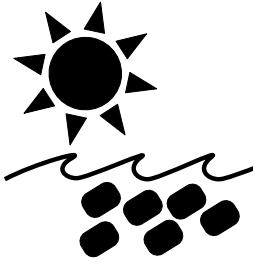
# A model of acquired phototrophy



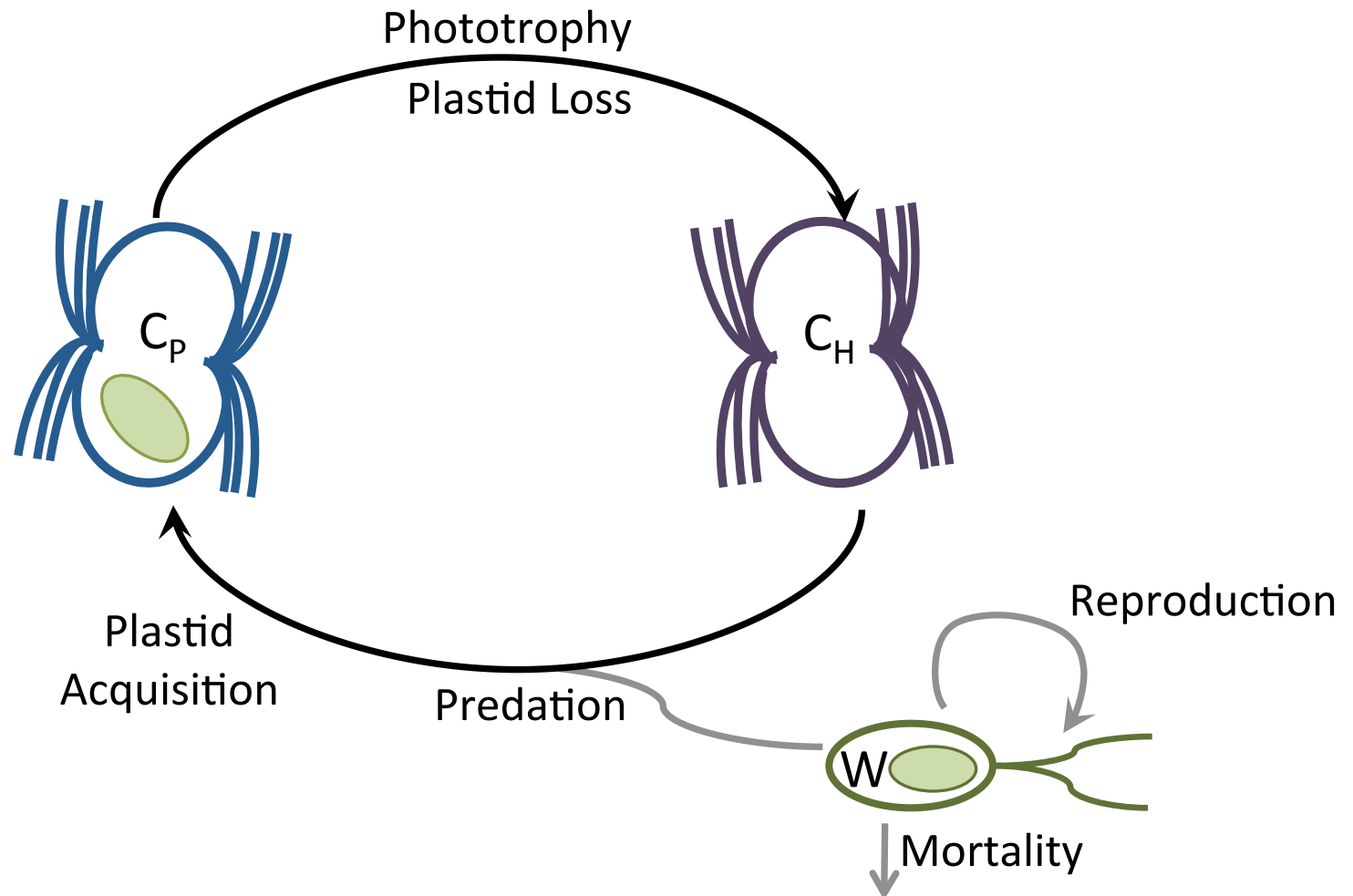


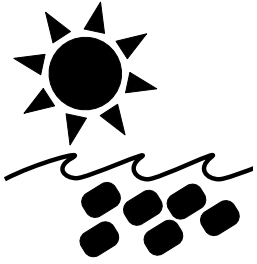
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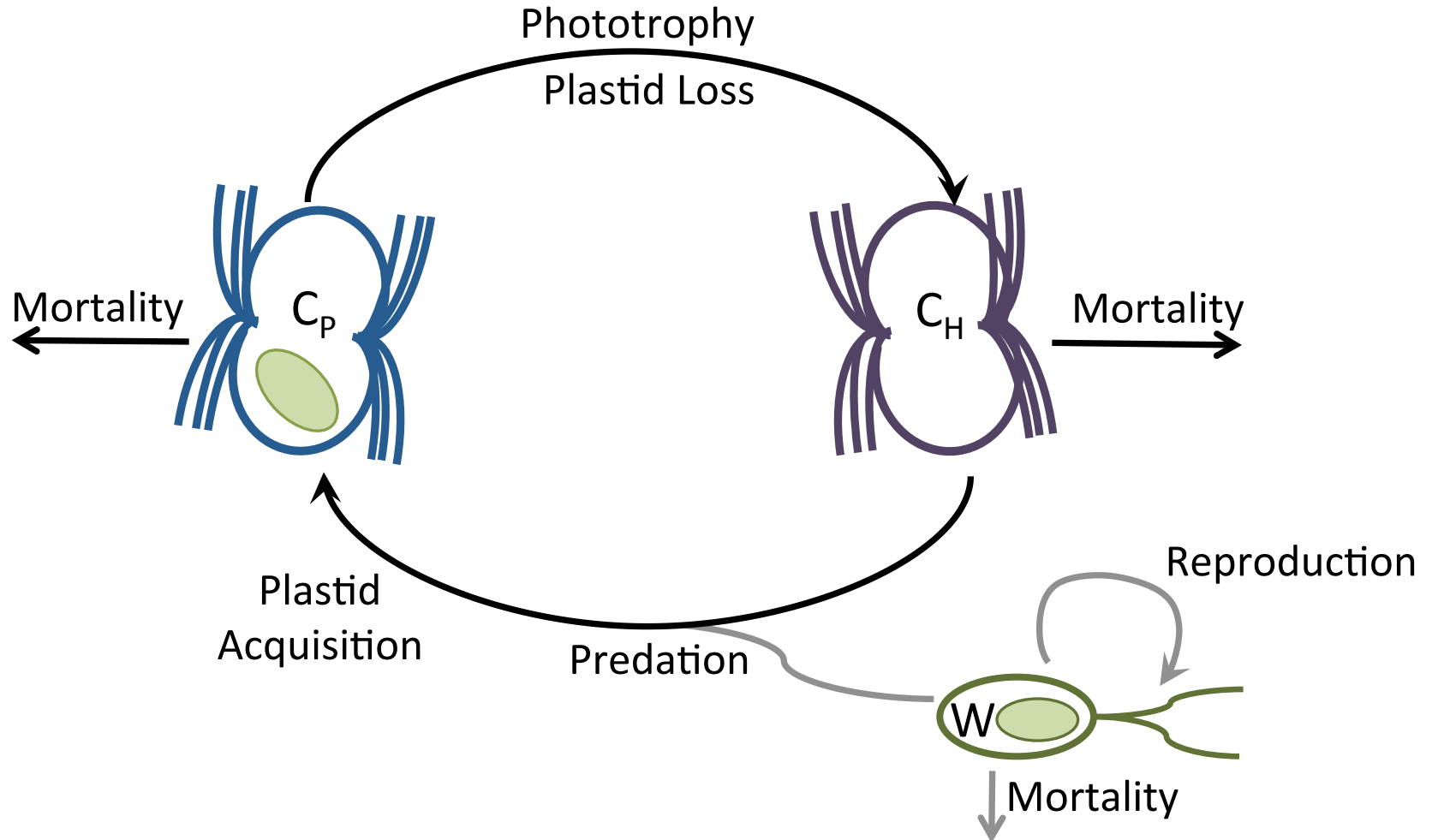


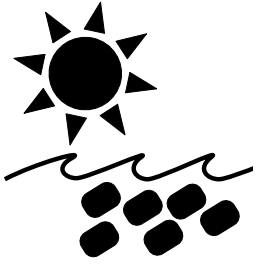
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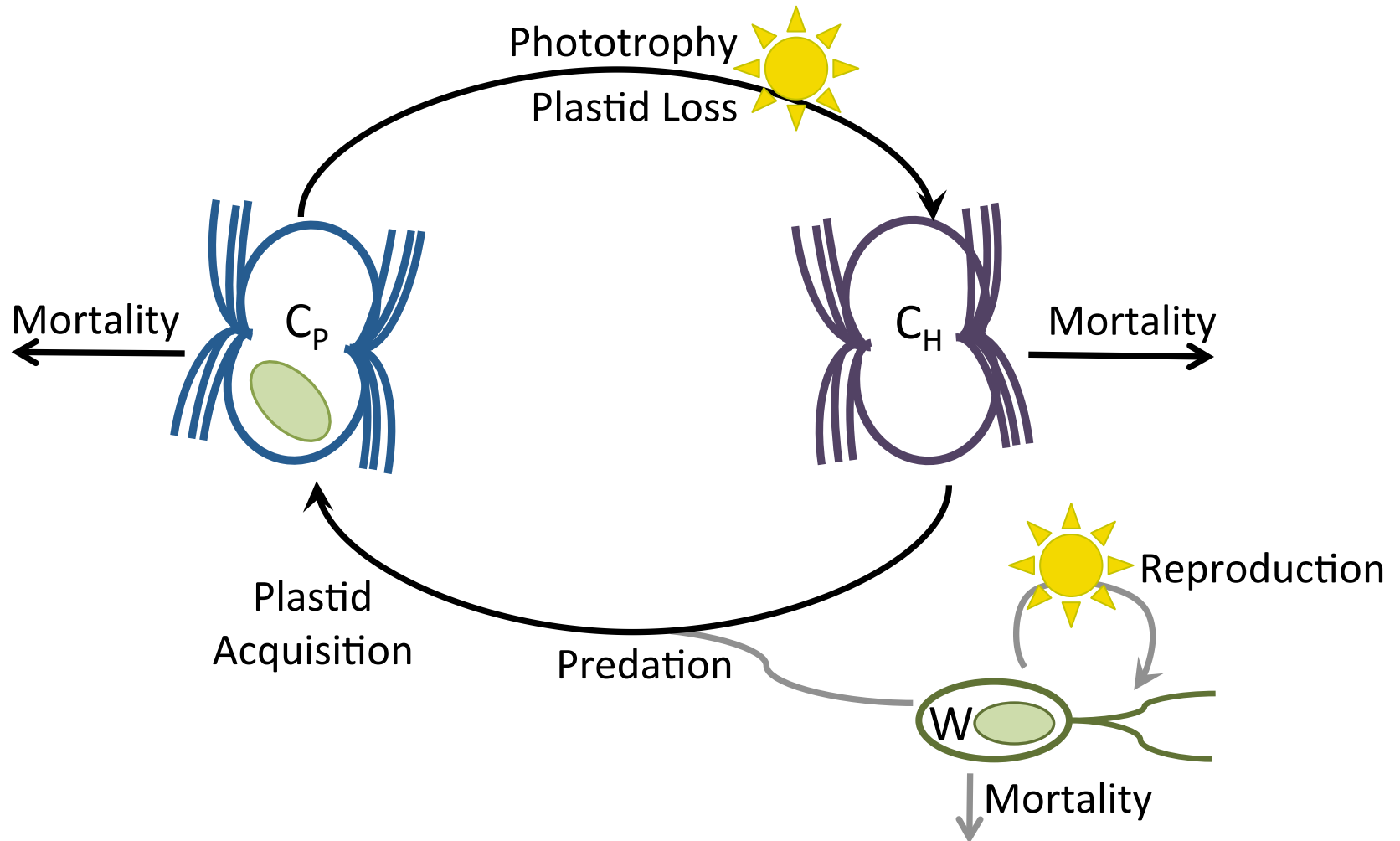


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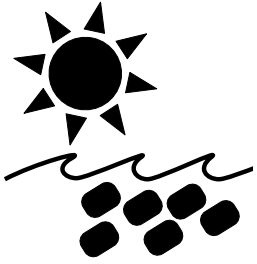




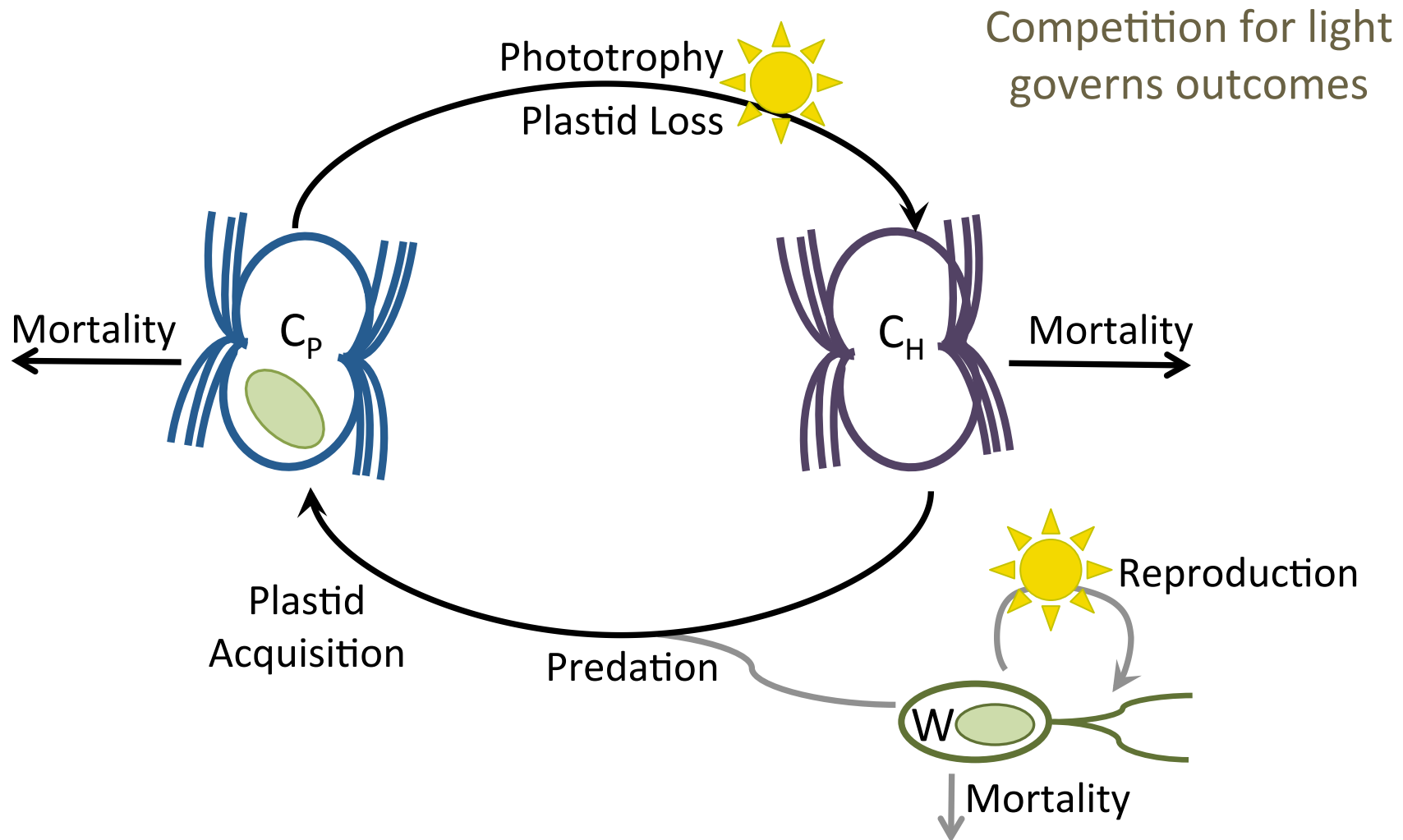
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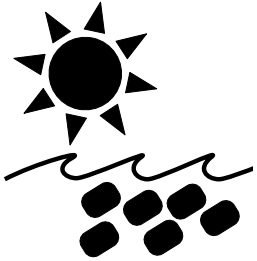




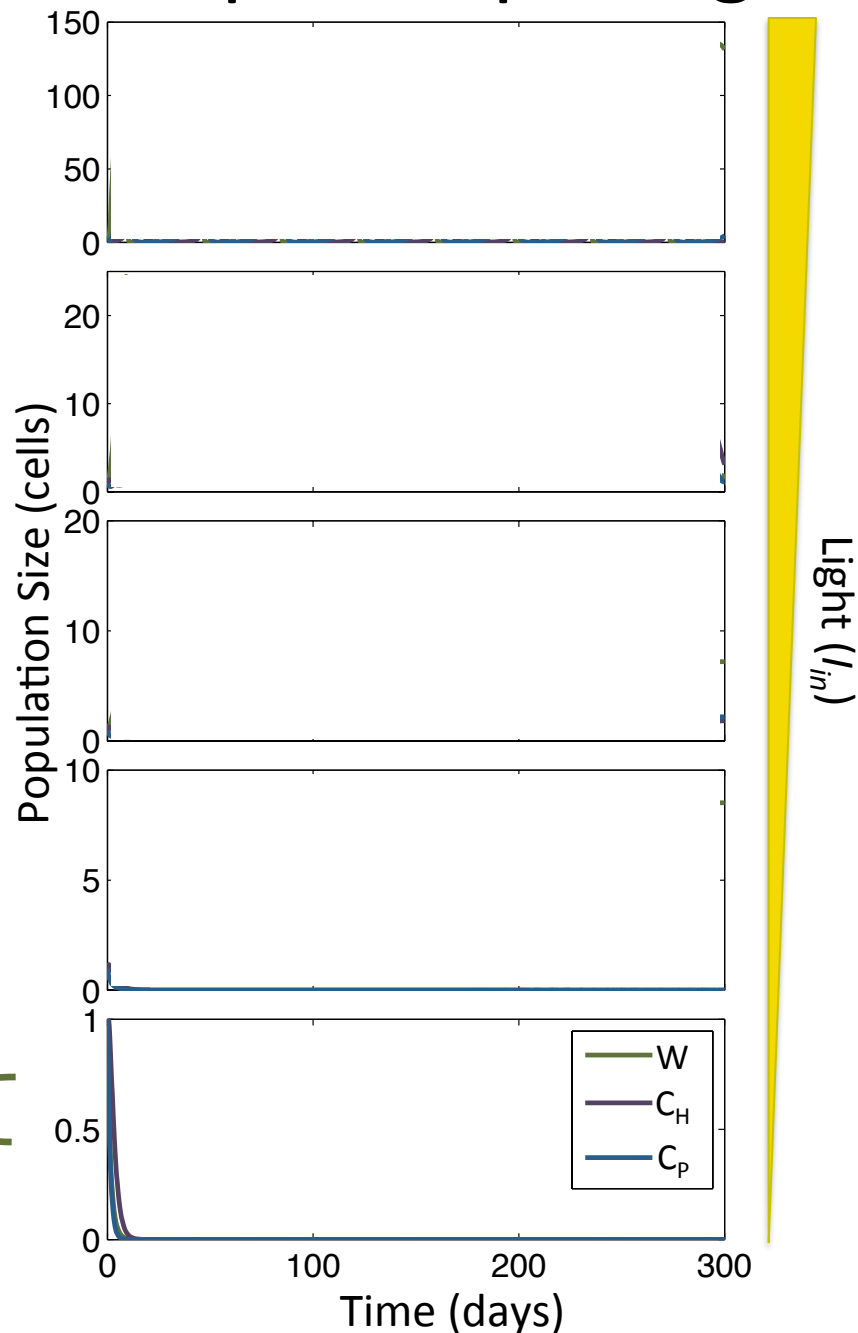
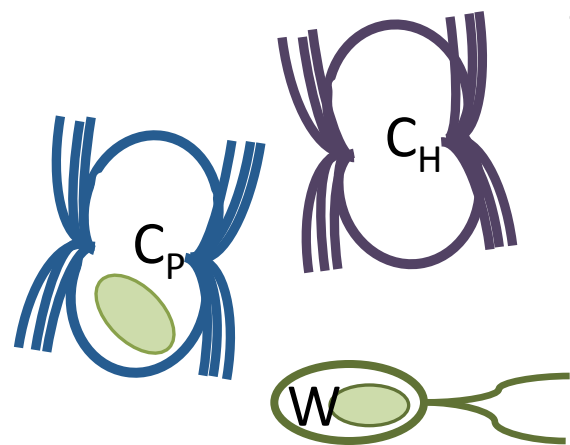


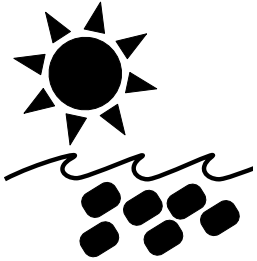
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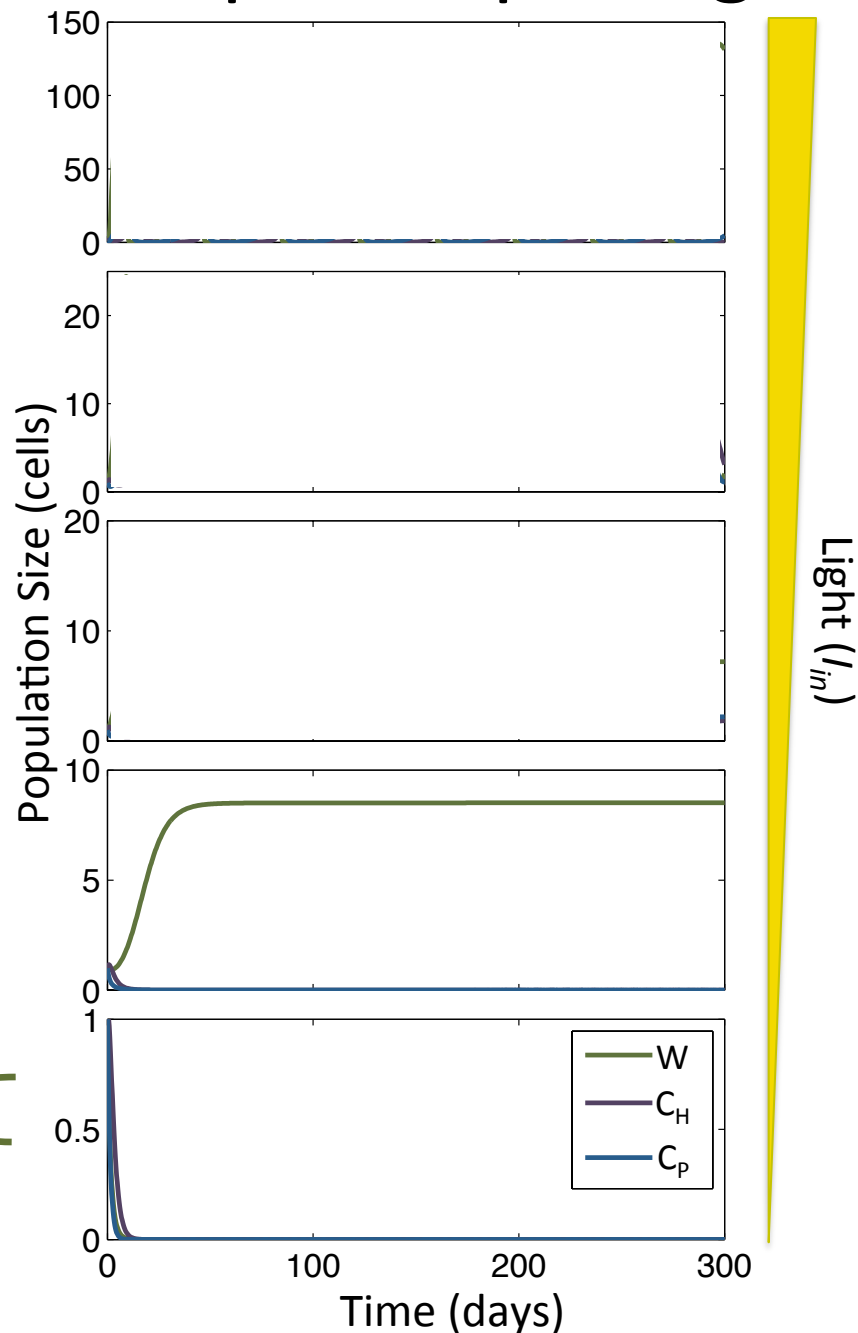
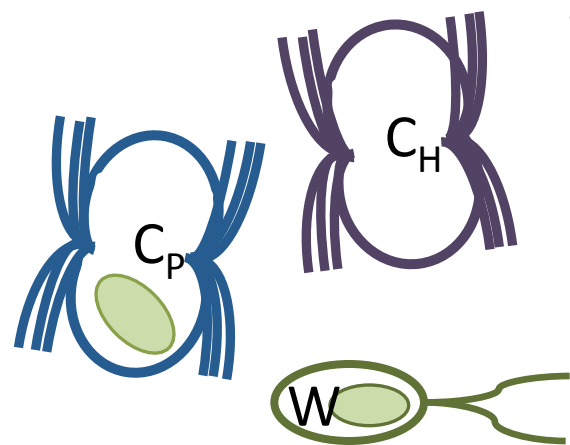


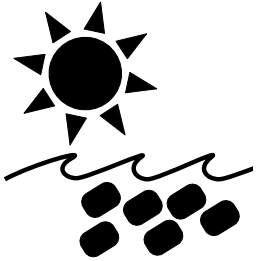
# Dynamics depend upon light



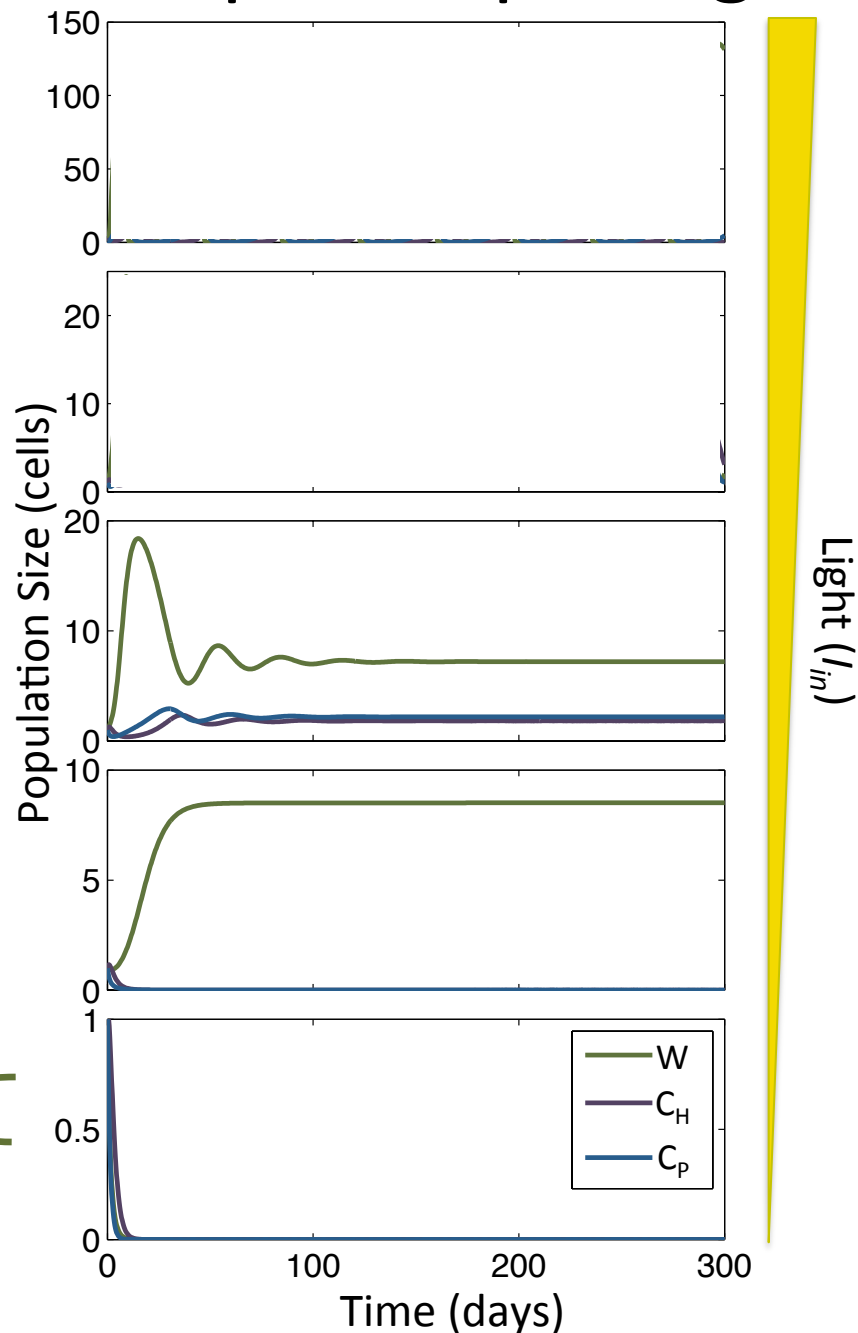
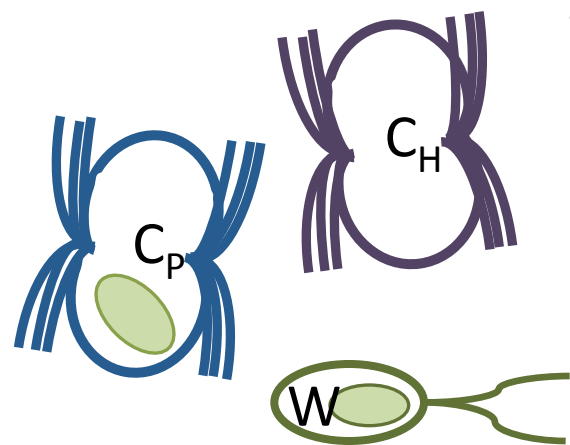


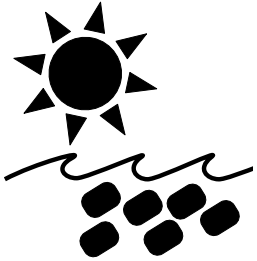
# Dynamics depend upon light



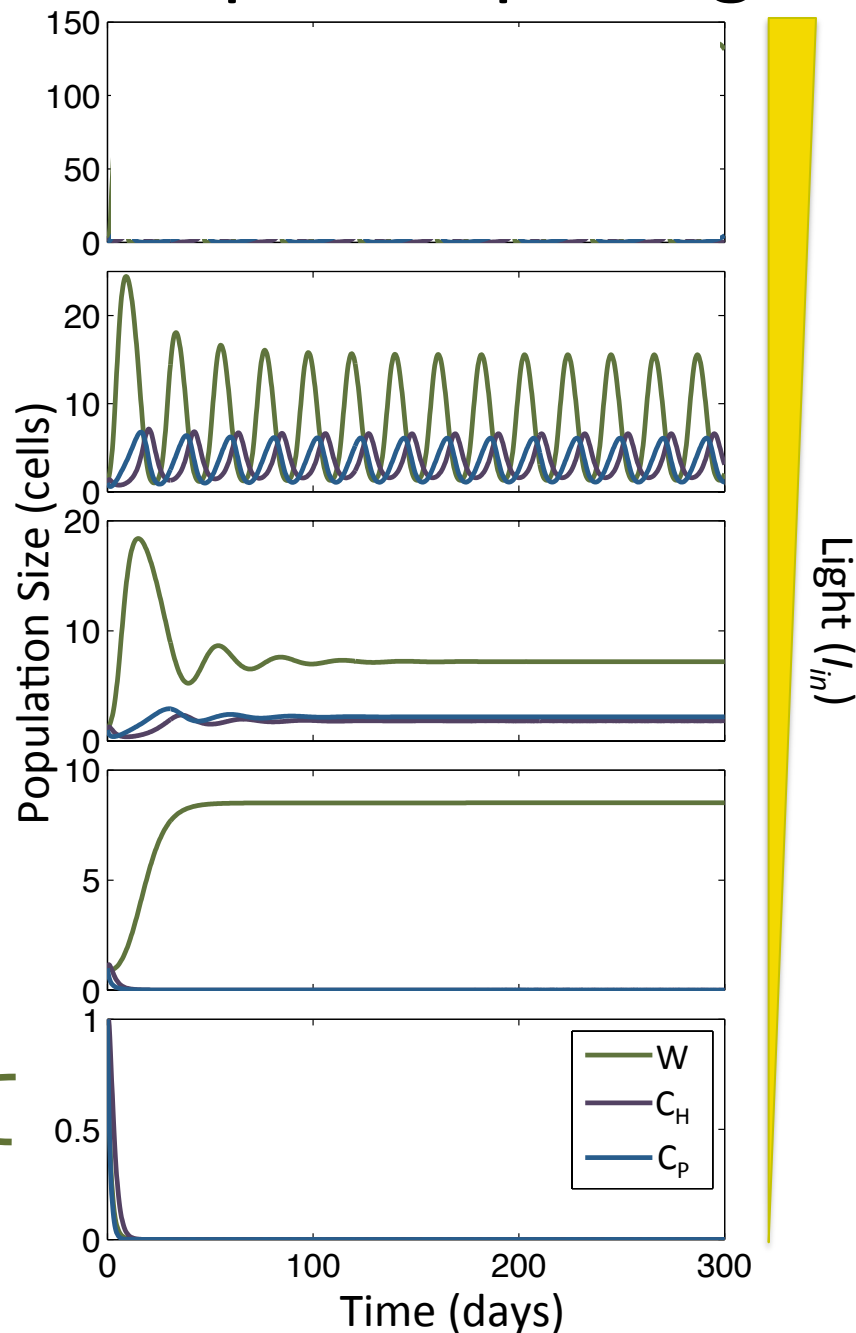
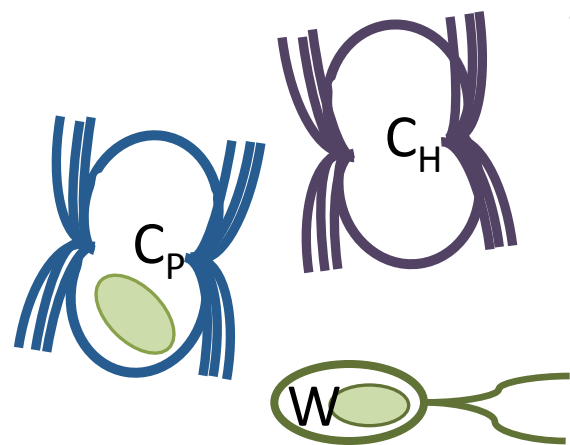


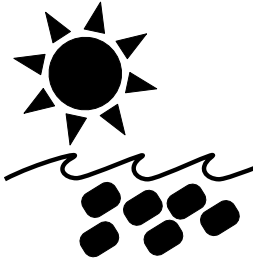
# Dynamics depend upon light



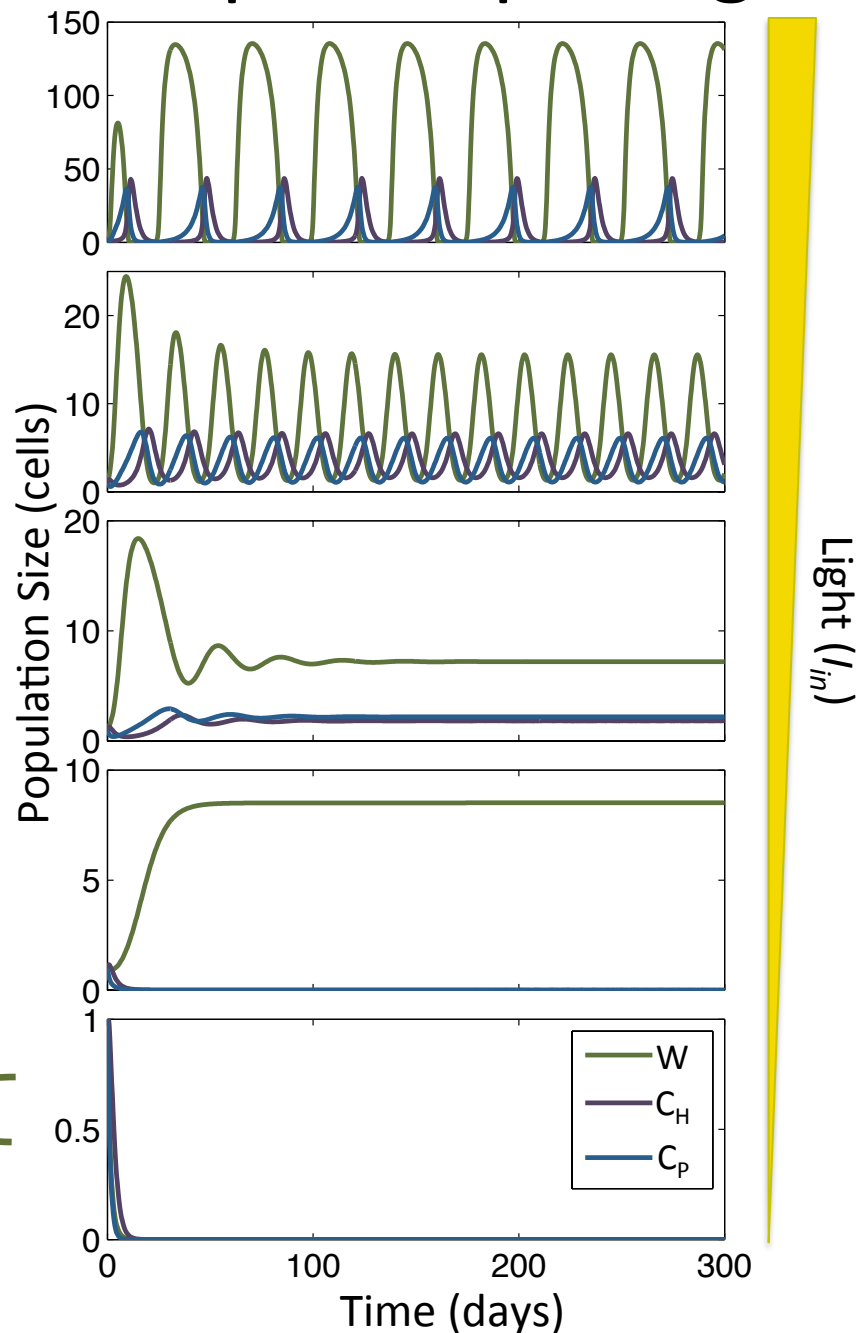
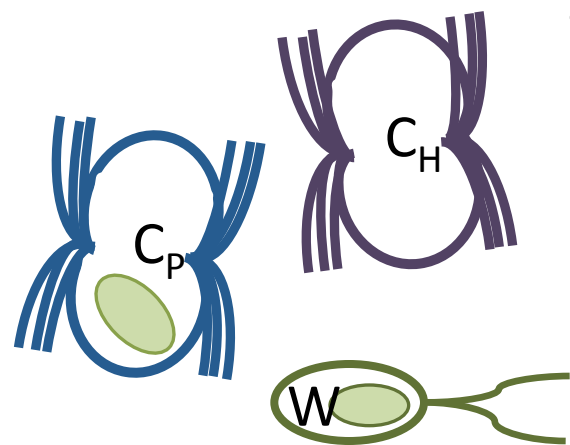


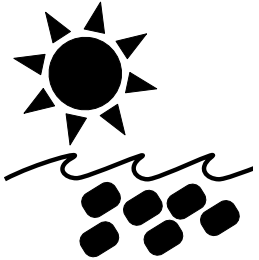
# Dynamics depend upon light





# Dynamics depend upon light

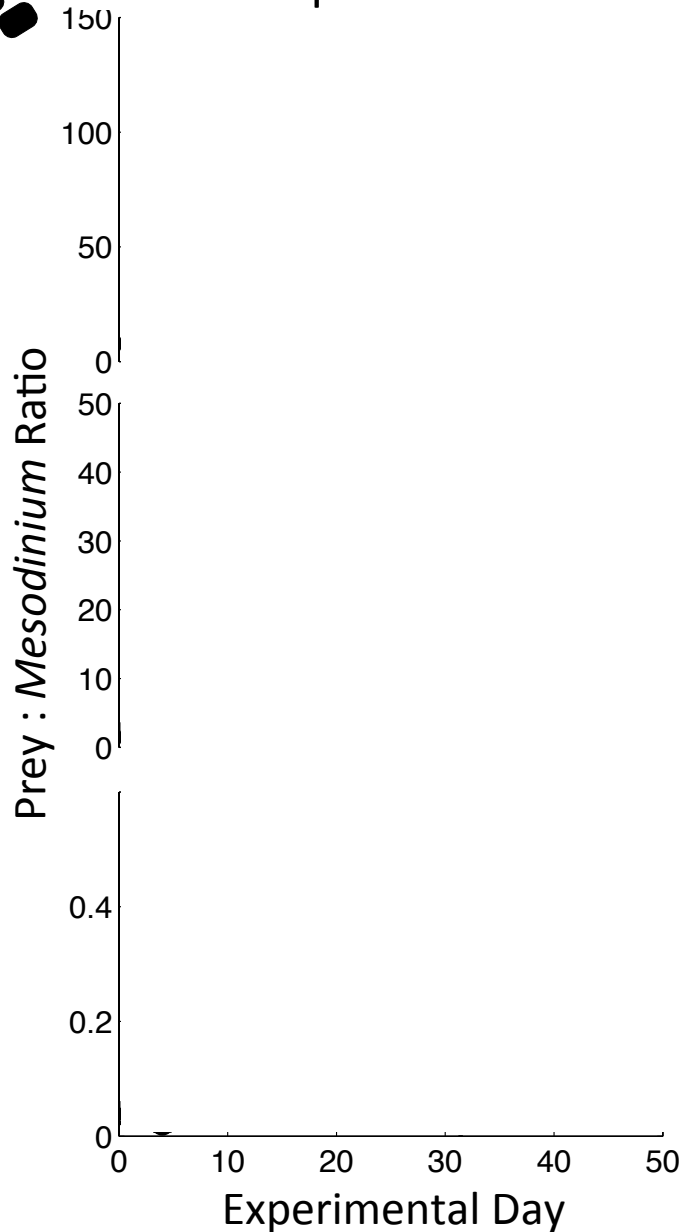




# Experimental validation

Empirical Data

Simulation Results



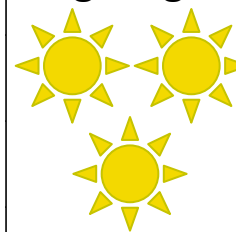
Low Light



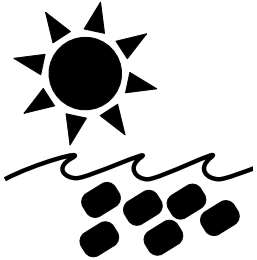
Med. Light



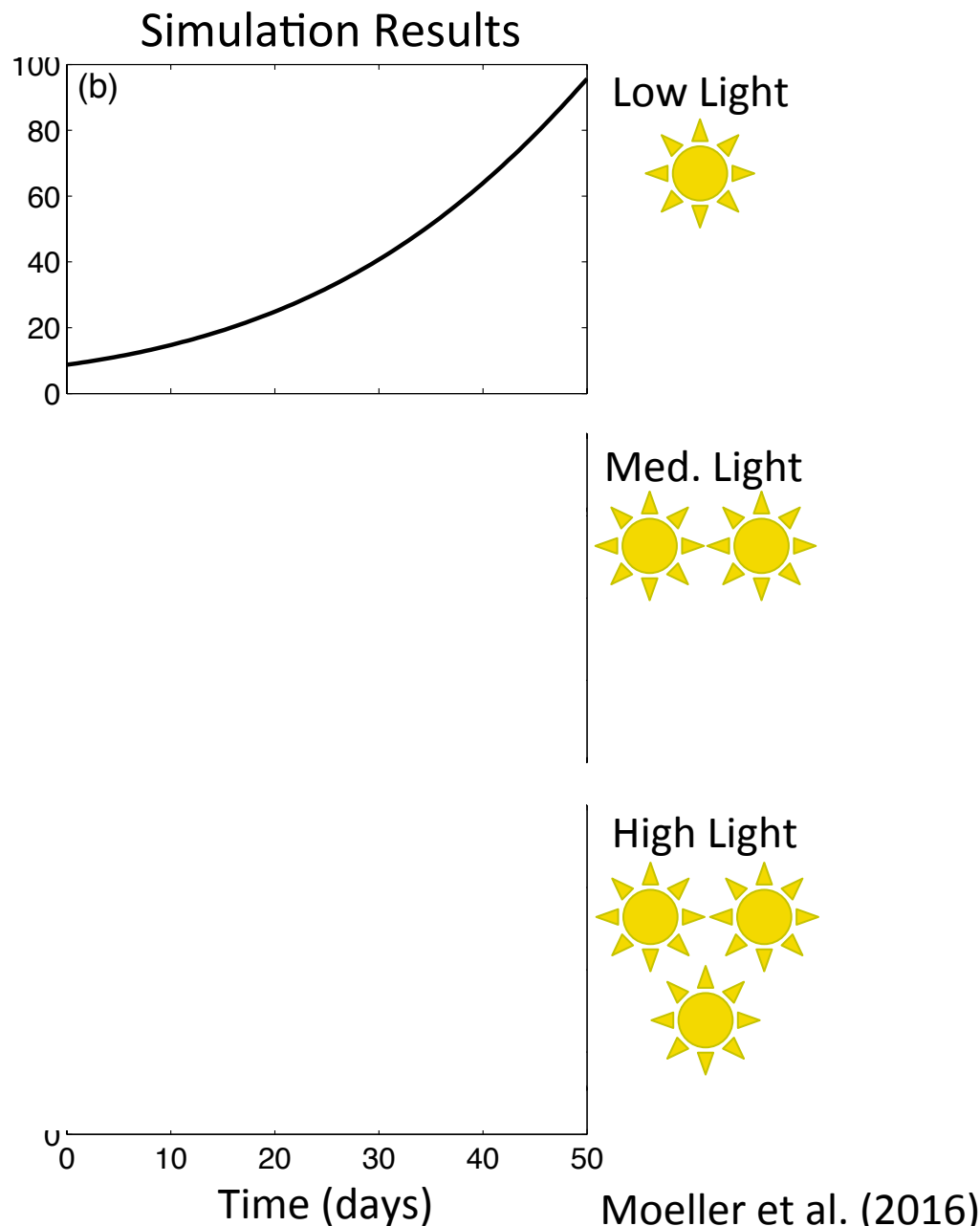
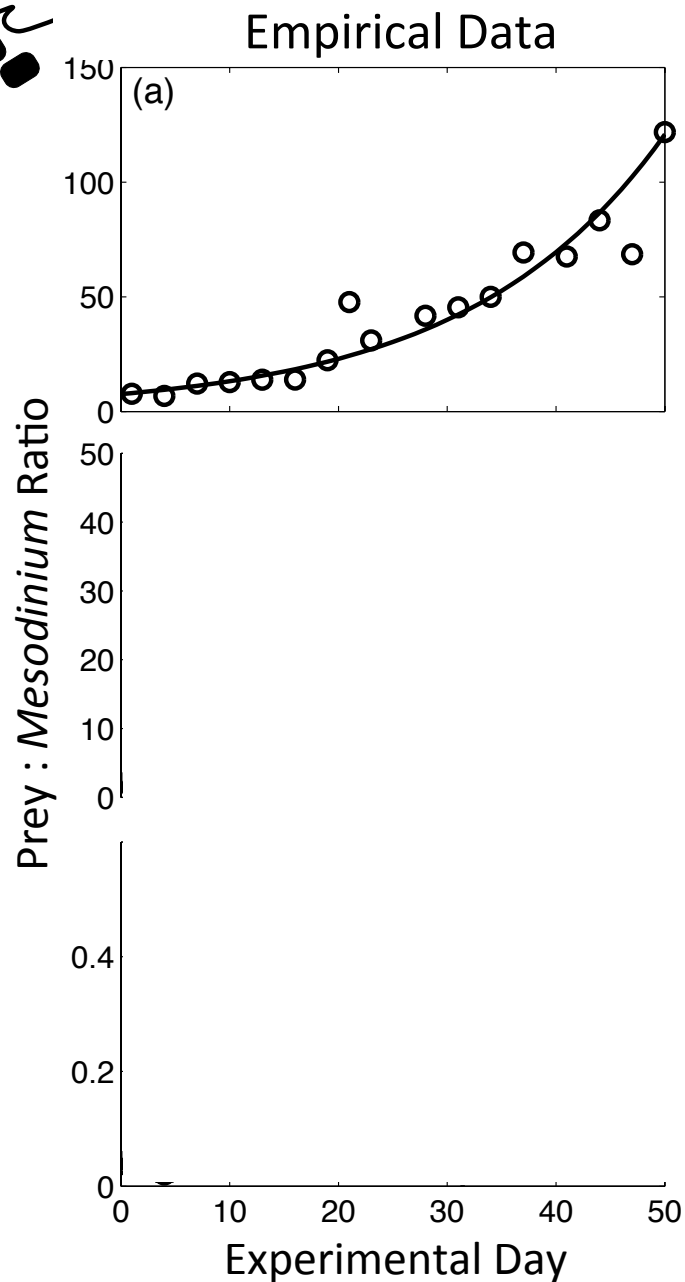
High Light



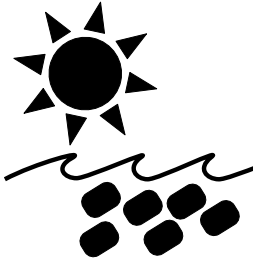
Moeller et al. (2016)



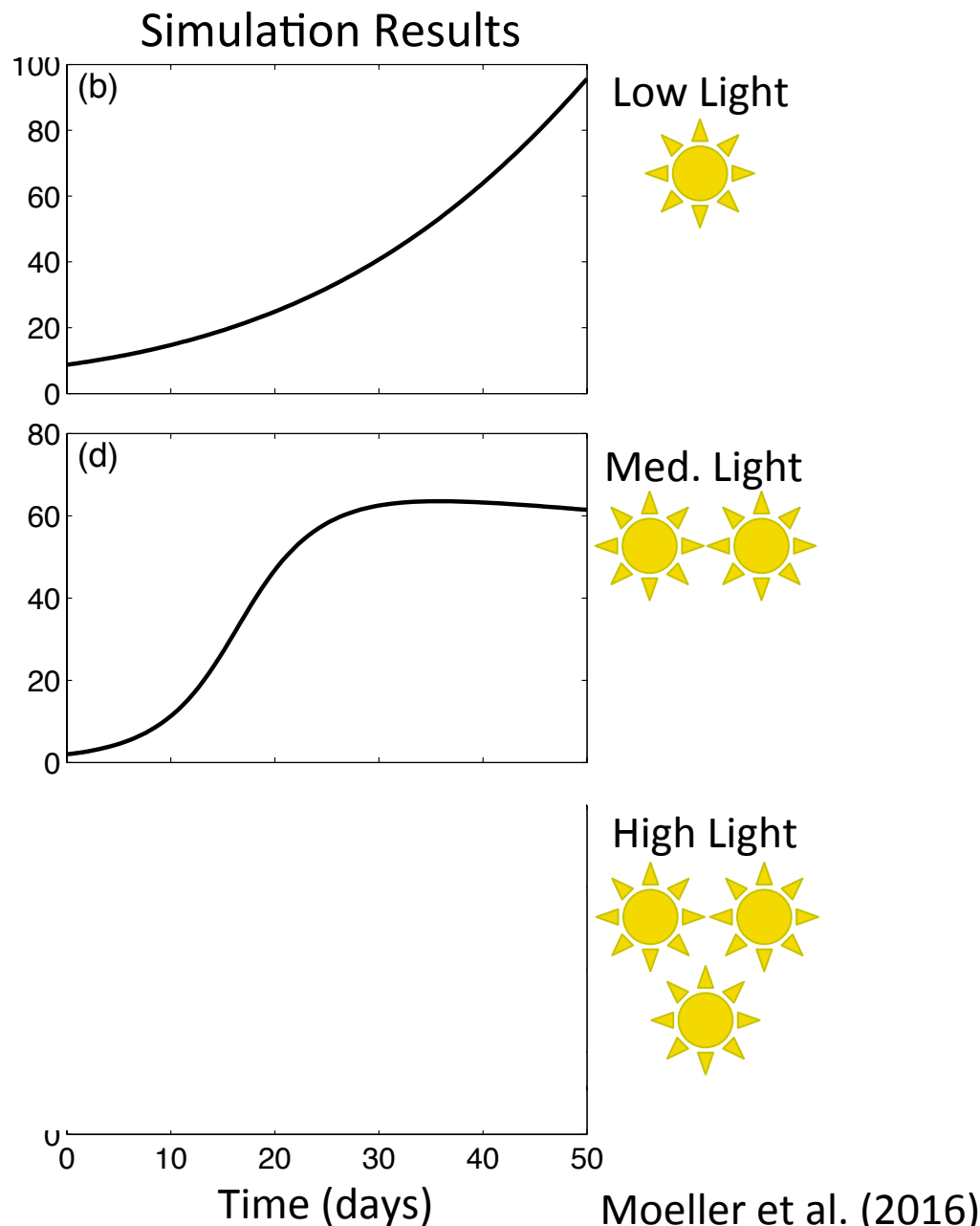
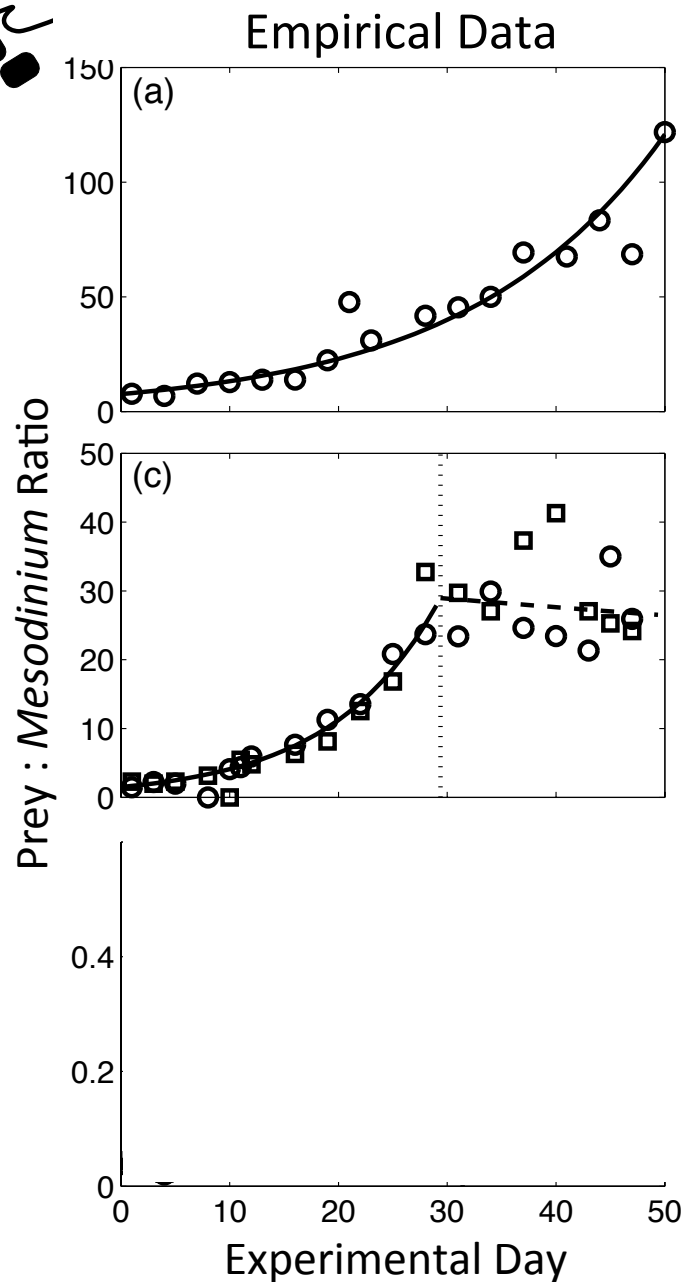
# Experimental validation

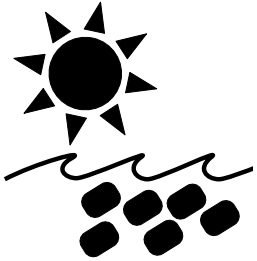




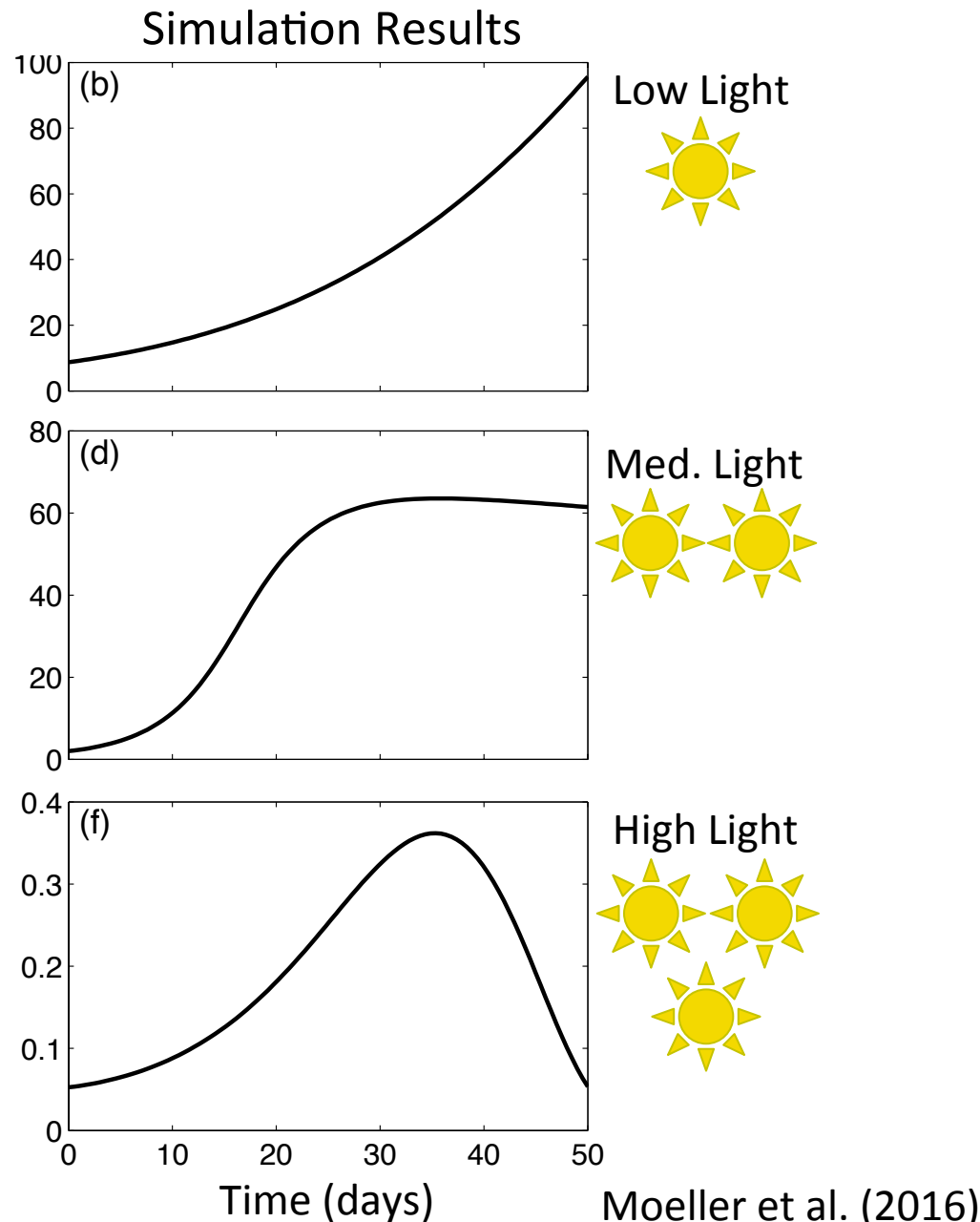
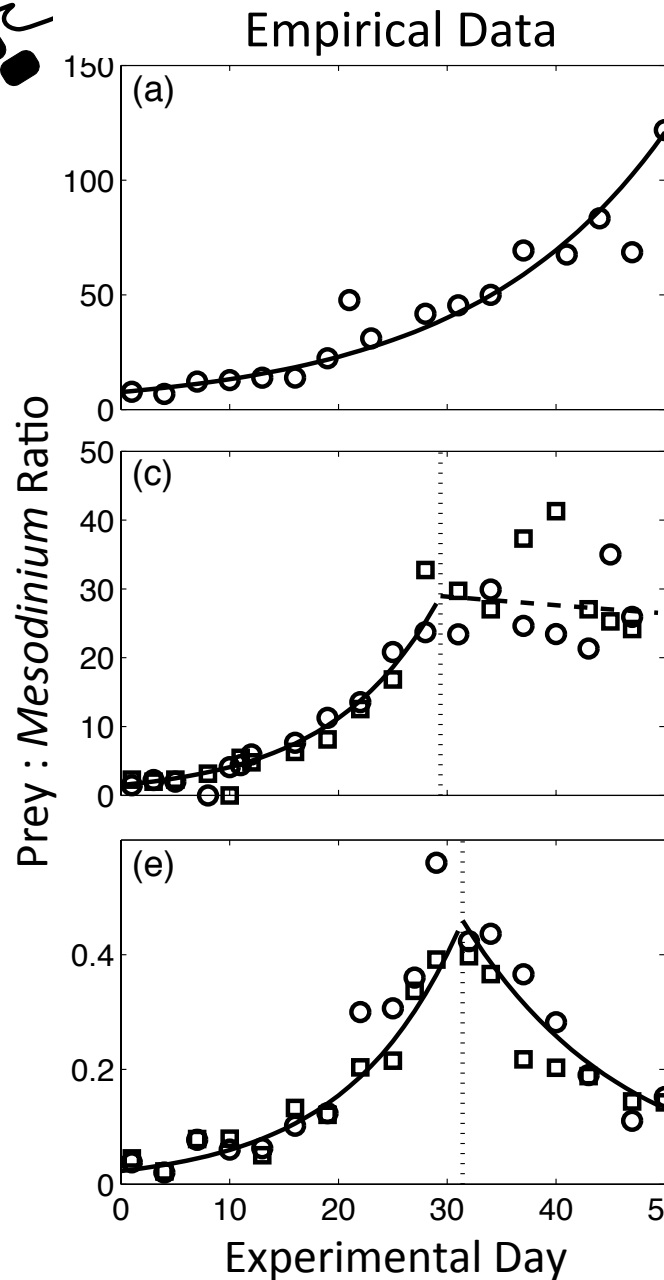


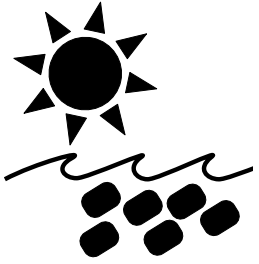
# Experimental validation



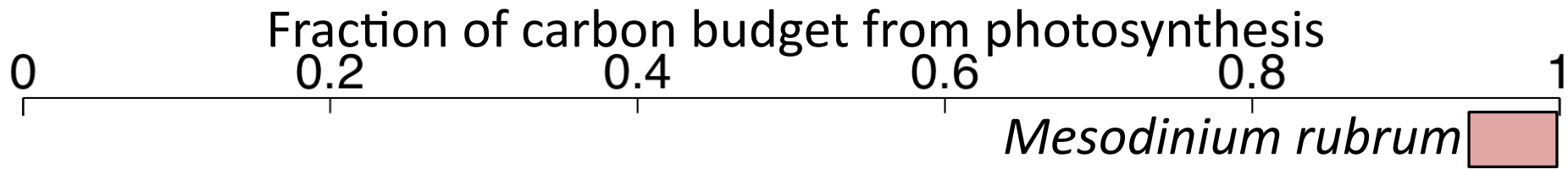


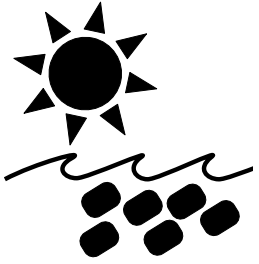
# Experimental validation



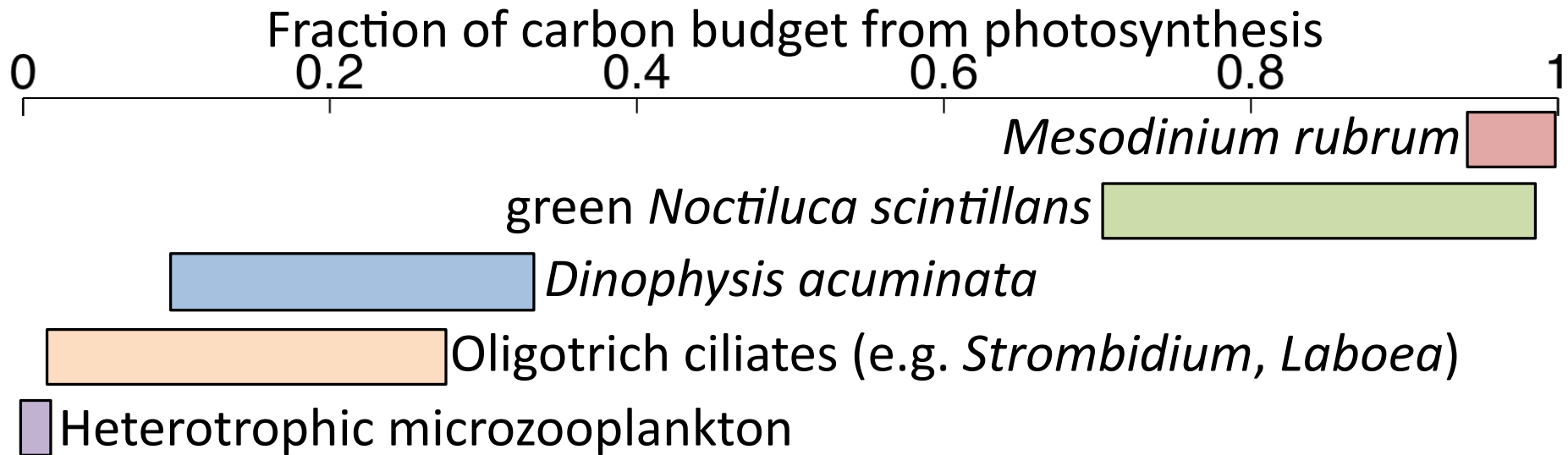


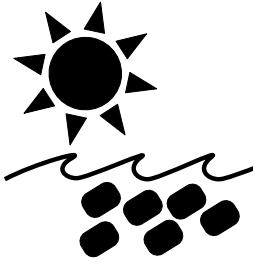
# Acquired phototrophs vary in carbon budget



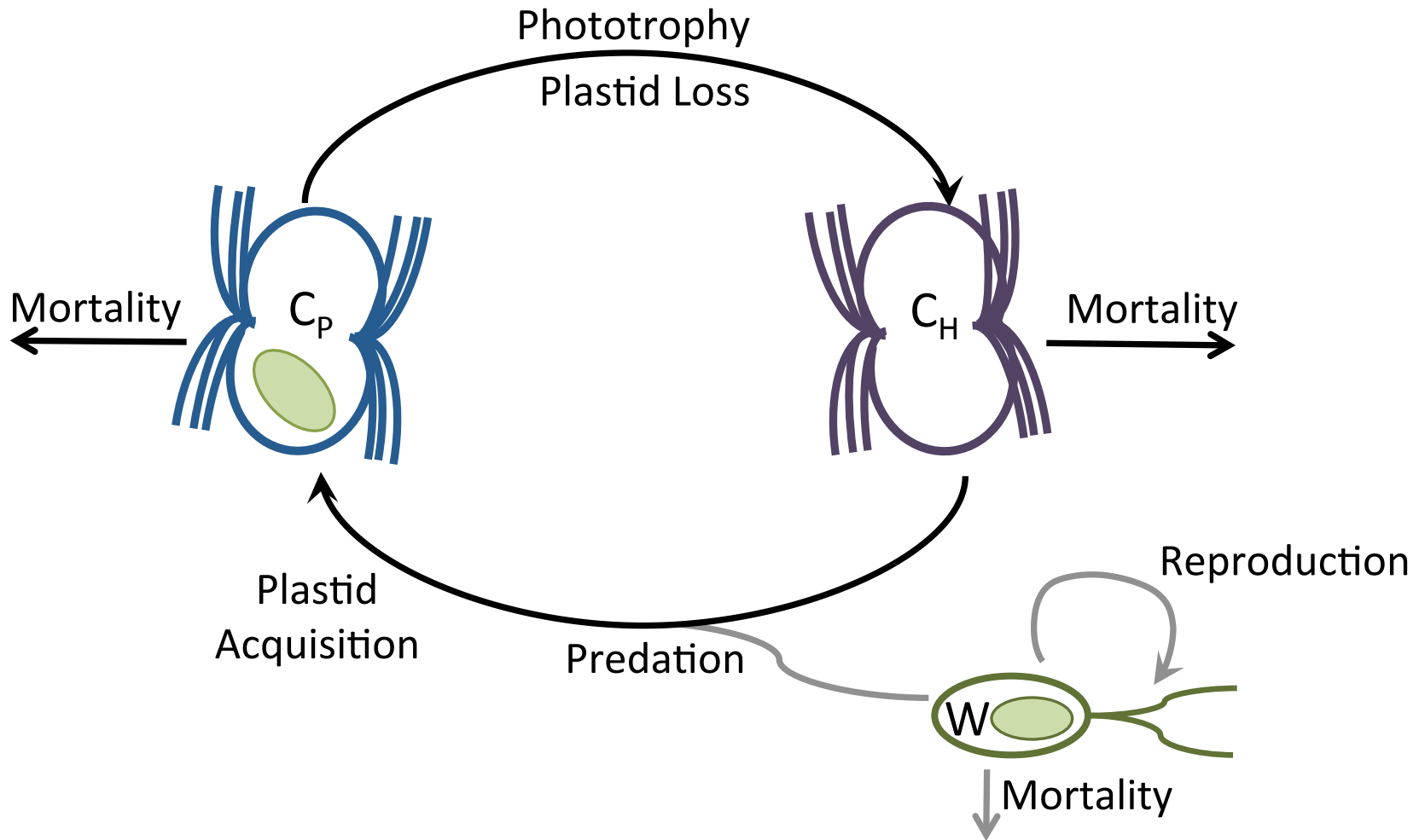


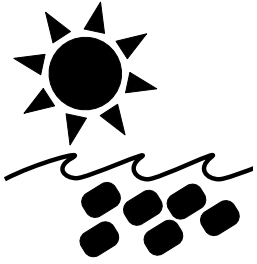
# Acquired phototrophs vary in carbon budget



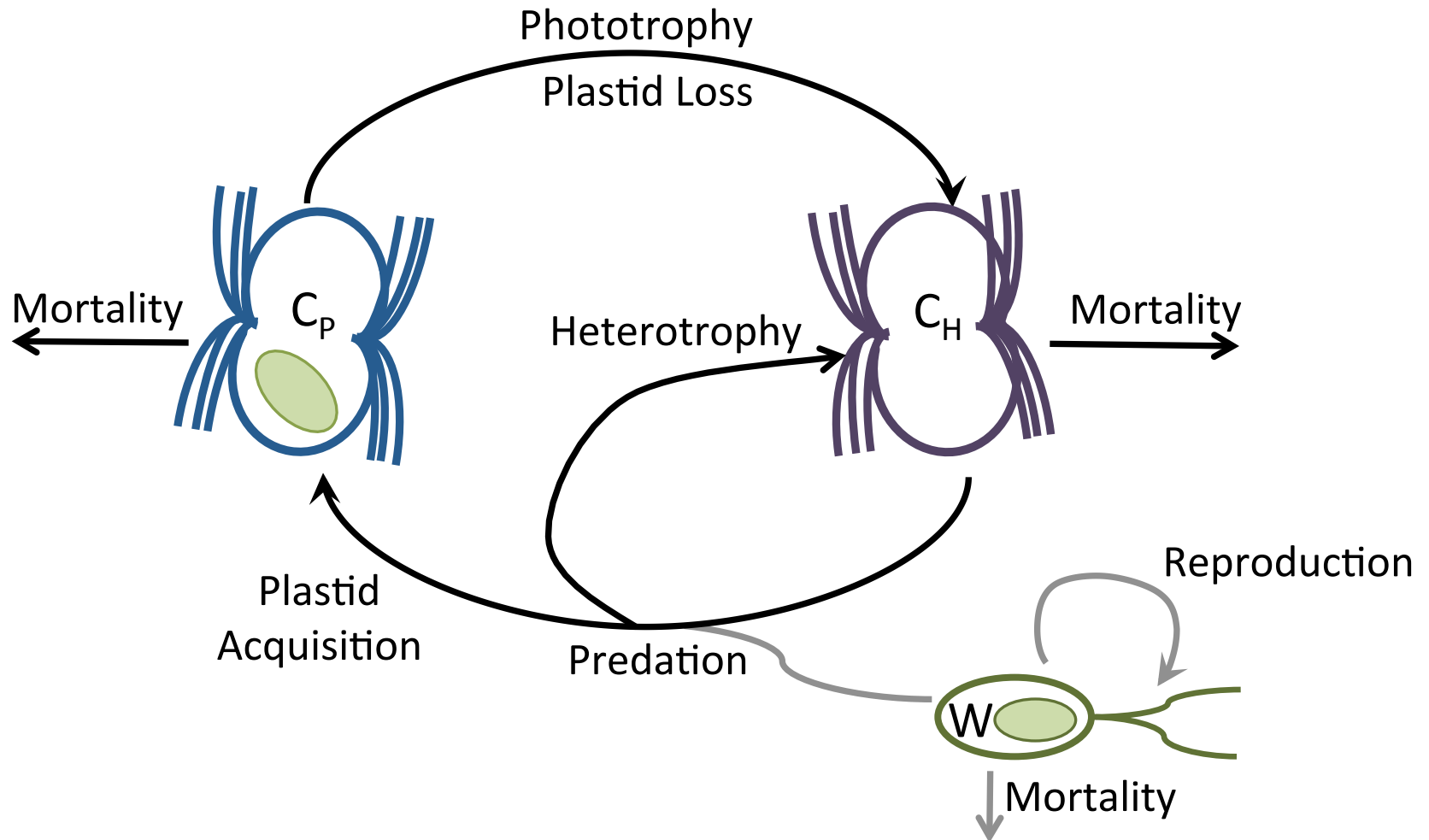


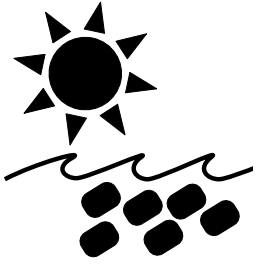
# A model of acquired phototrophy



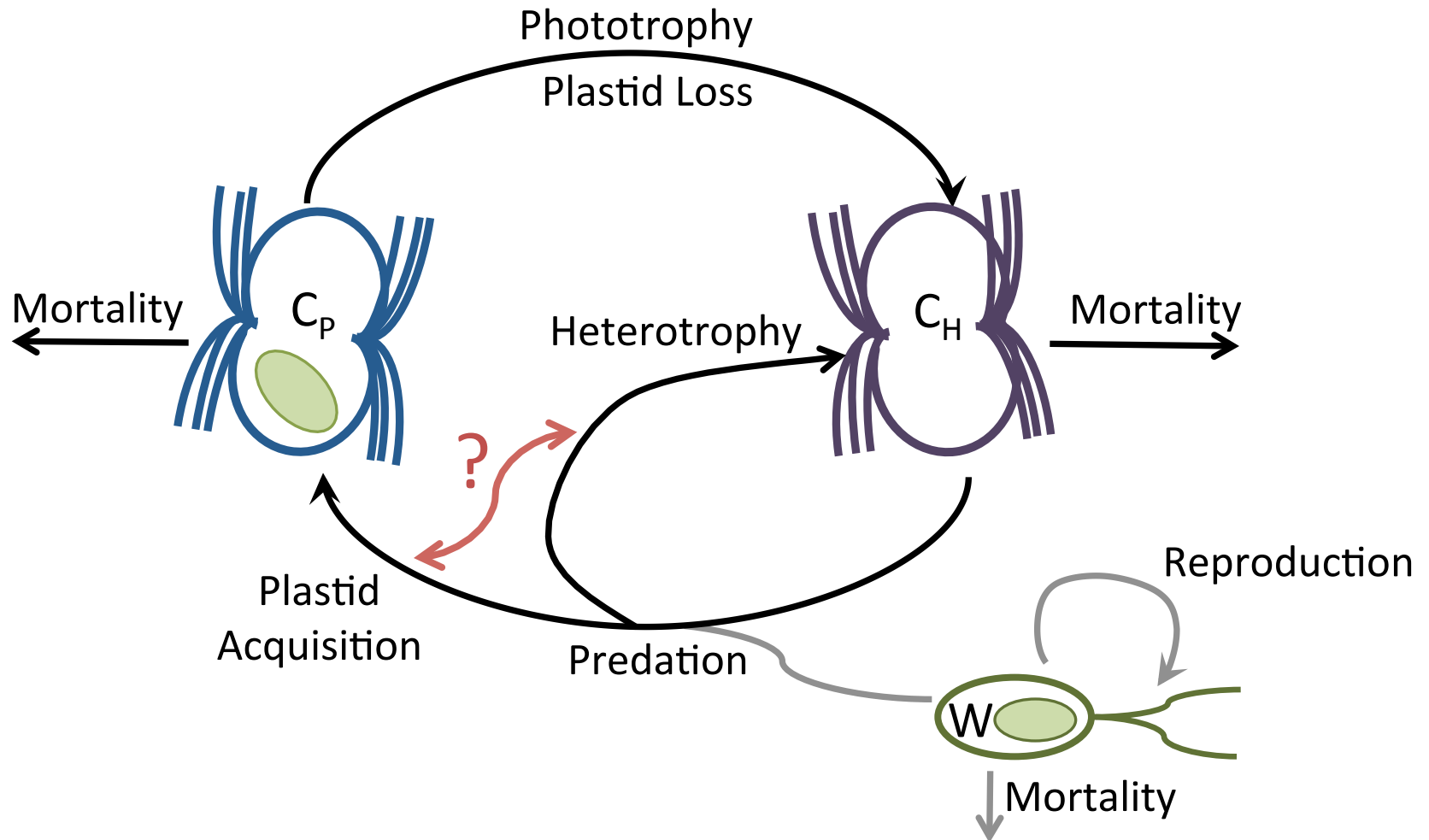


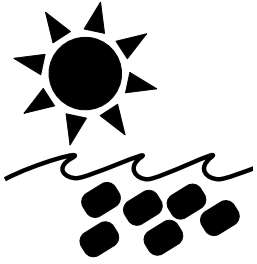
# A model of acquired phototrophy



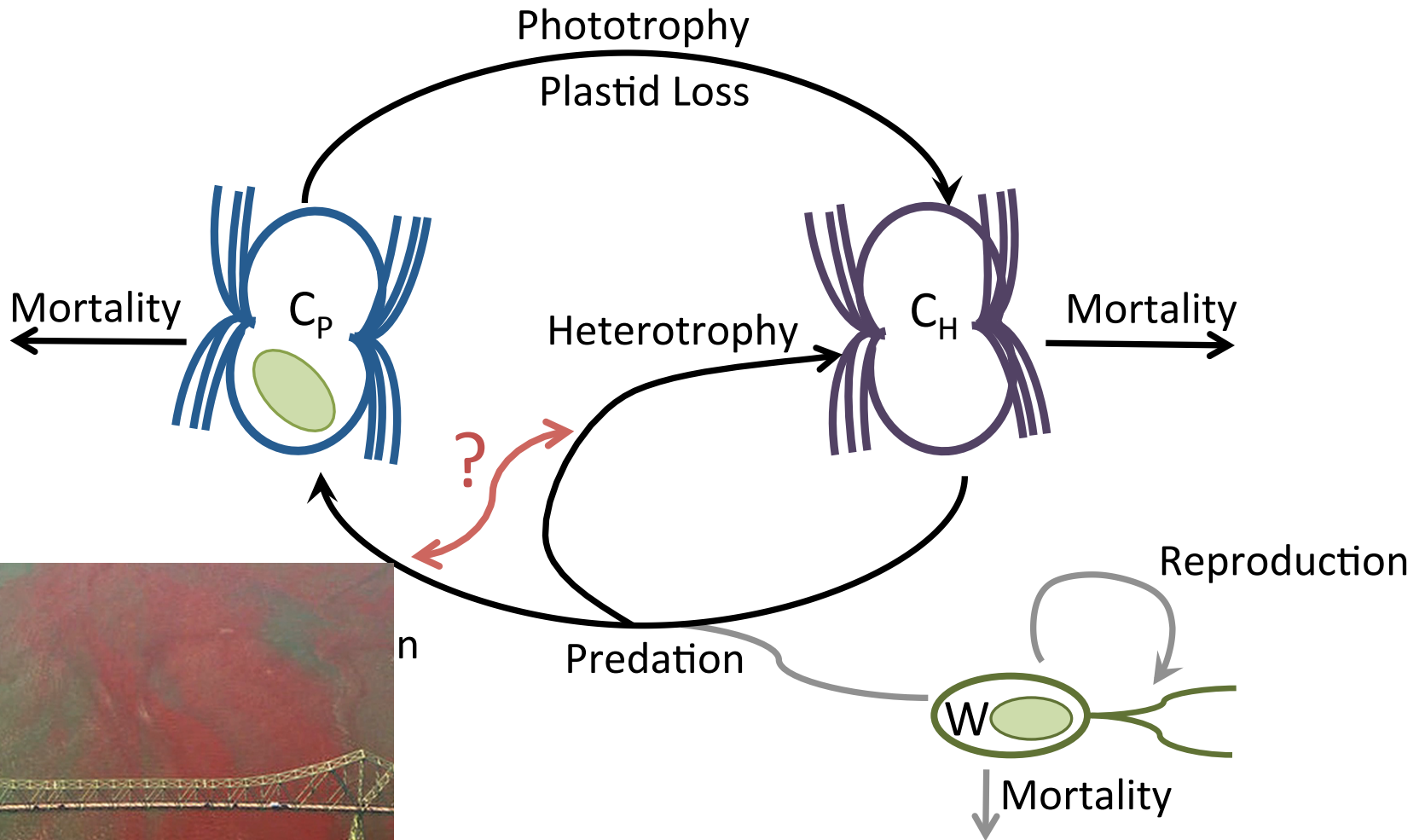


# A model of acquired phototrophy



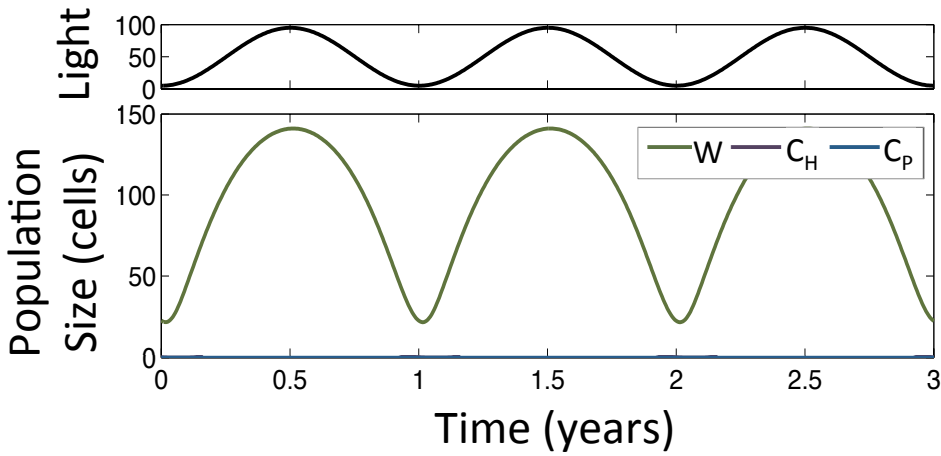
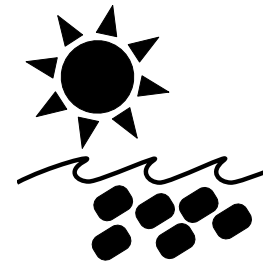


# A model of acquired phototrophy



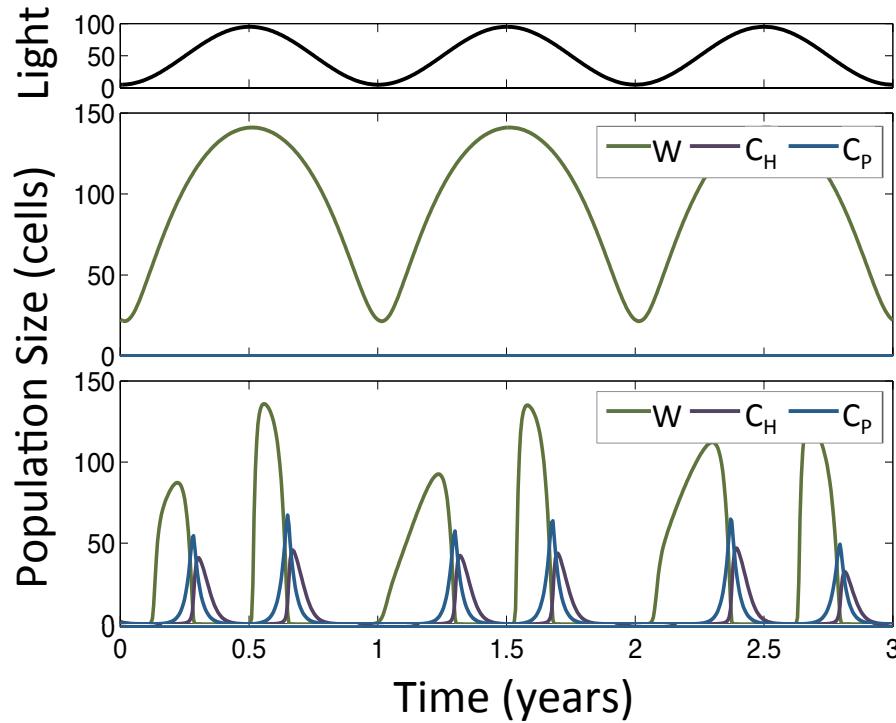
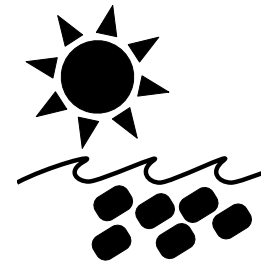


# Force the model with annual light cycles

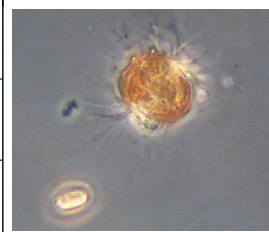


Prey only

# Blooms depend on degree of mixotrophy



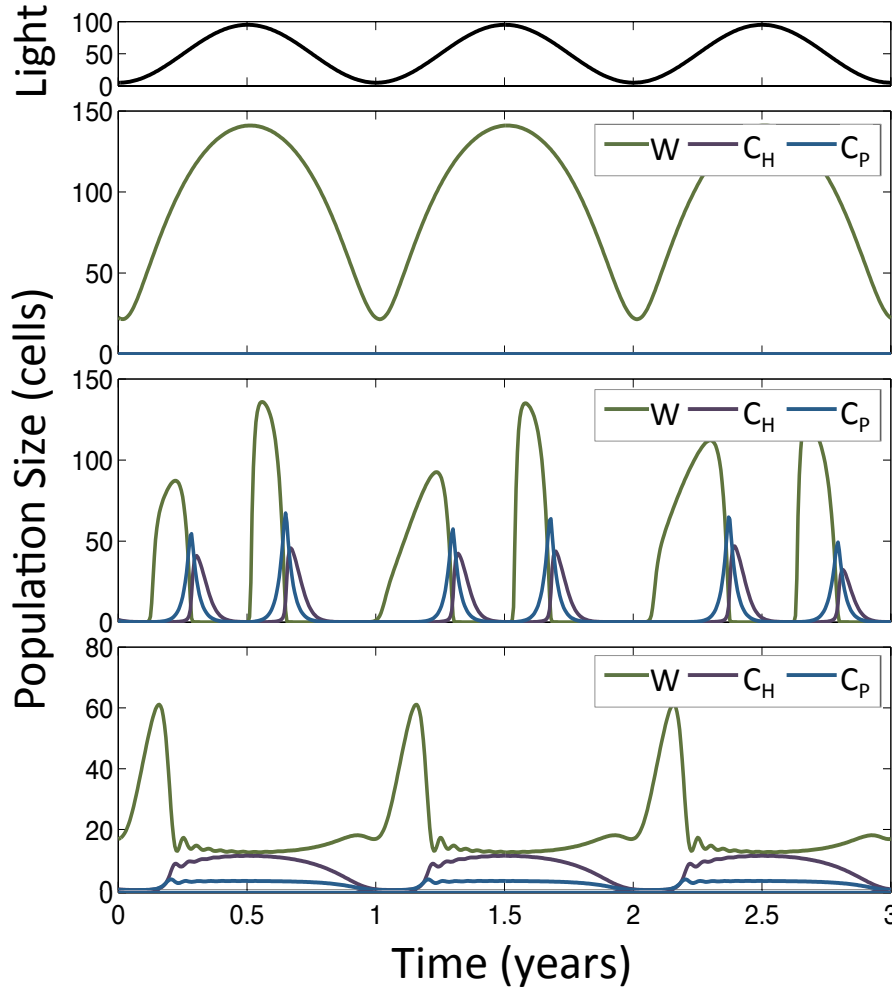
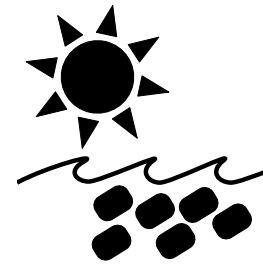
Prey only



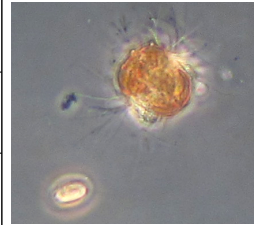
Strict acquired phototroph  
(e.g., *Mesodinium rubrum*)

(image by H. Moeller)

# Blooms depend on degree of mixotrophy



Prey only



Strict acquired phototroph  
(e.g., *Mesodinium rubrum*)

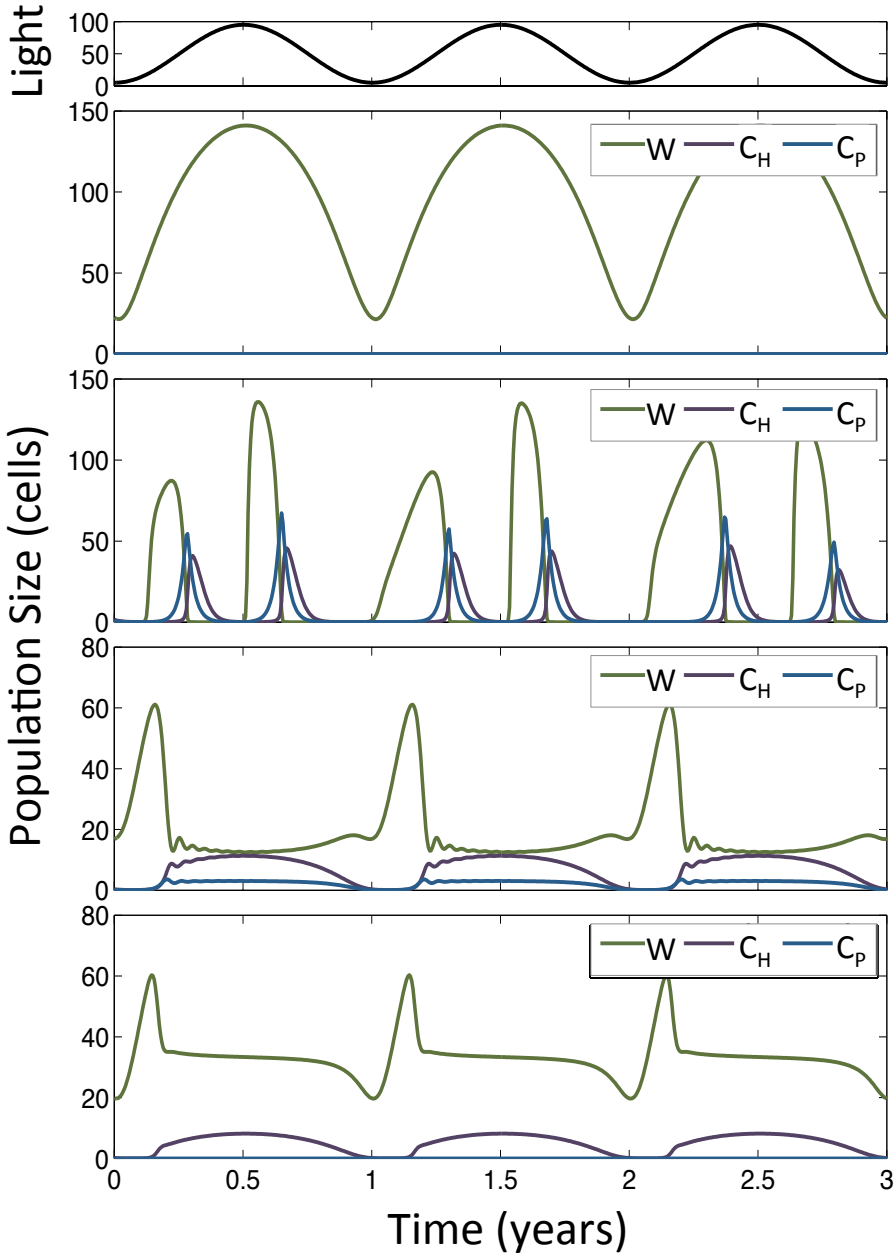
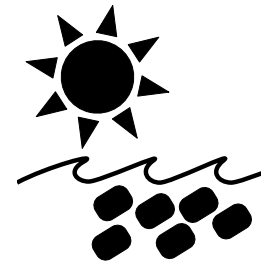
(image by H. Moeller)



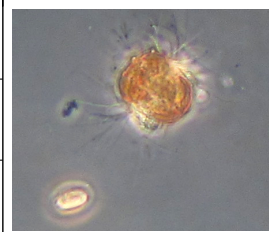
Mixotrophic acquired phototroph  
(e.g., *Strombidium*)

(image courtesy of G. McManus)

# Blooms depend on degree of mixotrophy

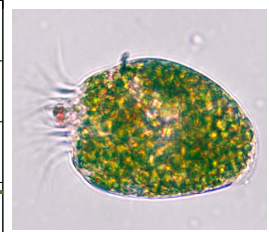


Prey only



Strict acquired phototroph  
(e.g., *Mesodinium rubrum*)

(image by H. Moeller)



Mixotrophic acquired phototroph  
(e.g., *Strombidium*)

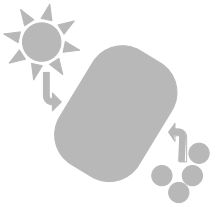
(image courtesy of G. McManus)



Strict heterotroph  
(e.g., *Protoperidinium*)

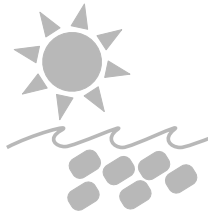
(image by M. Johnson)

# Mixotrophic Modulators of the Biological Pump

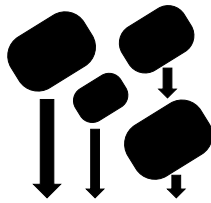


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



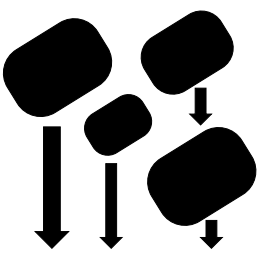
How mixotrophs modulate  
particle flux



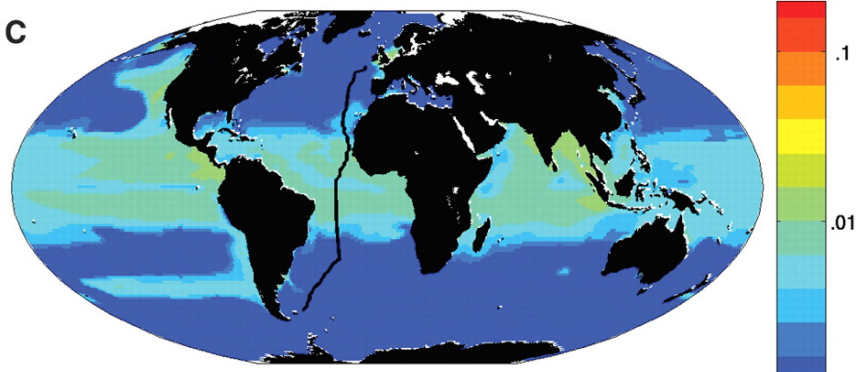
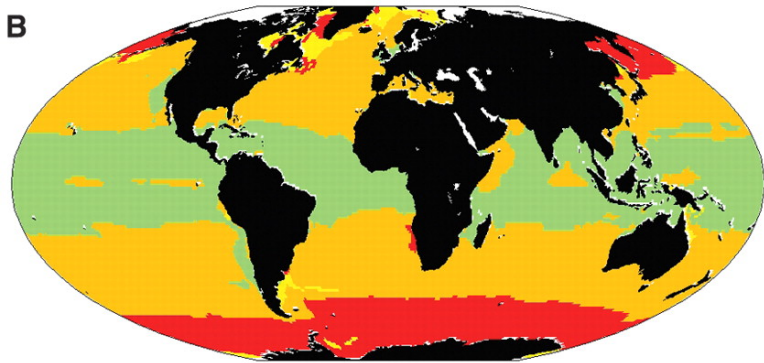
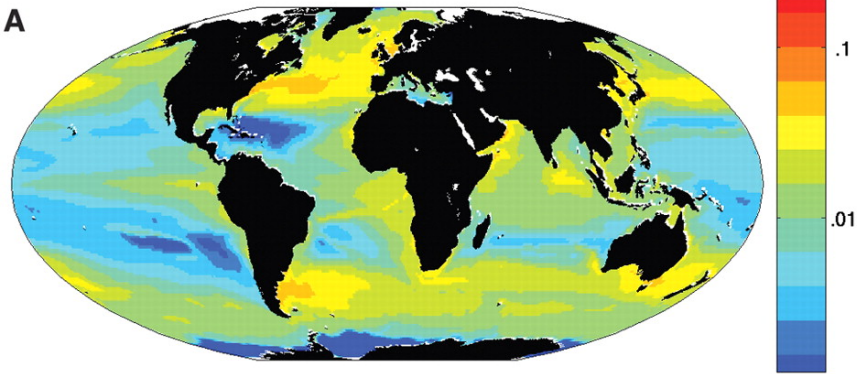
How mixotrophs modulate  
reminereralization rates

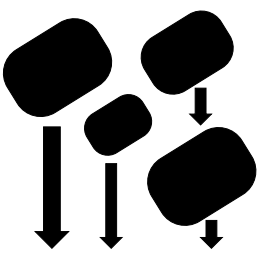


Where and when should mixotrophs matter?

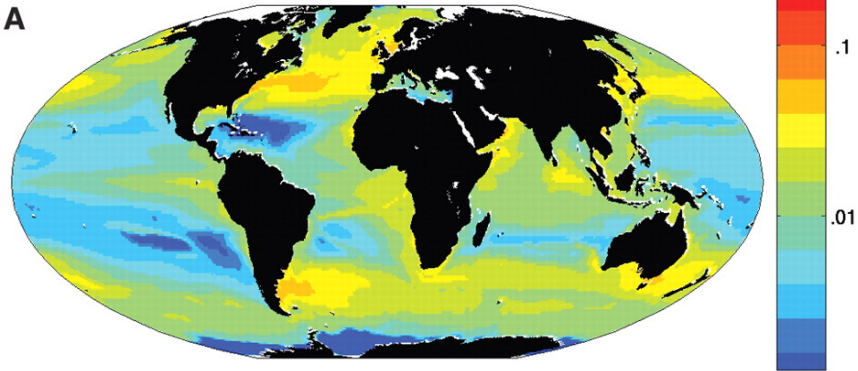


# Modeling mixotrophy at the global scale

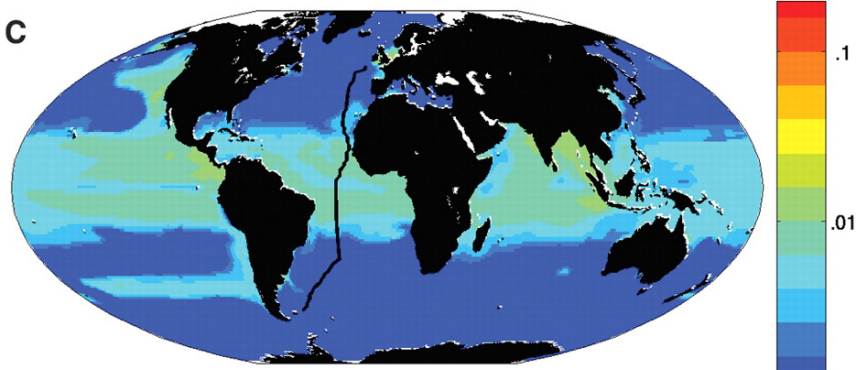
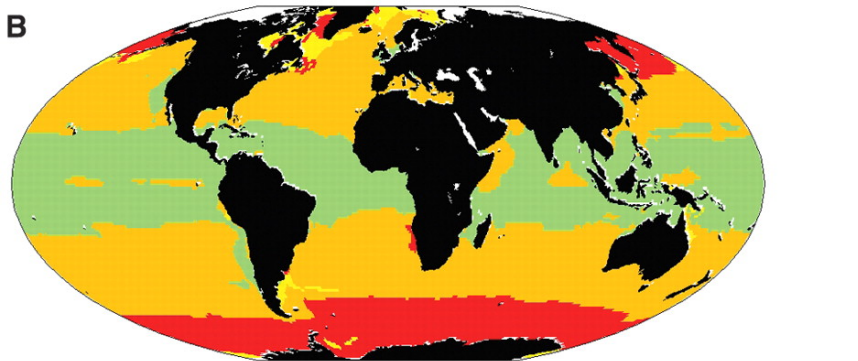




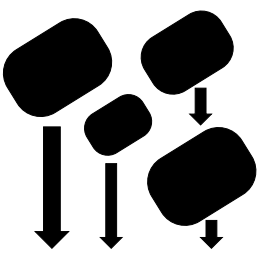
# Modeling mixotrophy at the global scale



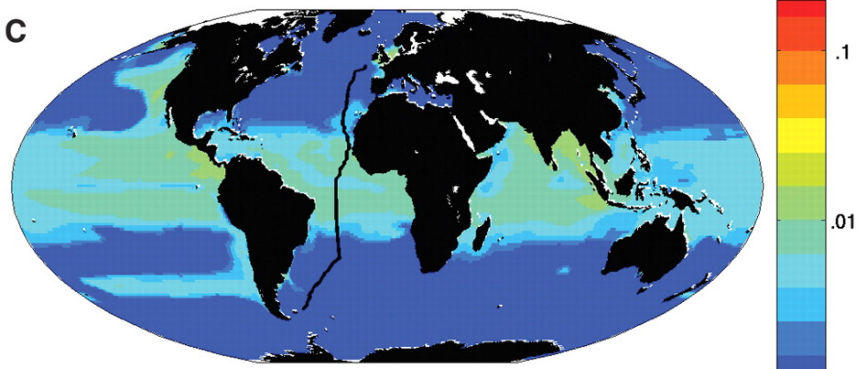
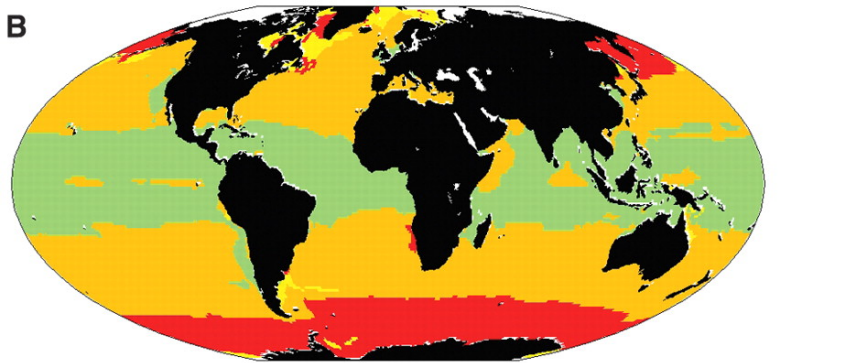
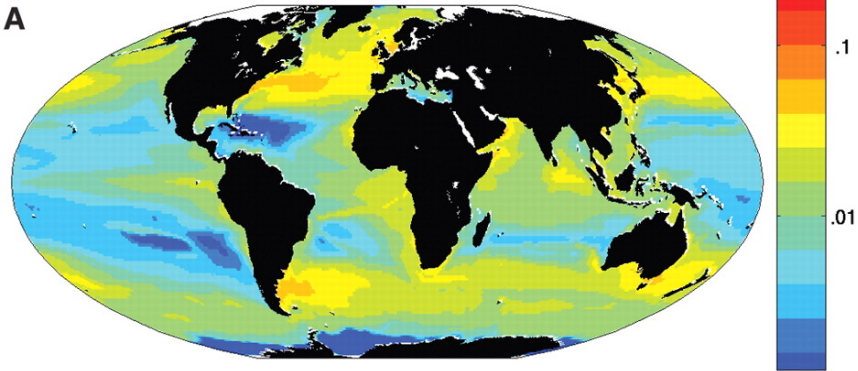
A trait-based approach to modeling marine plankton







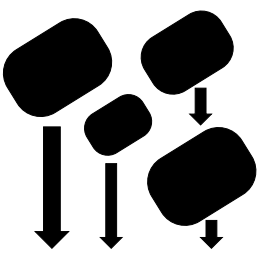
# Modeling mixotrophy at the global scale



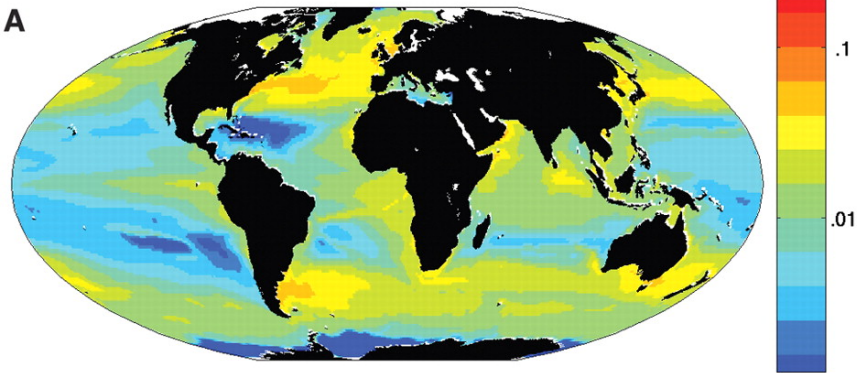
A trait-based approach to modeling marine plankton

- size
- nutrient uptake
- phototrophy or heterotrophy



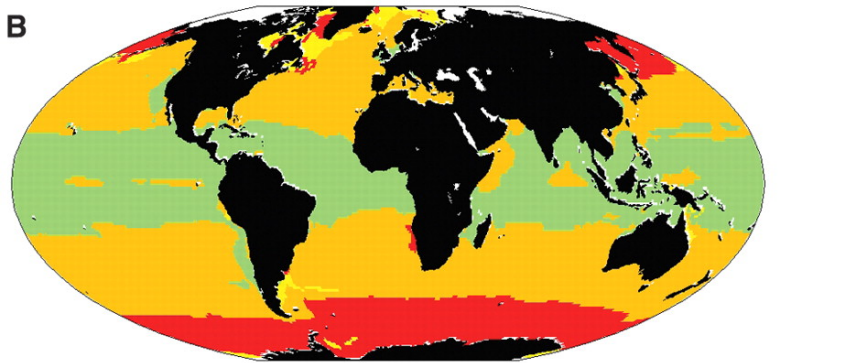


# Modeling mixotrophy at the global scale

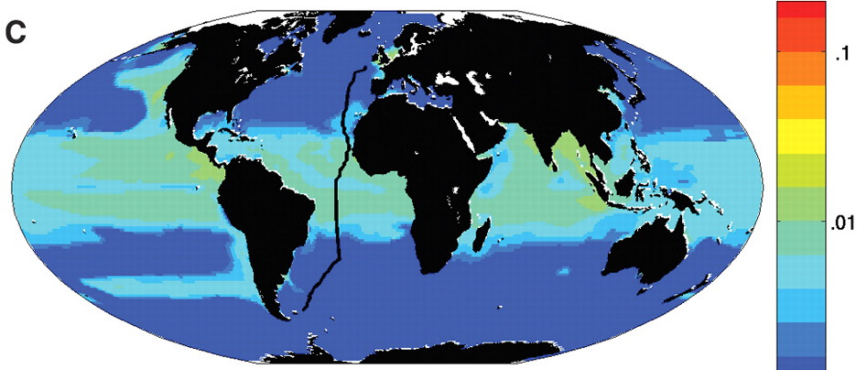


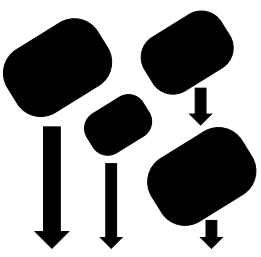
A trait-based approach to modeling marine plankton

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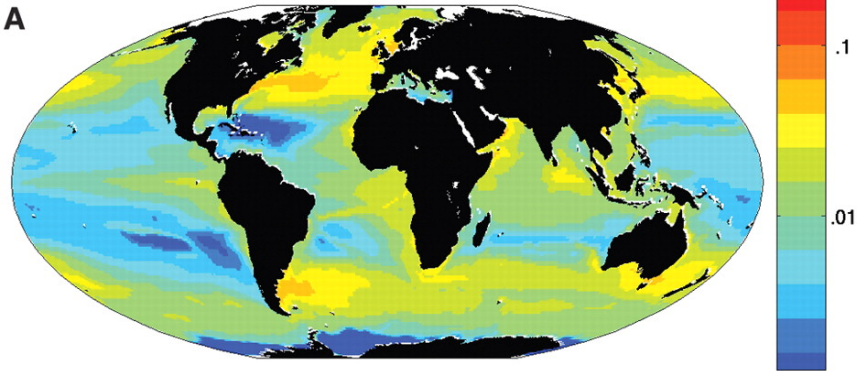


Seed with organisms randomly assigned traits



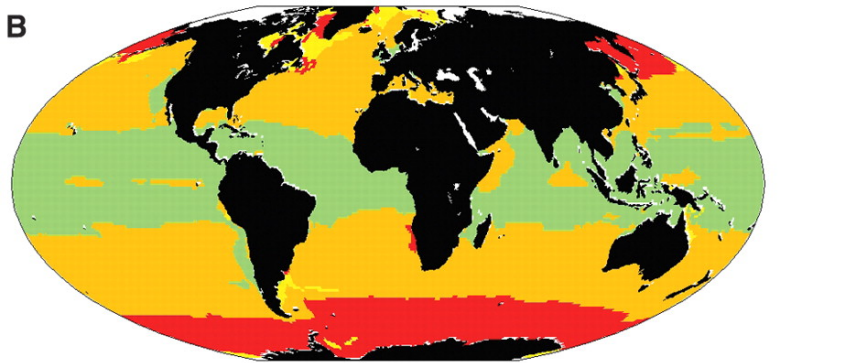


# Modeling mixotrophy at the global scale

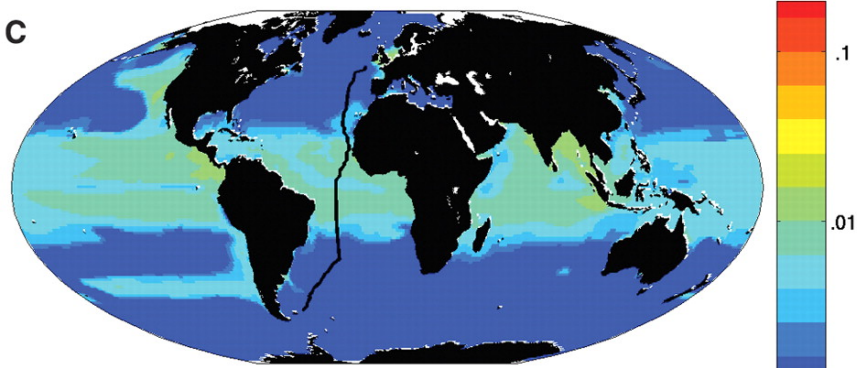


A trait-based approach to modeling marine plankton

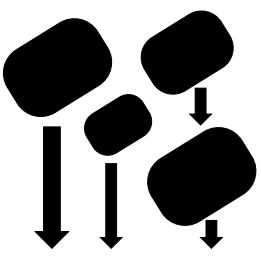
- size
- nutrient uptake
- phototrophy or heterotrophy



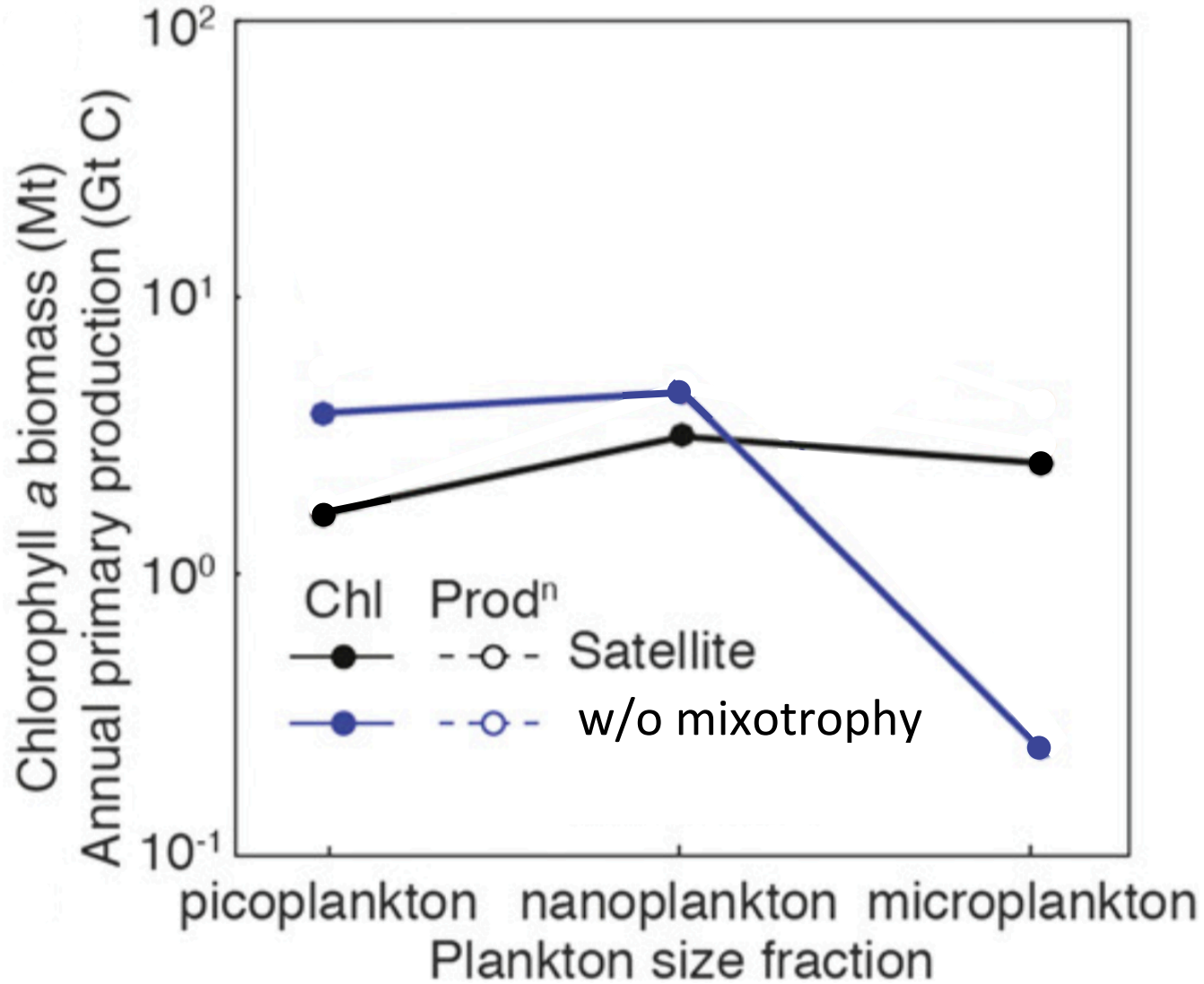
Seed with organisms randomly assigned traits

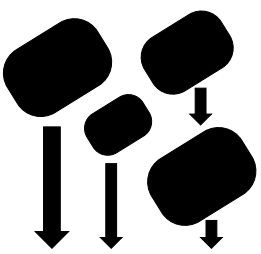


Observe emergent patterns

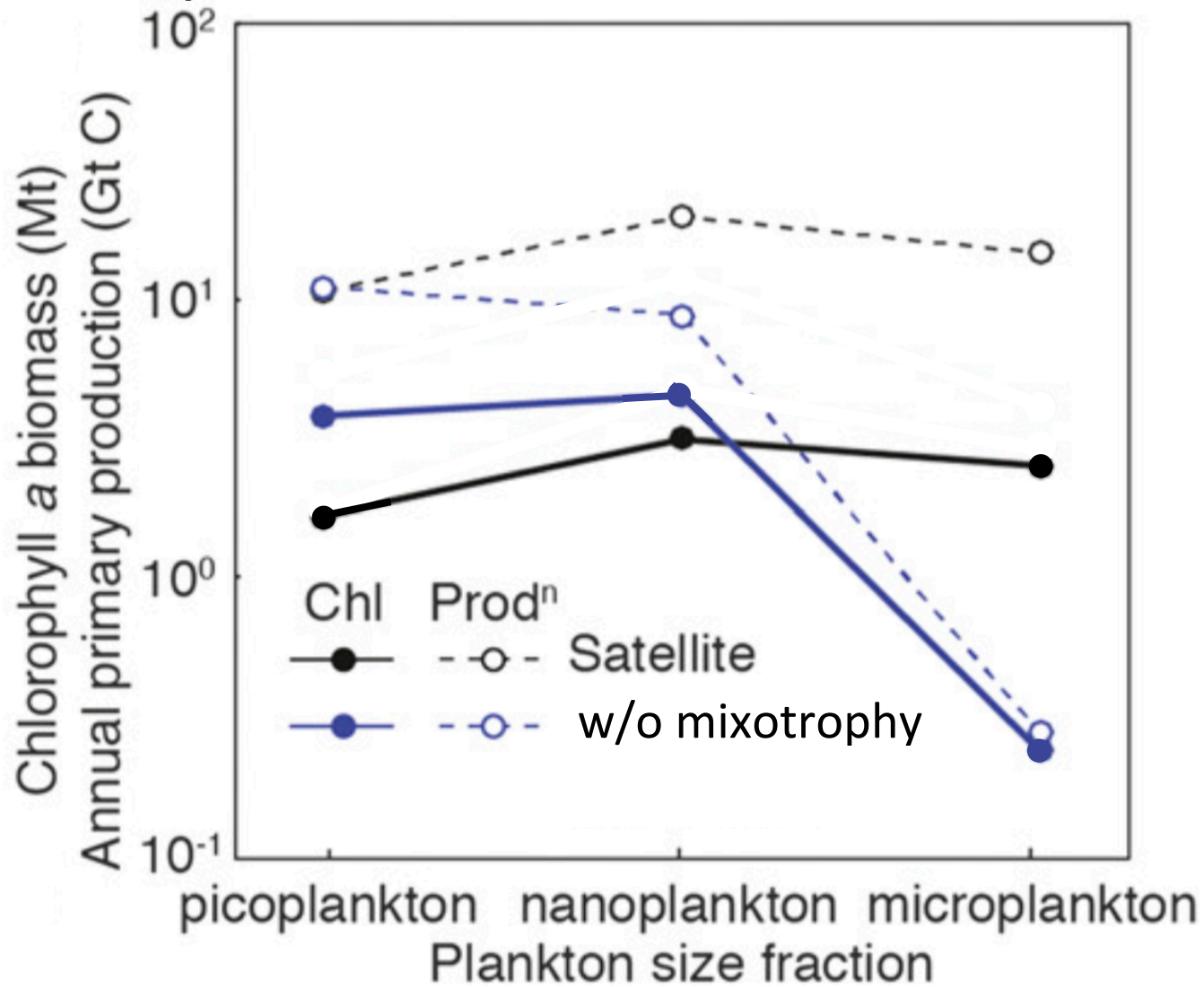


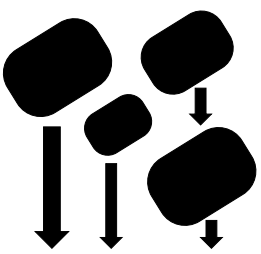
# Allowing for mixotrophy increases mean particle size



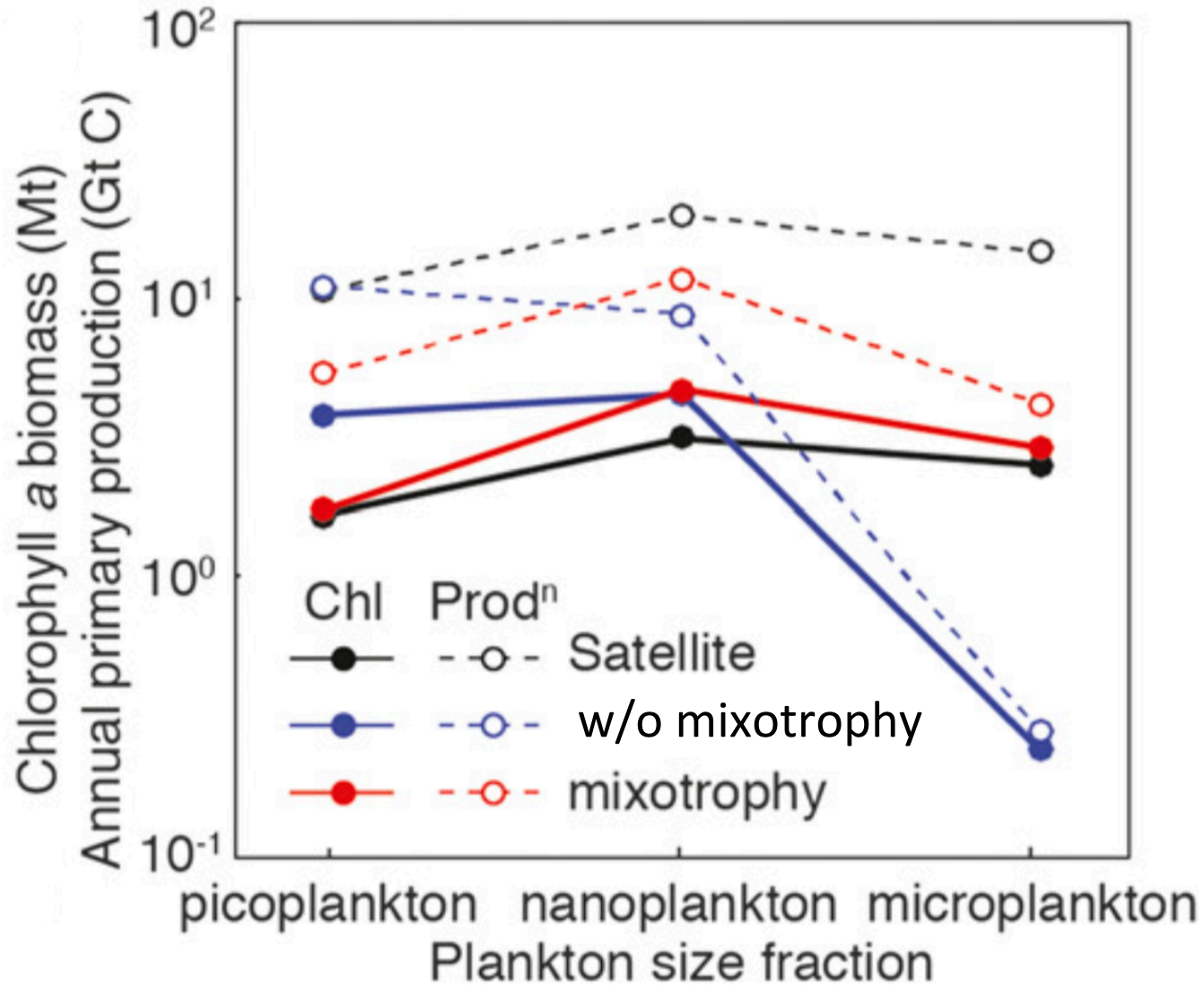


# Allowing for mixotrophy increases mean particle size

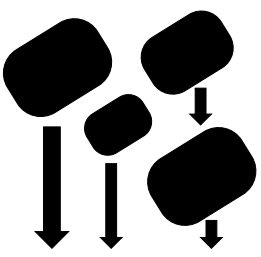




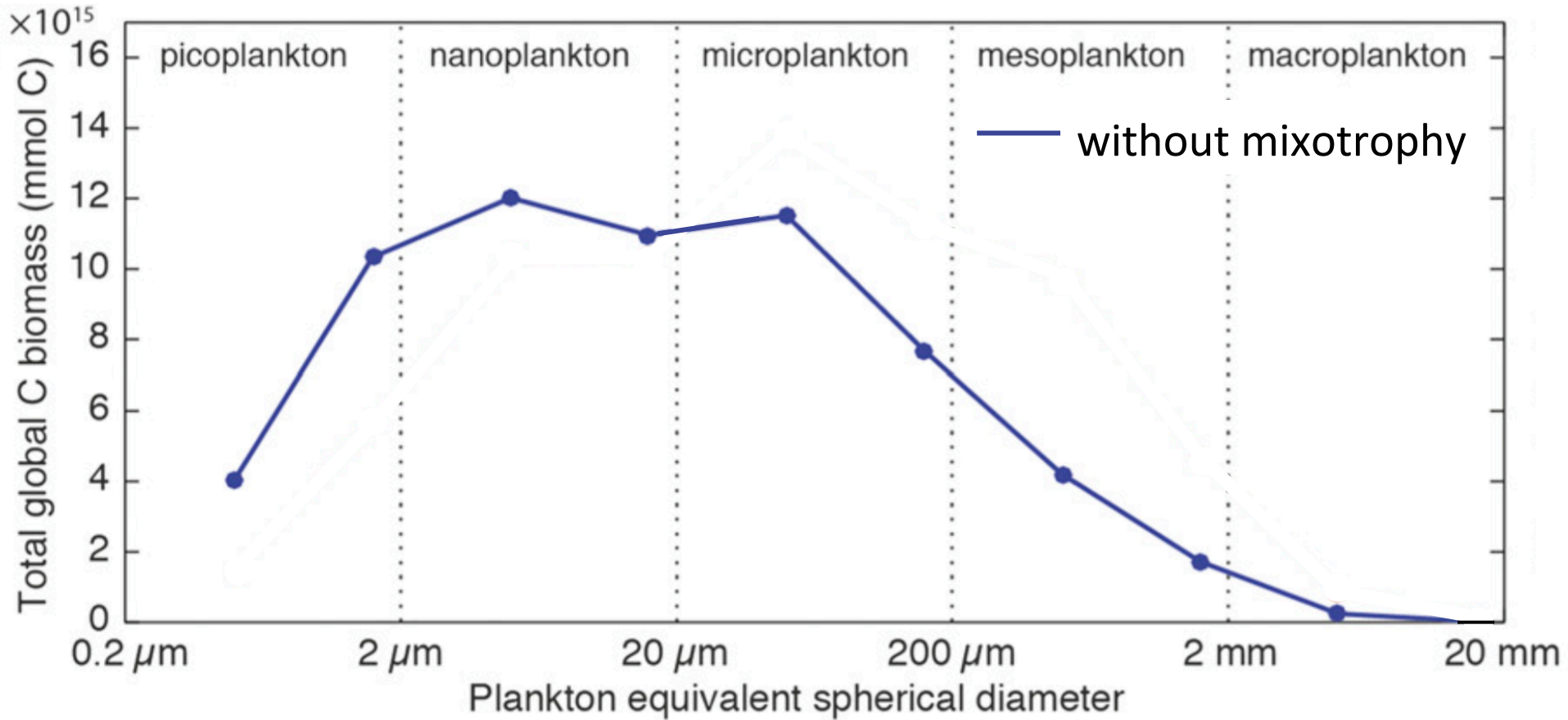
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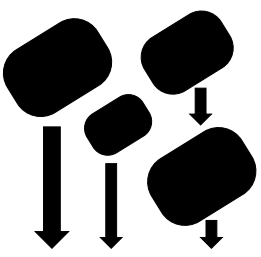




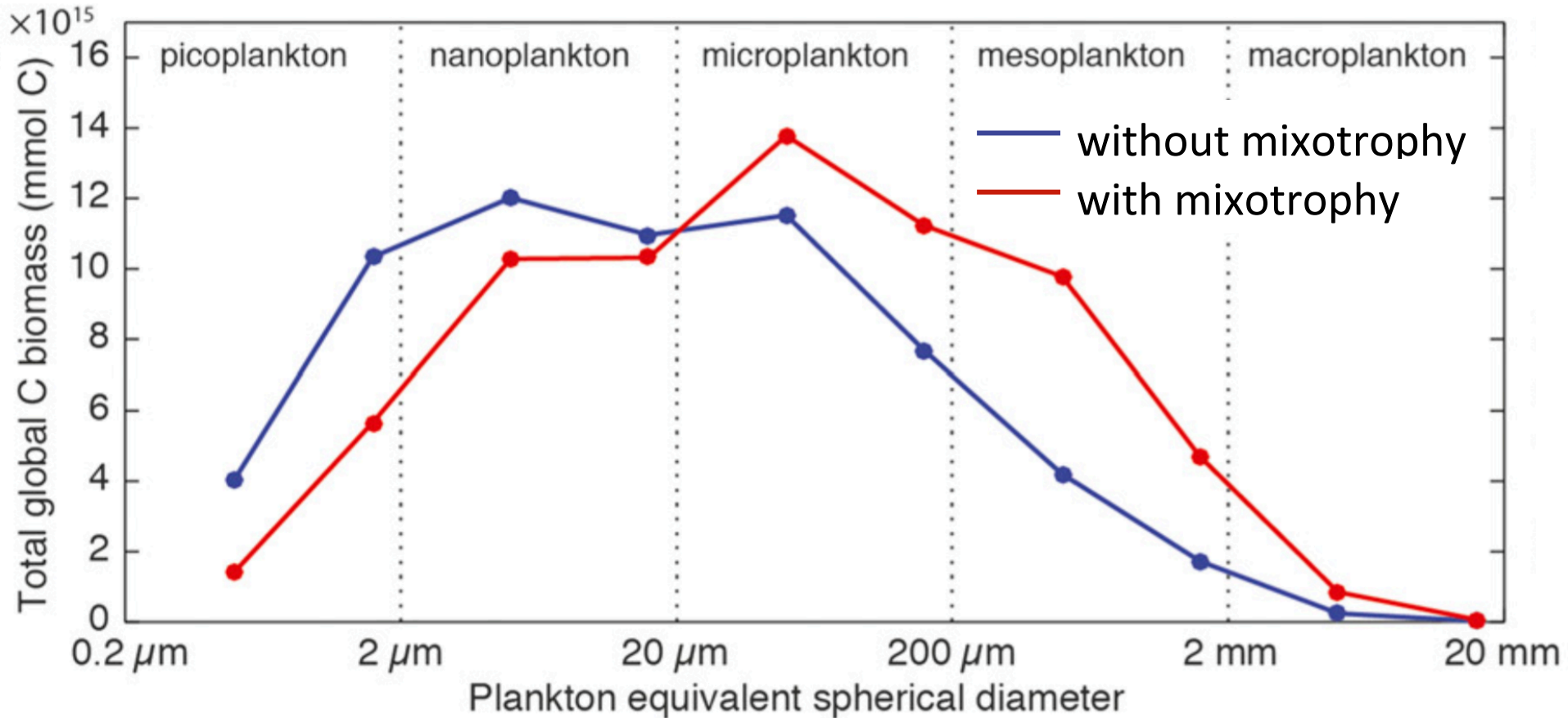


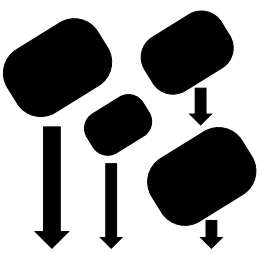
# Allowing for mixotrophy increases mean particle size



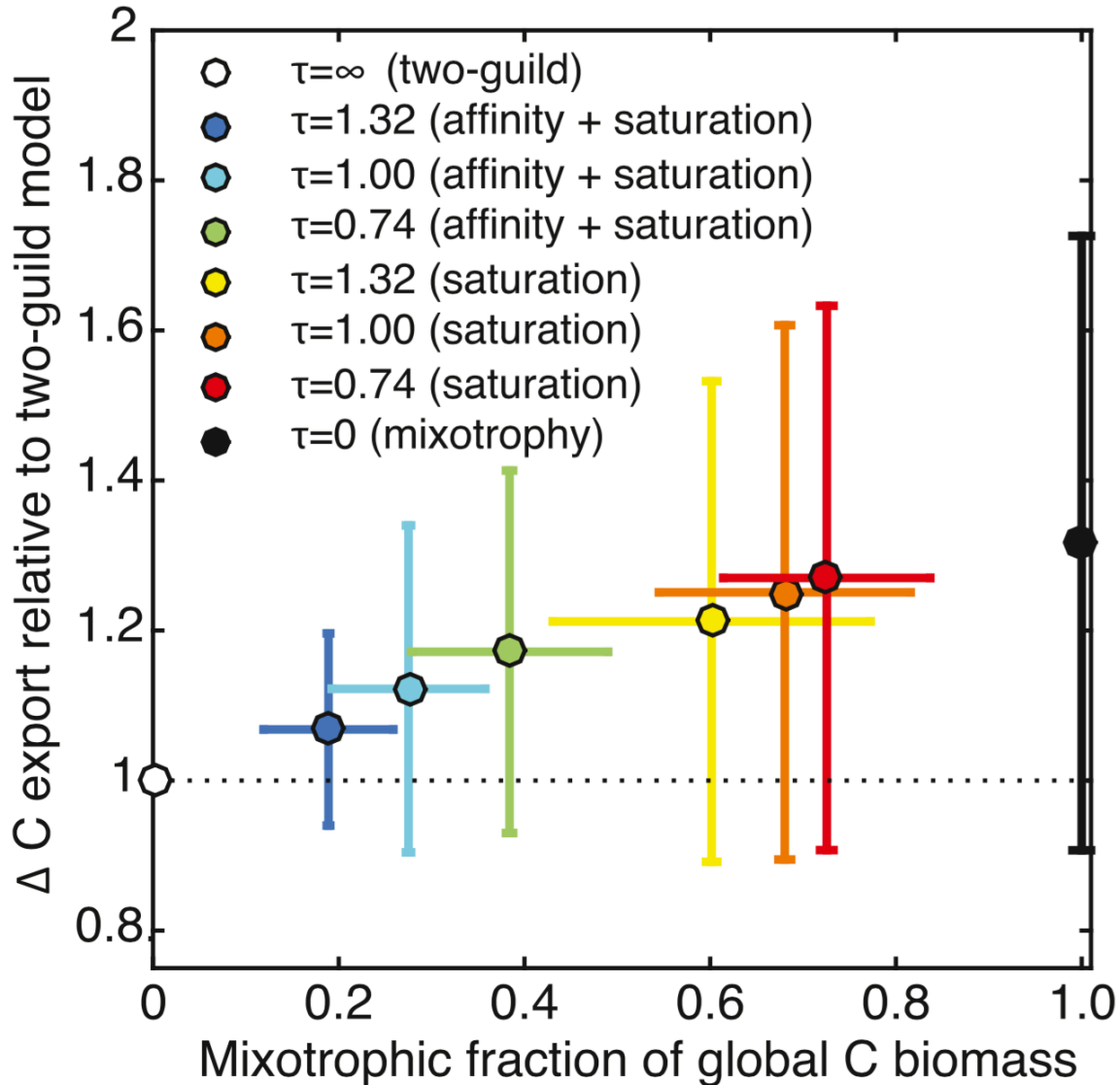


# Allowing for mixotrophy increases mean particle size

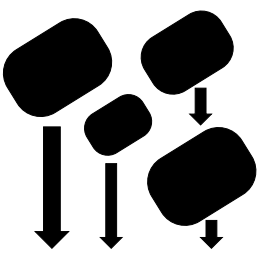




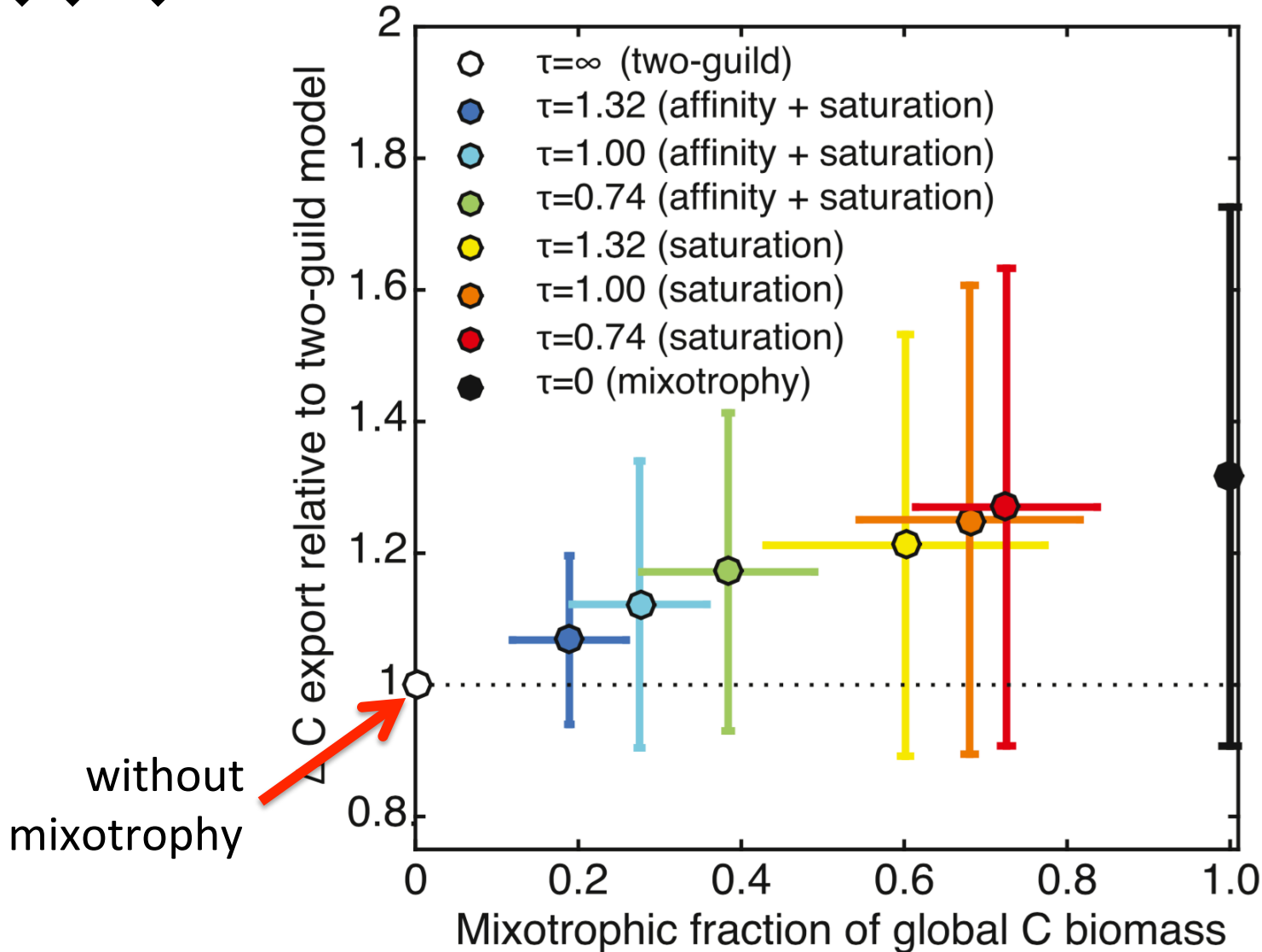
# Allowing for mixotrophy increases mean particle size, increasing C export

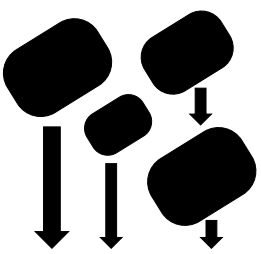




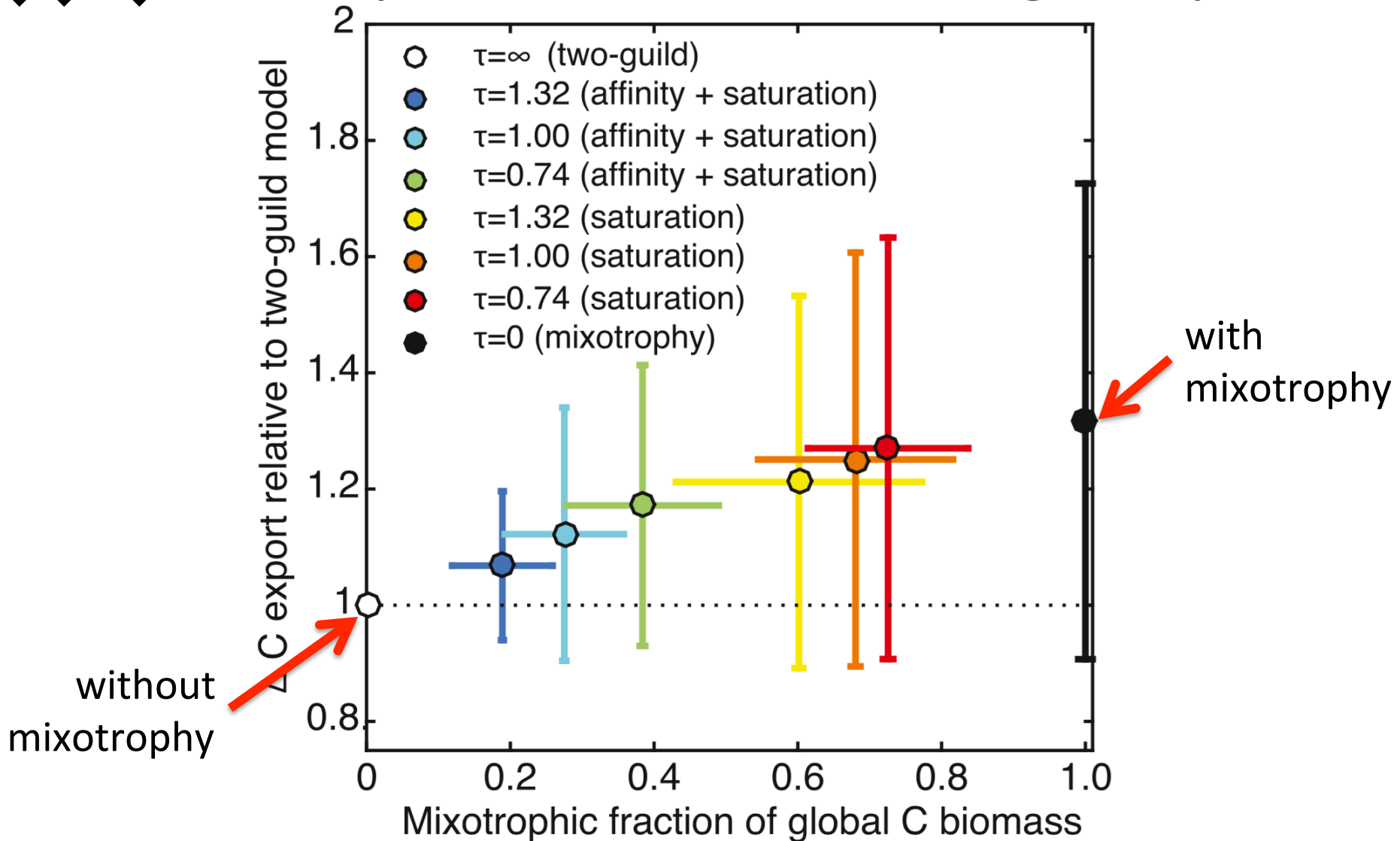


Allowing for mixotrophy increases  
mean particle size, increasing C export

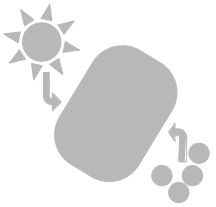




# Allowing for mixotrophy increases mean particle size, increasing C export

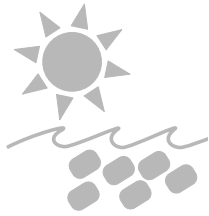


# Mixotrophic Modulators of the Biological Pump

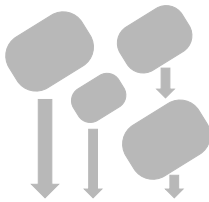


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



How mixotrophs modulate  
particle flux

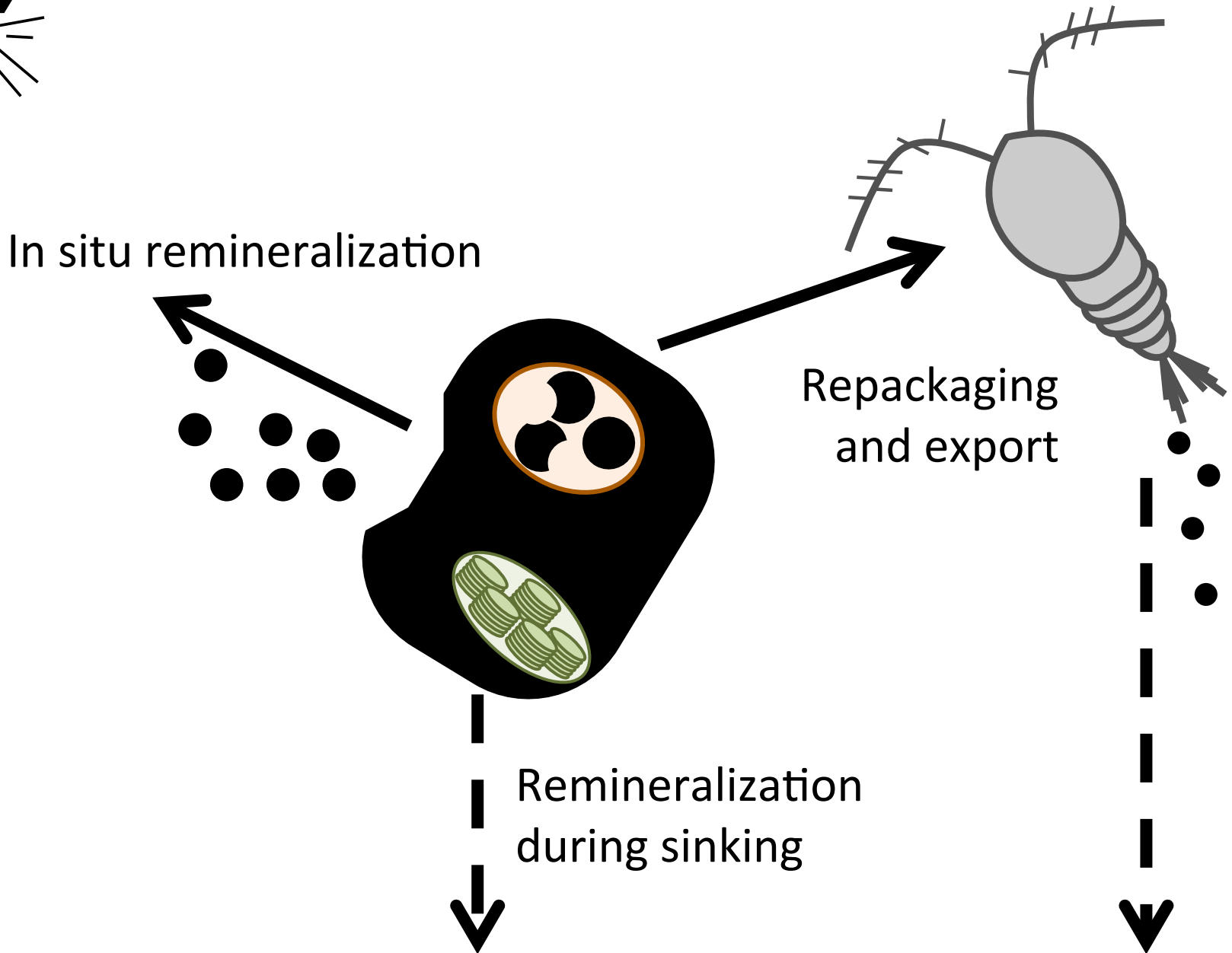


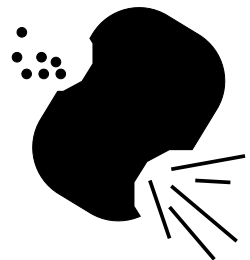
How mixotrophs modulate  
remineralization rates



Where and when should mixotrophs matter?

# Fate of carbon depends on palatability



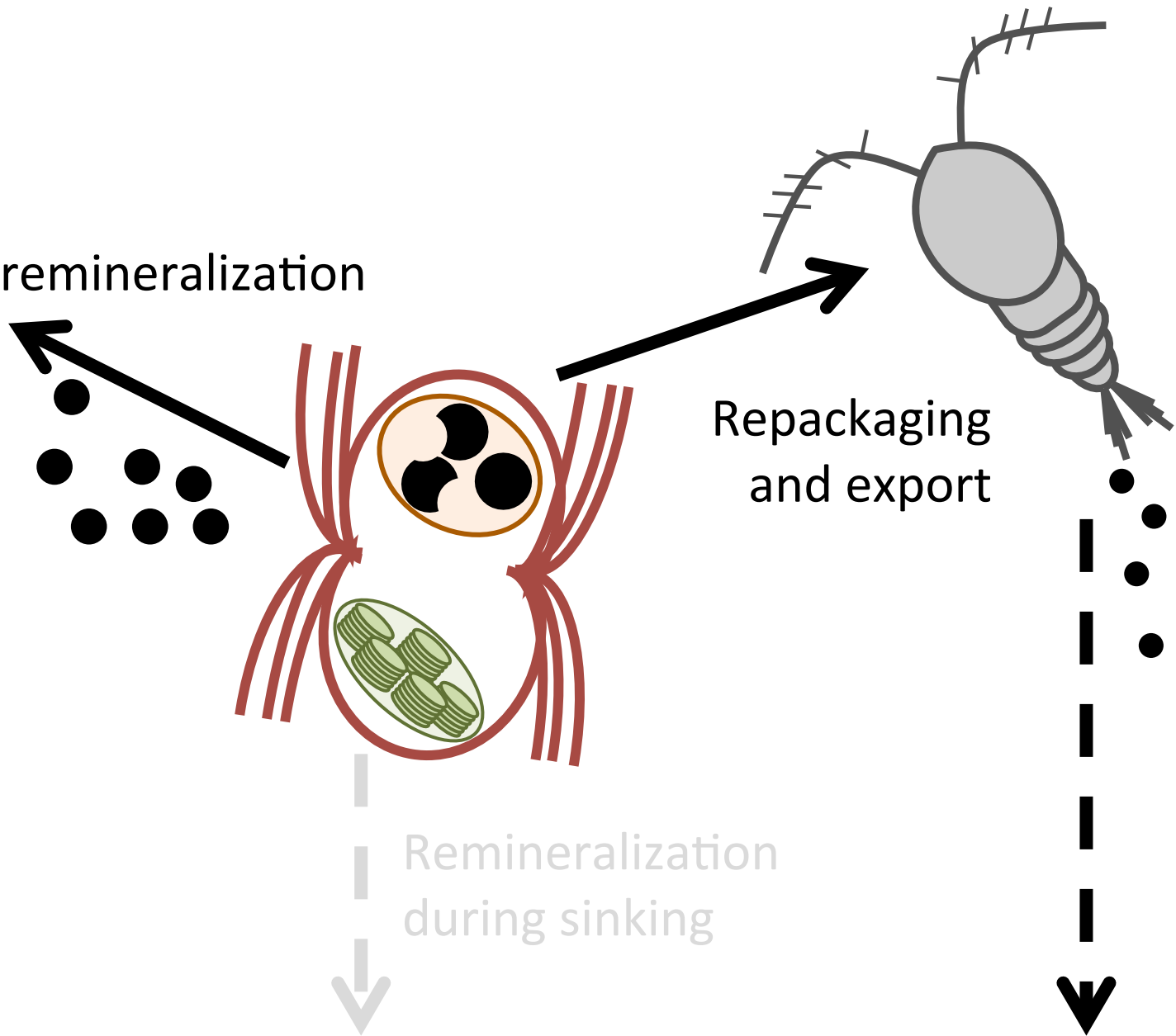


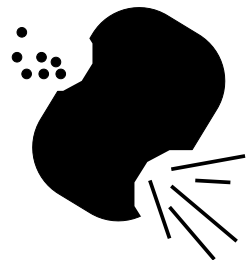
# Fate of carbon depends on palatability

In situ remineralization

Repackaging and export

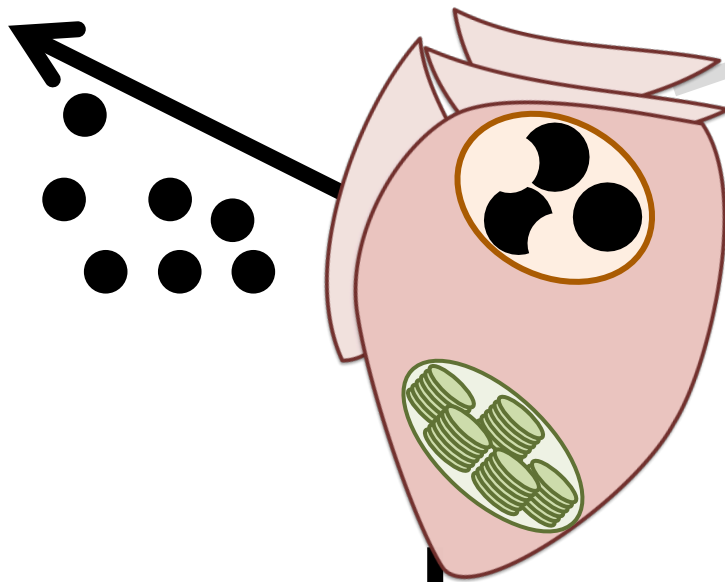
Remineralization during sinking



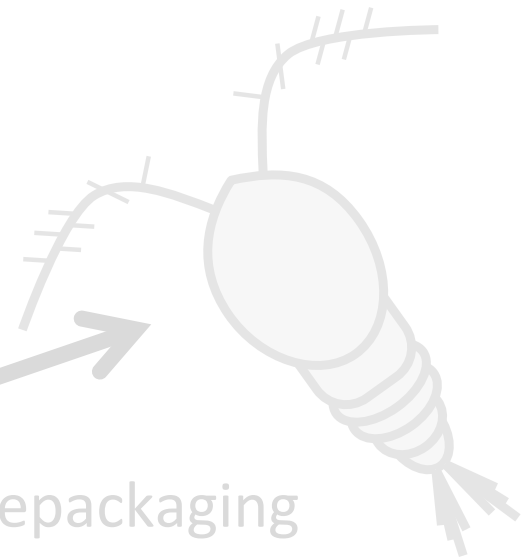


# Fate of carbon depends on palatability

In situ remineralization



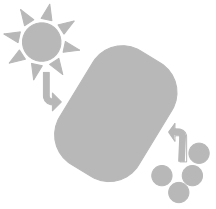
Repackaging and export



Remineralization during sinking

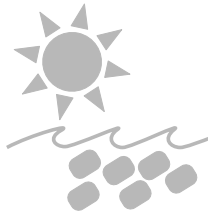


# Mixotrophic Modulators of the Biological Pump

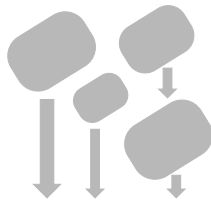


What is a mixotroph?

Impacts on the  
Biological Pump



How mixotrophs modulate  
primary productivity



How mixotrophs modulate  
particle flux



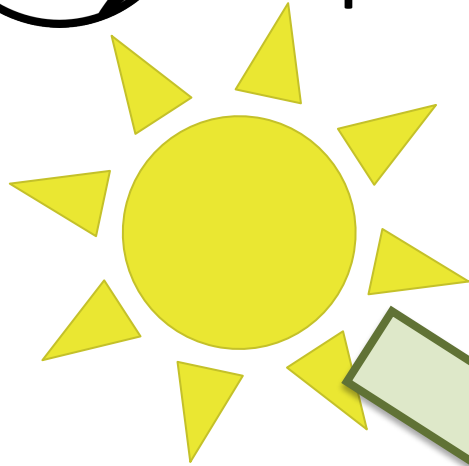
How mixotrophs modulate  
remineralization rates



Where and when should mixotrophs matter?

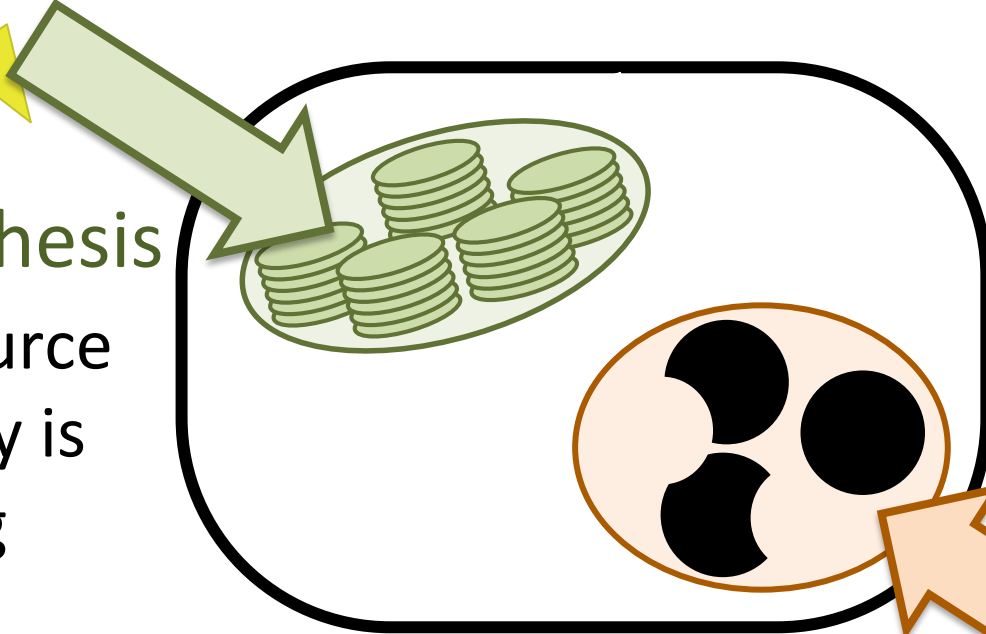


# The mixotroph advantage: Should these “superbugs” be universally dominant?



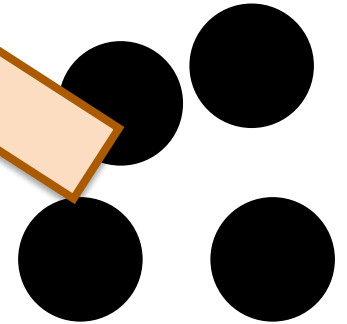
Photosynthesis

Carbon source  
when prey is  
limiting



Nutrient source  
when nutrients  
are limiting

Grazing



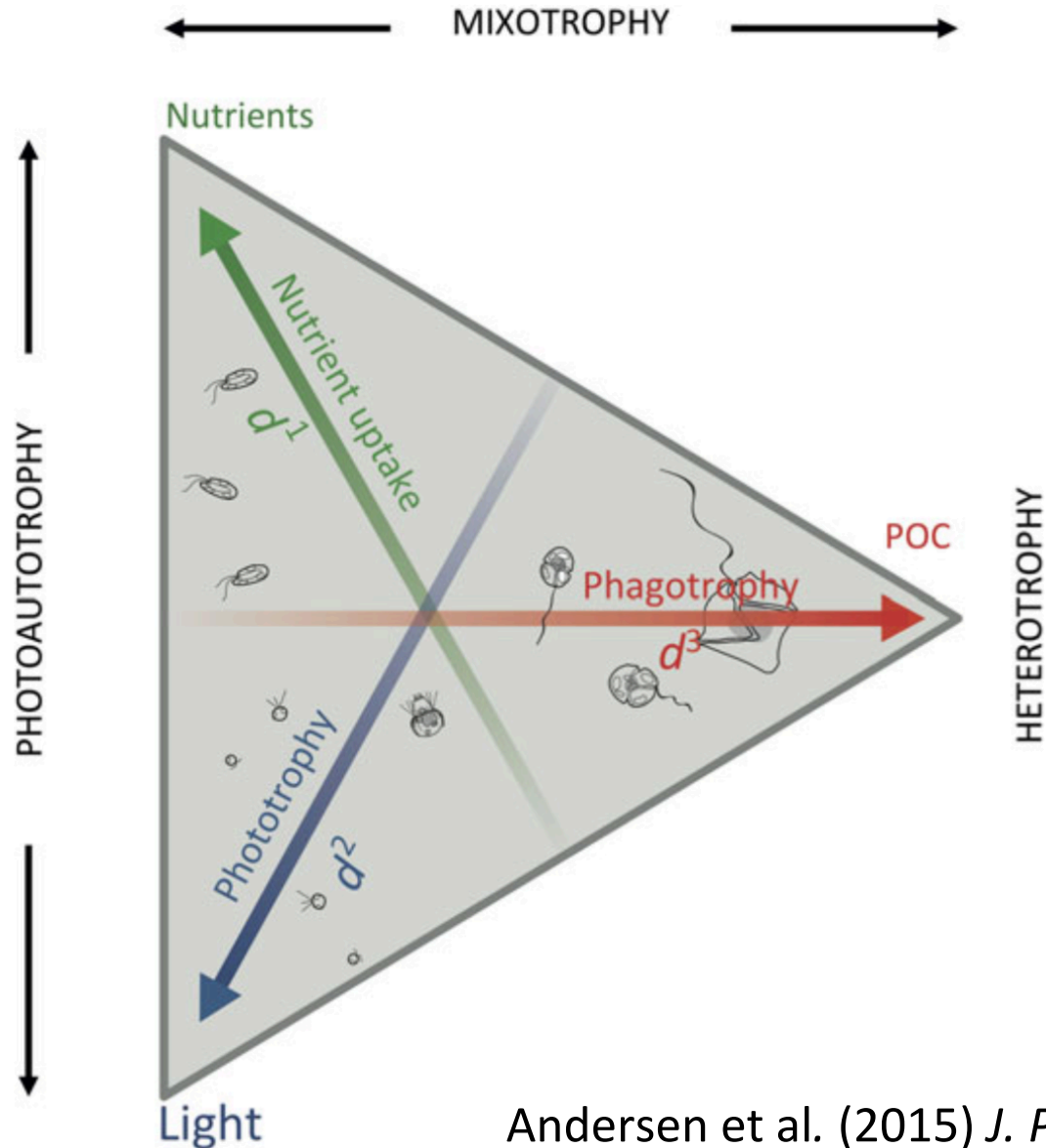
Tittel et al. (2003) *PNAS*

Flynn & Mitra (2009) *J. Plankton Research*



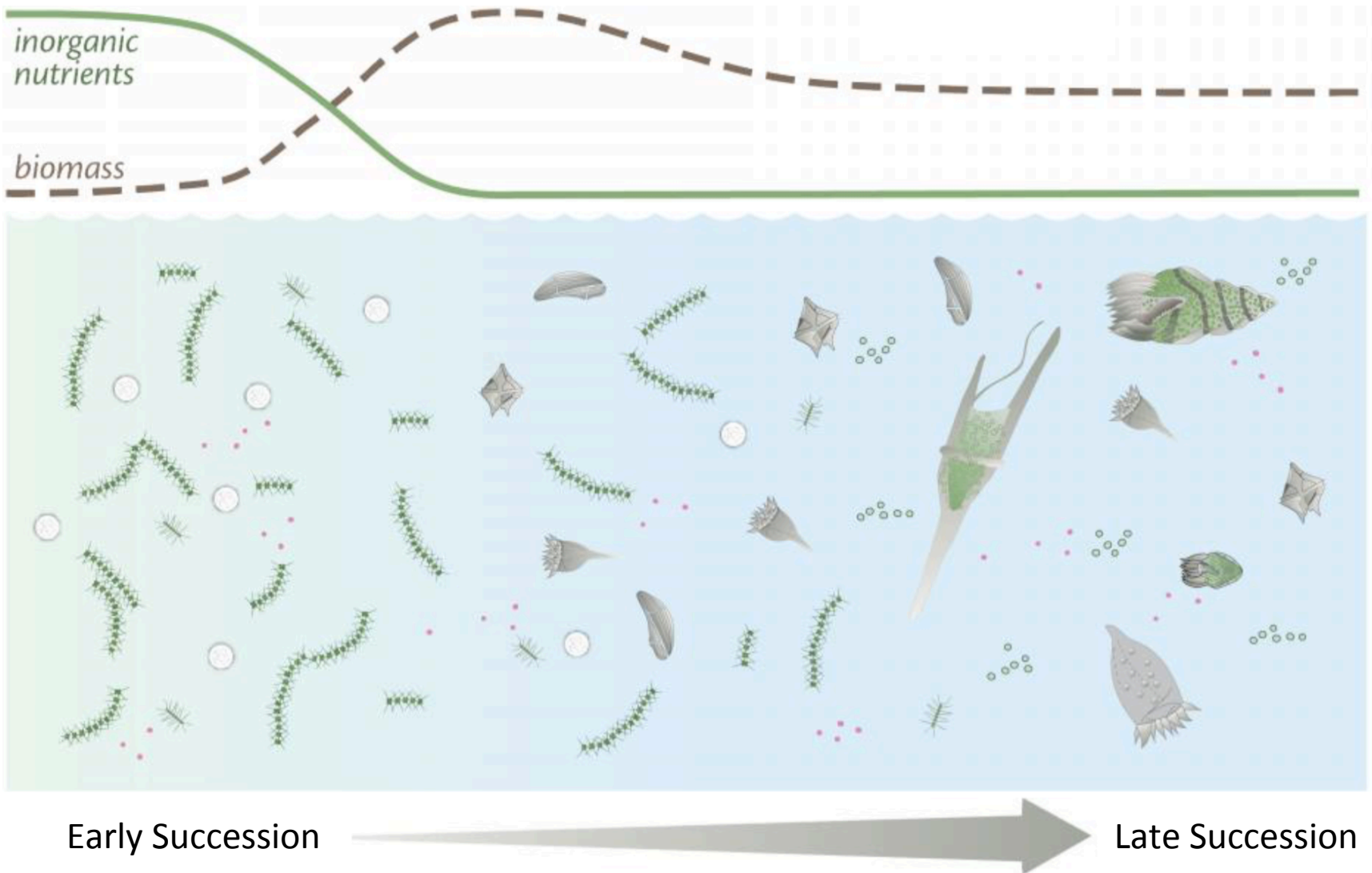


# Key: Quantifying tradeoffs in resource acquisition strategies



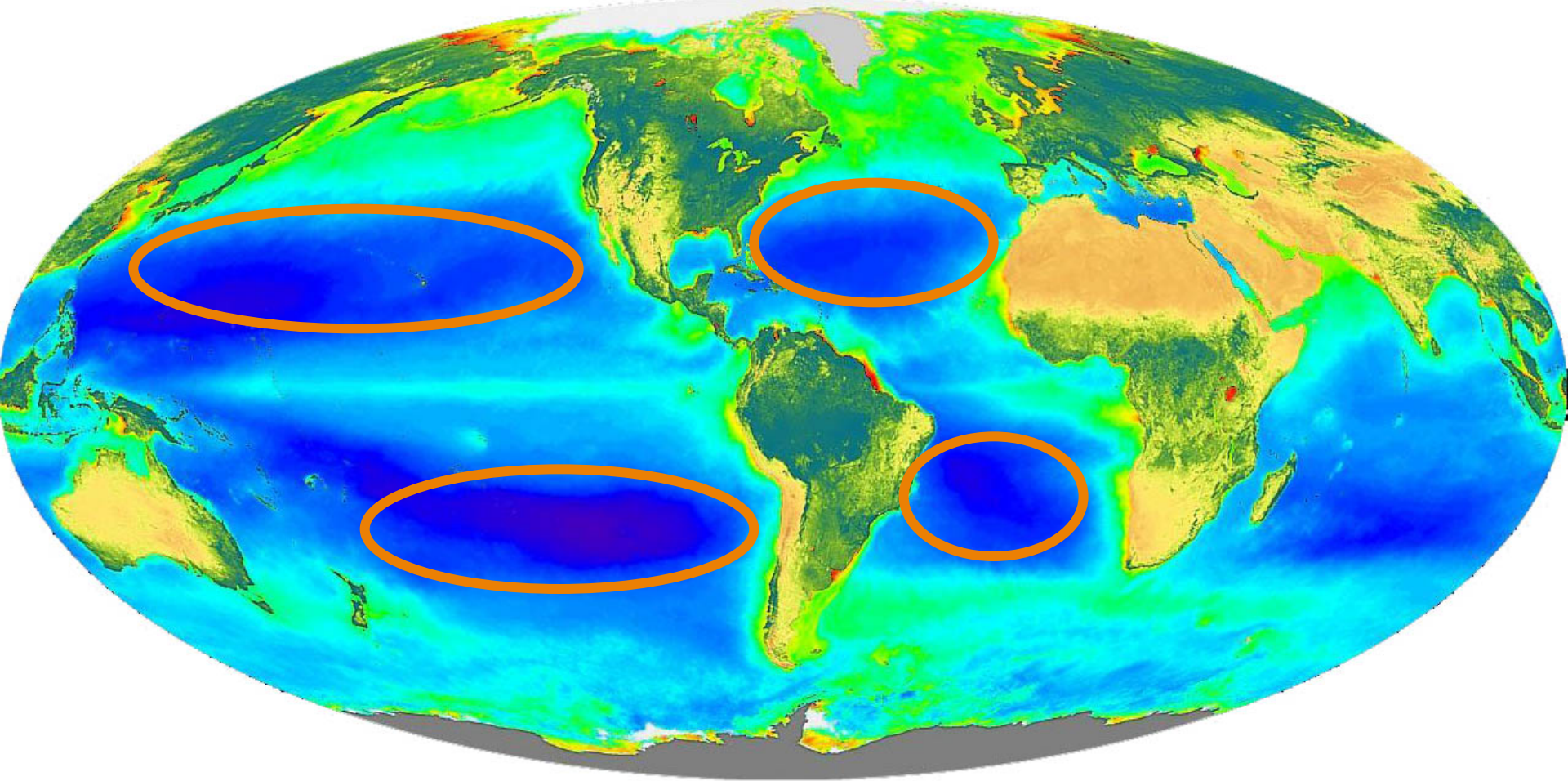


# Mixotrophs have an advantage in low-nutrient, “mature” regimes





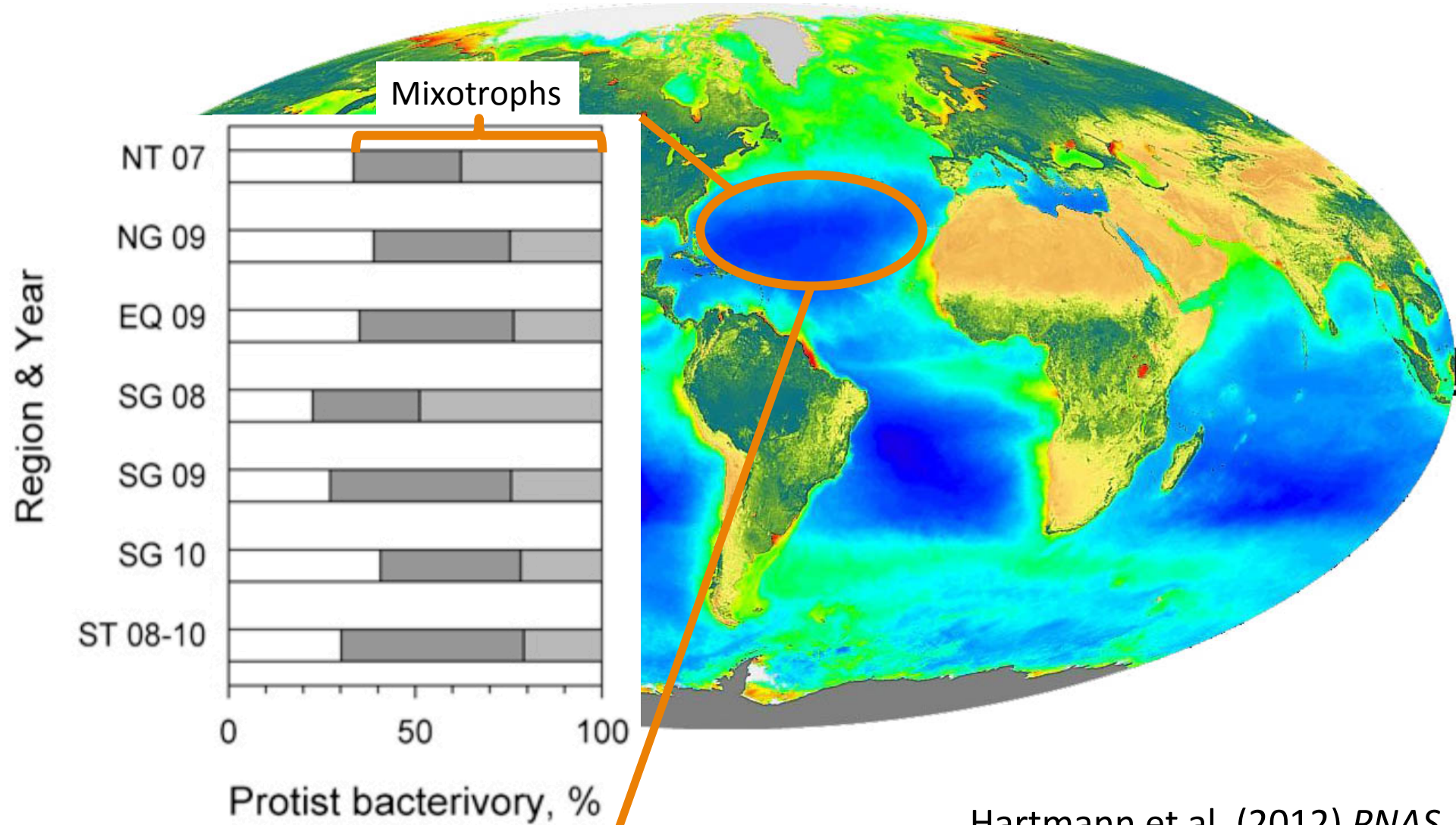
Mixotrophs have an advantage in low-nutrient, “mature” regimes





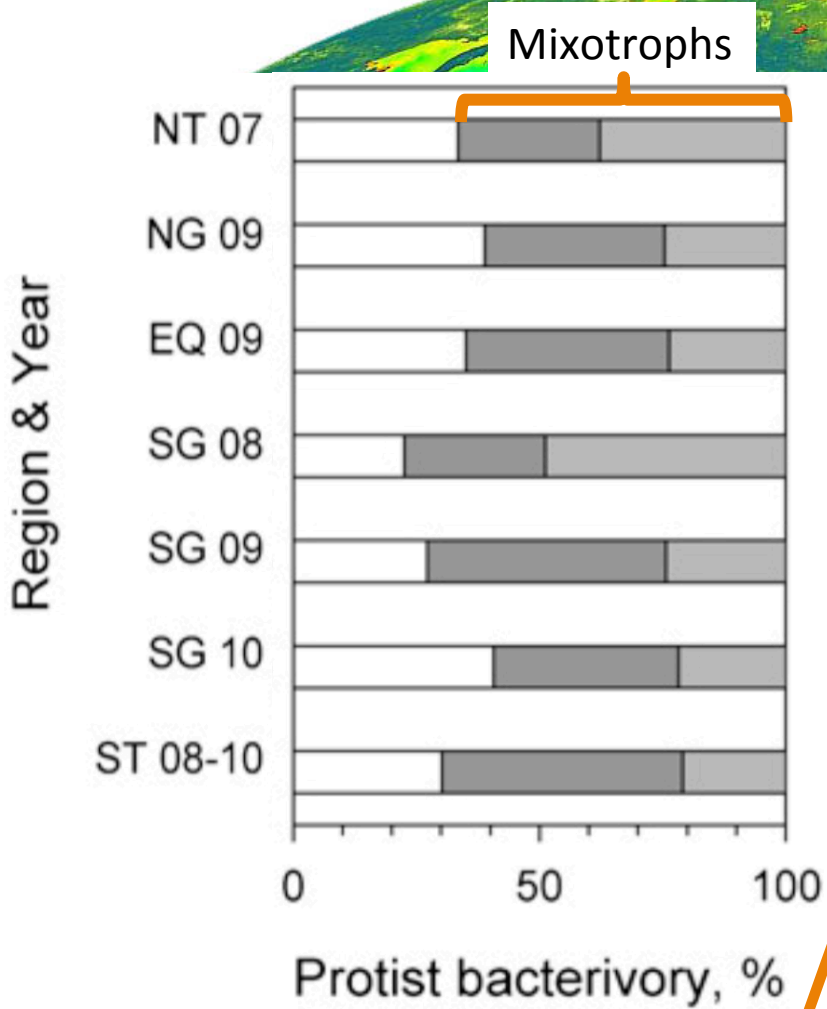
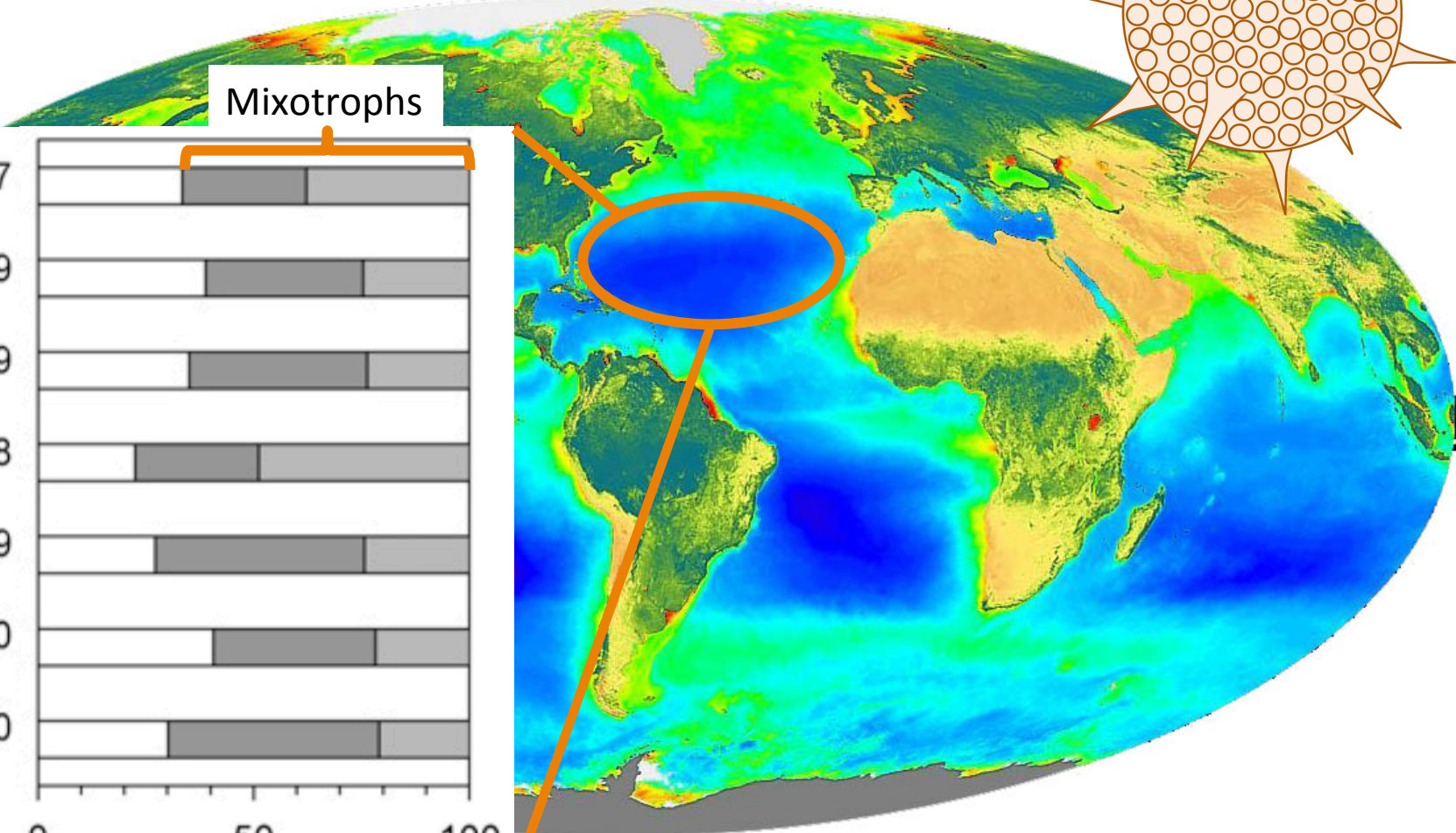
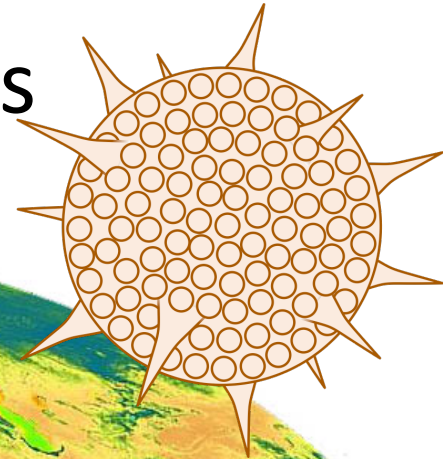


# Mixotrophs have an advantage in low-nutrient, “mature” regimes





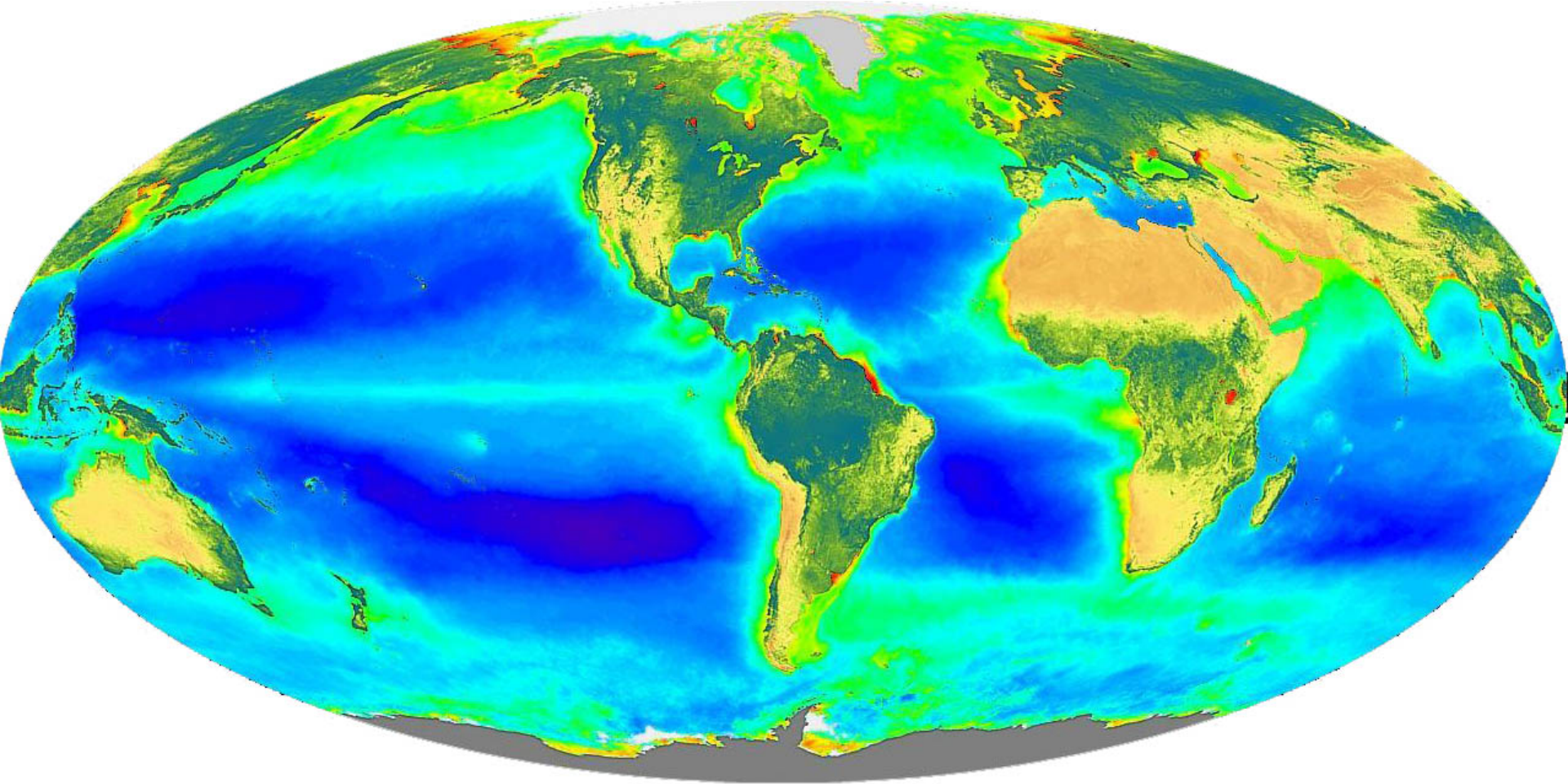
# Mixotrophs have an advantage in low-nutrient, “mature” regimes





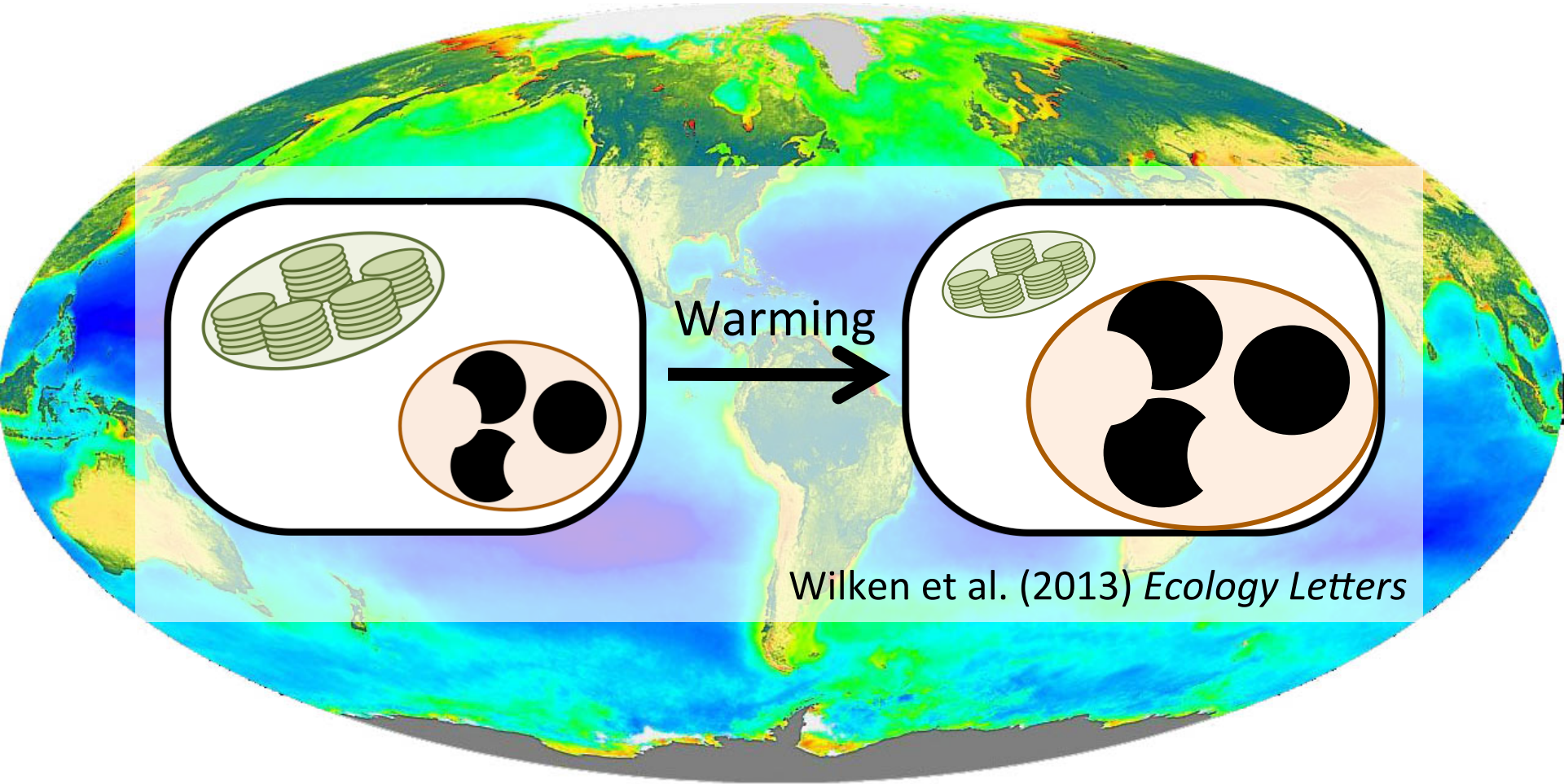


Oligotrophic gyres are also expanding and warming





Oligotrophic gyres are also expanding and warming

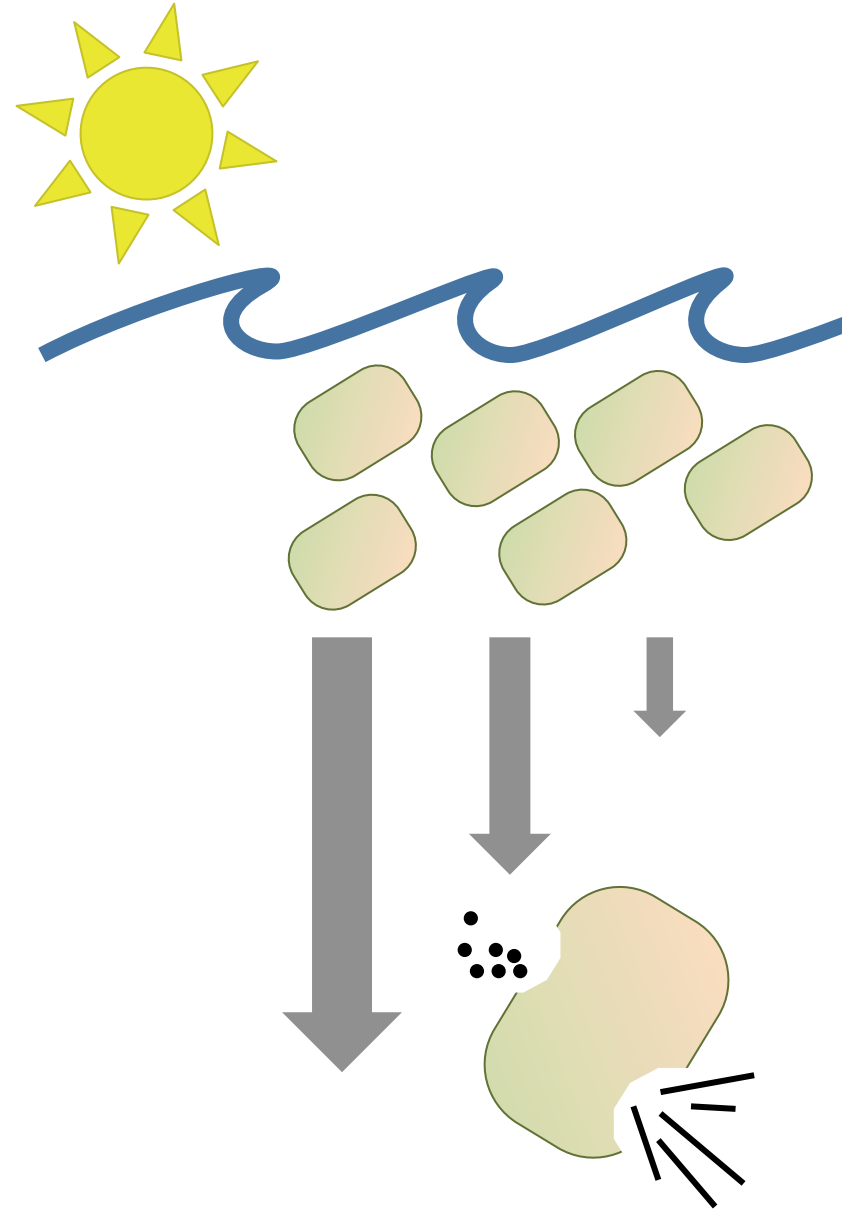


Wilken et al. (2013) *Ecology Letters*

Polovina et al. (2008) *Geophys. Res. Lett.*



# Moving forward with mixotrophy

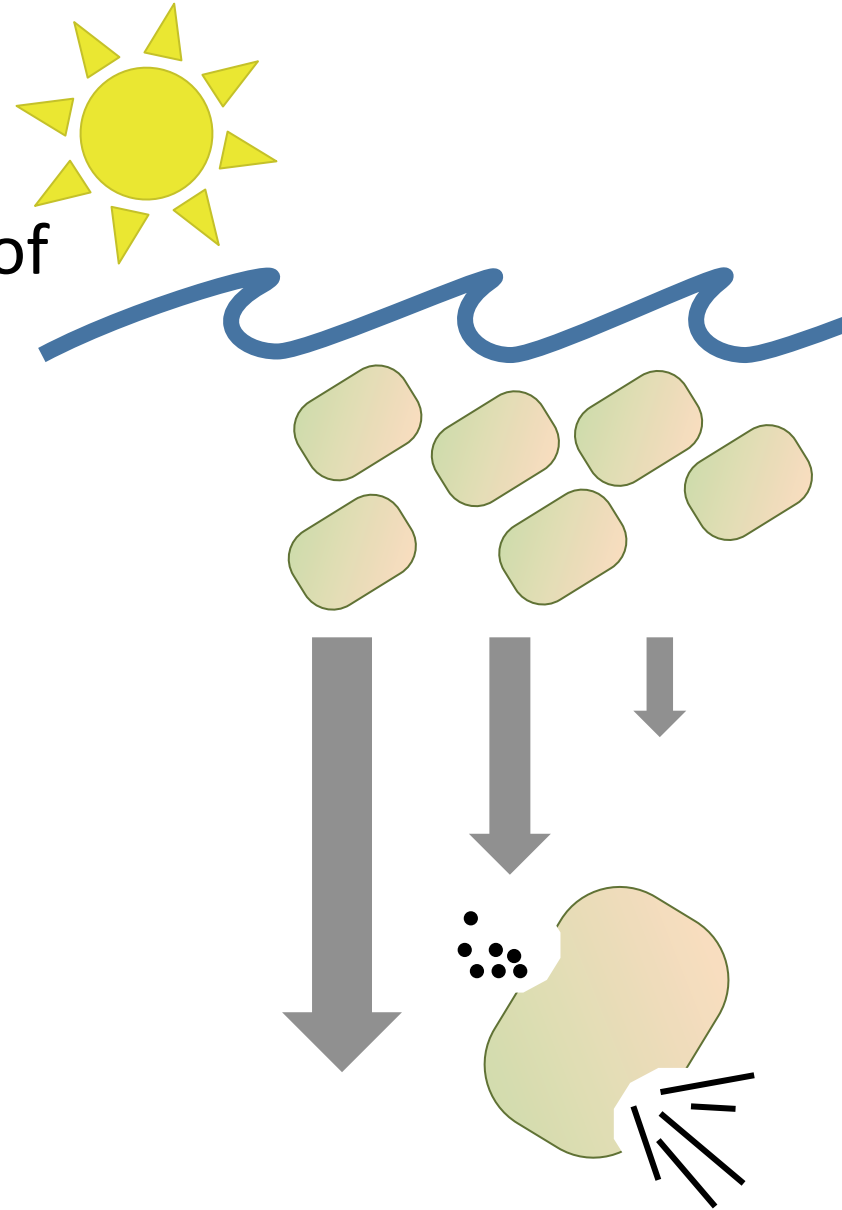






# Moving forward with mixotrophy

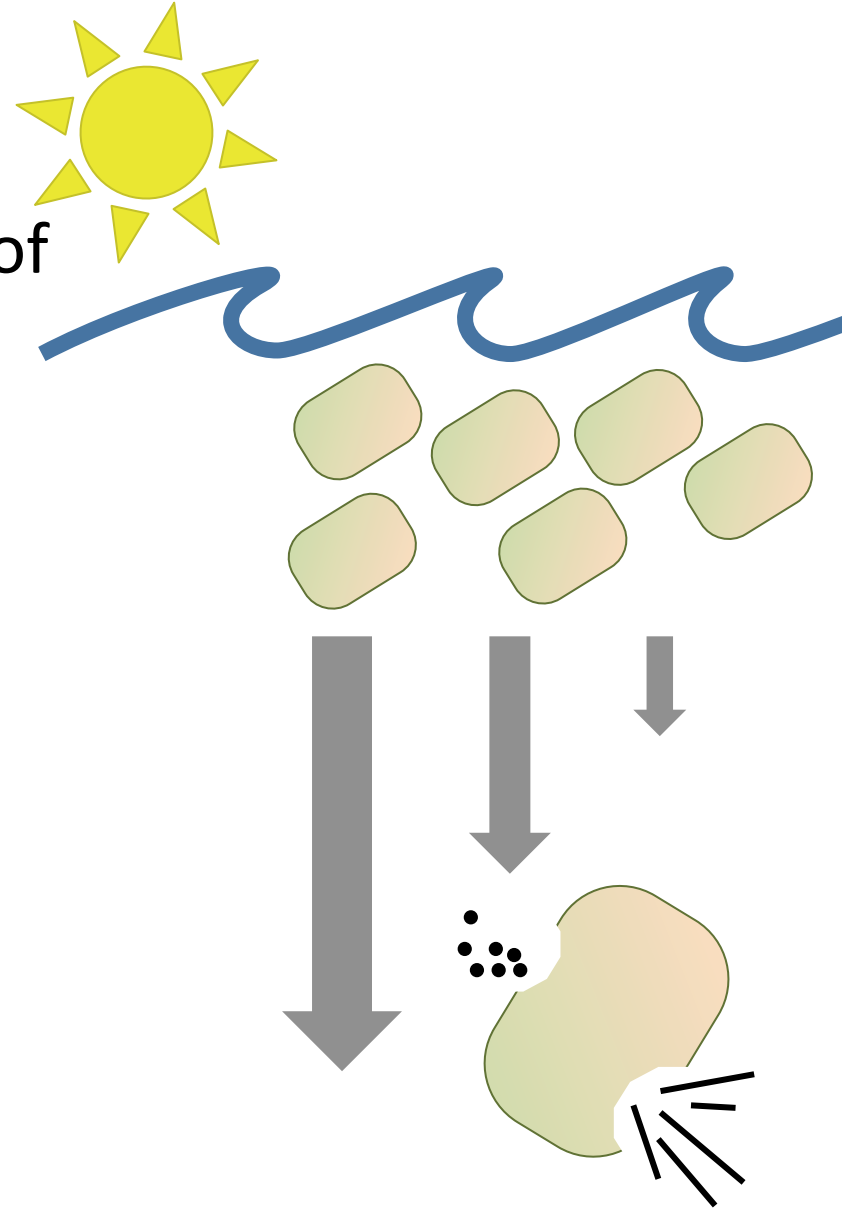
1. Mixotrophy affects the amount of primary production





# Moving forward with mixotrophy

1. Mixotrophy affects the amount of primary production
  - Allows extra carbon fixation

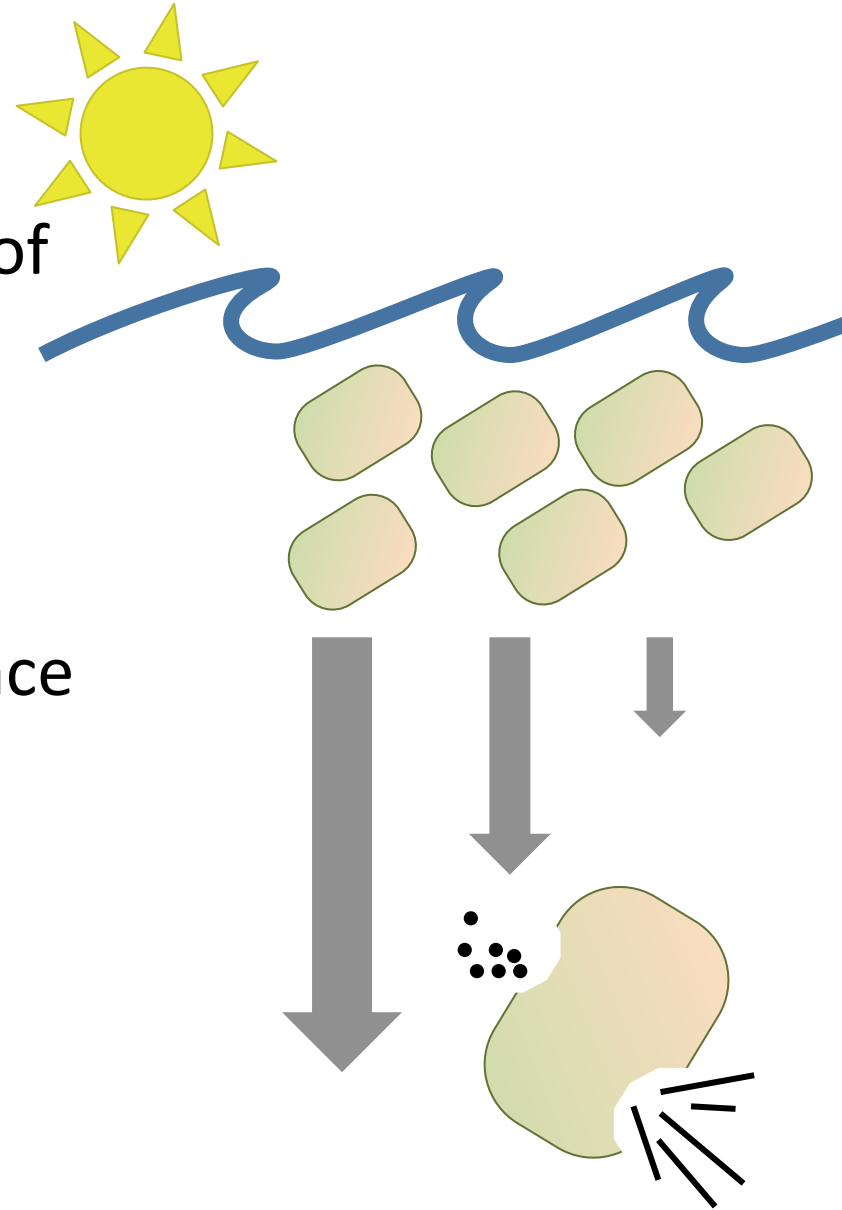




# Moving forward with mixotrophy

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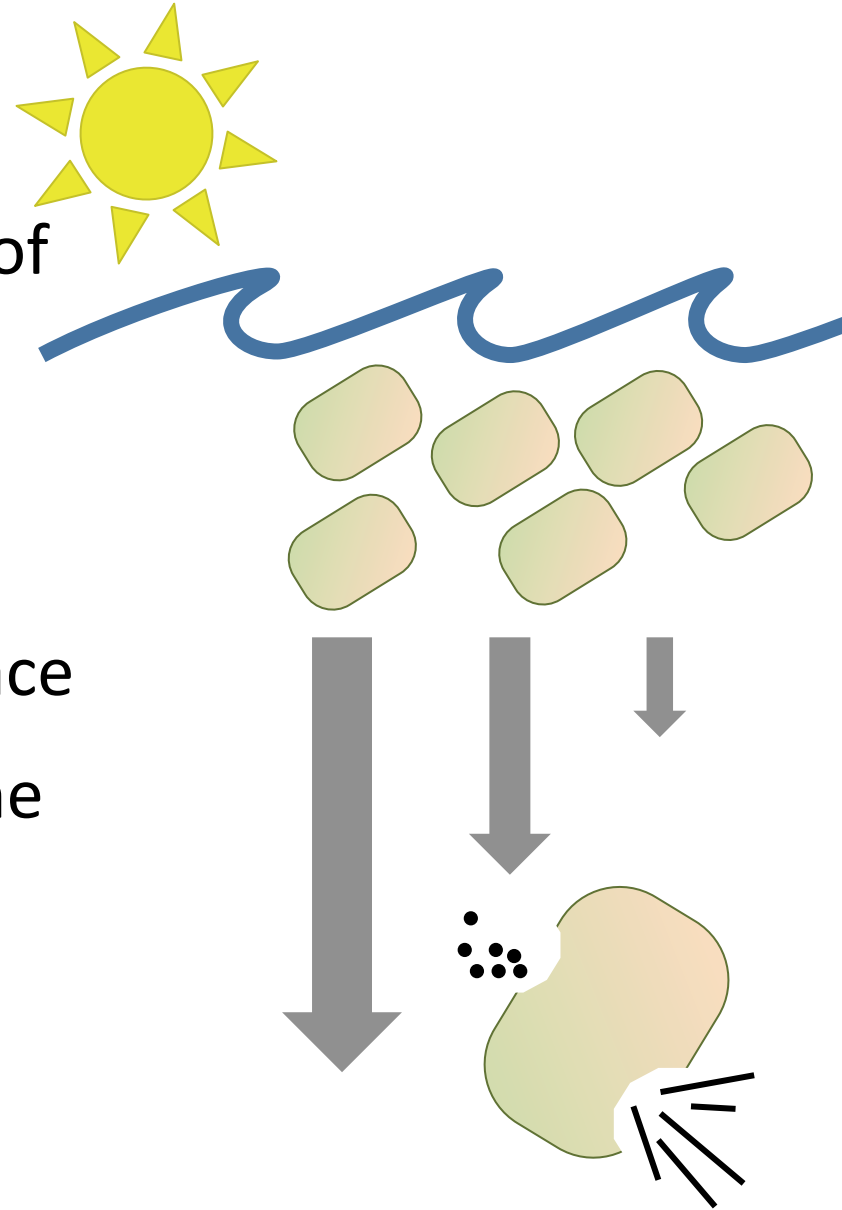
- Allows extra carbon fixation
- Provides a “short-circuit” in remineralization at the surface





# Moving forward with mixotrophy

1. Mixotrophy affects the amount of primary production
  - Allows extra carbon fixation
  - Provides a “short-circuit” in remineralization at the surface
2. Density and palatability affect the fate of this organic C





# Moving forward with mixotrophy

1. Mixotrophy affects the amount of primary production
  - Allows extra carbon fixation
  - Provides a “short-circuit” in remineralization at the surface
2. Density and palatability affect the fate of this organic C
3. Focused studies on oligotrophic gyre communities can provide climatically relevant insight

