Acquired Phototrophy in Ciliates: Does it boost trophic transfer to mesozooplankton?

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Food web efficiency depends on the number of trophic levels as well as the efficiency of each level.

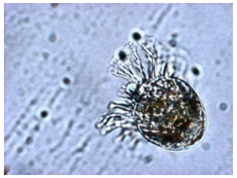
Although microzooplankton (ciliates and hetertrophic dinoflagellates) are a trophic link from phytoplankton to copepods, MZ respiration leads to loss of organic carbon.

The gross growth efficiency (GGE) of the MZ link influences transfer efficiency of primary production to mesozooplankton.

Does photosynthesis in ciliates affect microbial food web efficiency (C available to copepods)?

Planktonic ciliates are an important component of copepod diets

- **Strong selection for ciliates over phytoplankton (reviewed in Saiz & Calbet 2010):**
  - **Optimum prey size (~20-100 µm)**
  - **Encounter rate increased by ciliate swimming**
  - **Hydrodynamic signals from ciliate increase detection**
- **Ciliates are high quality food with lower C:N than most phytoplankton and high PUFA content. Ingestion of ciliates along with phytoplankton can boost egg production (Dutz & Peters 2008)**



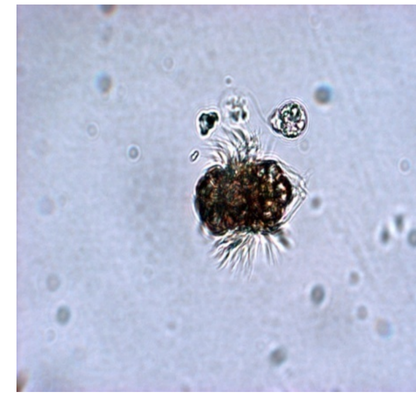
Many ciliate species have acquired phototrophy and are mixotrophs; they ingest small phytoplankton but are also photosynthetic.

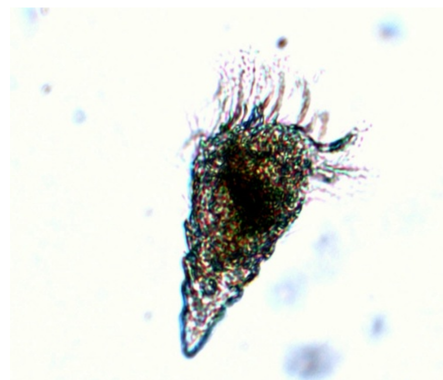
Mixotrophic oligotrichs include *Laboea strobila*, *Tontonia* spp. and many *Strombidium* spp.

The mixotrophic litosome ciliate *Mesodinium rubrum* can bloom in coastal and upwelling waters.

Large, mixotrophic ciliates are particularly important as prey for copepods (Dutz &Peters 2008, Christaki et al 2009)

Mesodinium rubrum (=*Myrionecta rubra*)





Laboea, a large mixotrophic choreotrich

Contribution of Ciliates with Acquired Phototrophy to Ciliate Abundance and Biomass

- **Annual average, ~30% of ciliates in upper water column have acquired chloroplasts (Stoecker et al. 1987; Dolan & Perez 2000)**
- **In late spring-summer, mixotrophic oligotirichs can account for >50% ciliate abundance and/or biomass in surface waters (Christaki et al. 2008; Stoecker et al. 1987; Bernard & Rassoulzadegan 1994; Dolan & Marrase 1995)**
- **In estuaries and upwelling areas, especially under low light conditions, *Mesodinium rubrum* can dominate ciliate abundance and biomass (Witek 1998; Crawford et al. 1997; Sanders 1995)**

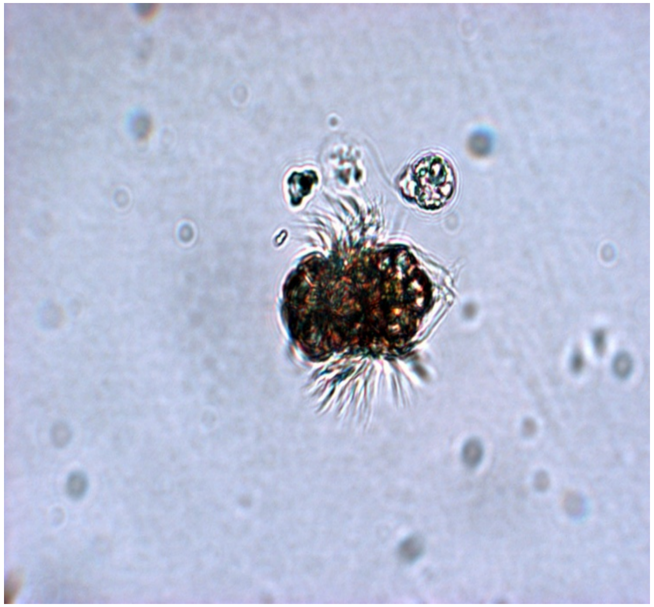
Does Acquired Phototrophy Increase Gross Growth Efficiency of Ciliates?

Gross growth efficiency (GGE) of ~30% commonly assumed for heterotrophic ciliates (Straile 1997, Landry & Calbet 2004).

Do mixotrophic ciliates with acquired phototrophy have higher GGE than heterotrophic ciliates because photosynthesis spares ingested carbon from being respired?

Mesodinium rubrum (=*Myrionecta rubra*) can have GGE as high as 50-70%

(from Johnson & Stoecker 2005)



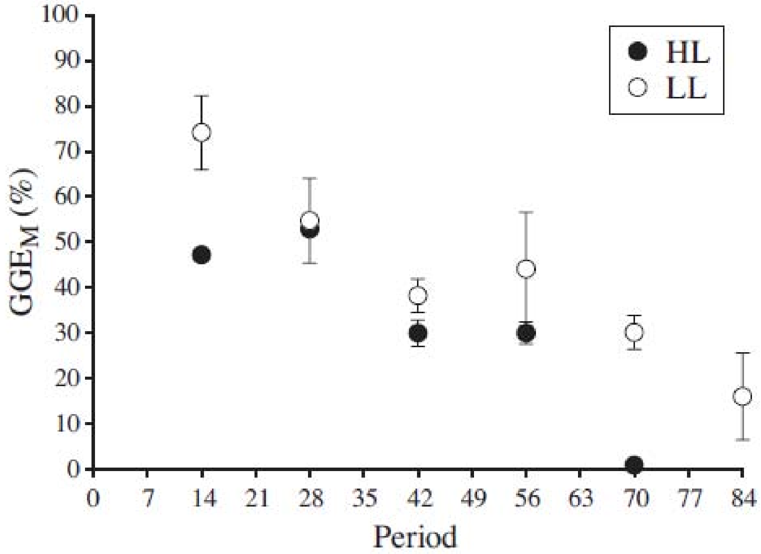


Fig. 8. *Myrionecta rubra*. Estimated mixotrophic gross growth efficiencies (GGE_M; means ± SE) for combined autotrophic and heterotrophic growth. Experimental conditions as in Fig. 2. GGE_M estimated for each 2 wk period (see Fig. 1)

Does Phototrophy increase GGE of Mixotrophic Oligotrichs with respect to ingested C?

- **No direct estimates.**

- **If assimilation efficiency of ciliates is close to 100% and GGE of heterotrophic ciliates is ~30% (Straile 1997, Landry & Calbet 2004) can assume ~70% of ingested C is respired.**

- **In mixotrophic oligotrichs up to 100% of respiratory demand for C can be met by photosynthesis in the light (Stoecker & Michaels 1991). Stored photosynthate is preferentially respired by the ciliates in the dark (Putt 1990).**

- **If assume photosynthesis and stored photosynthate covers respiratory demand for C for 12 h/d, sparing ~35% of ingested C from respiration, then the GGE of mixotrophic oligotrichs for ingested C is ca. 65% (Stoecker et al. 2009).**

Simplified scenario based on average values:

GGE of strictly heterotrophic ciliates is 30%

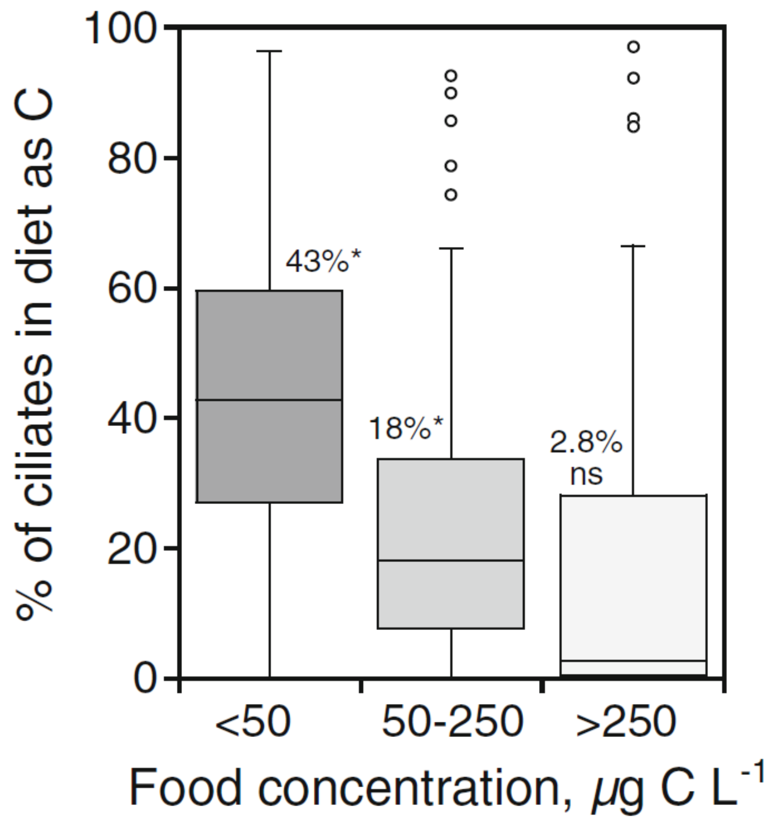
GGE of mixotrophic ciliates is 65%

30% of the ciliates are mixotrophic

Then the average GGE of the ciliate assemblage is ~40%

How would a change in average GGE of ciliates from 30% to 40% effect transfer of C to copepods?

It would depend on the relative contribution of ciliates to the diet of copepods.



(from Saiz & Calbet 2010)

Ca. carbon available to copepods as a percent of primary production based on estimated dietary contribution of ciliates (assumes no consumption by other MZ)

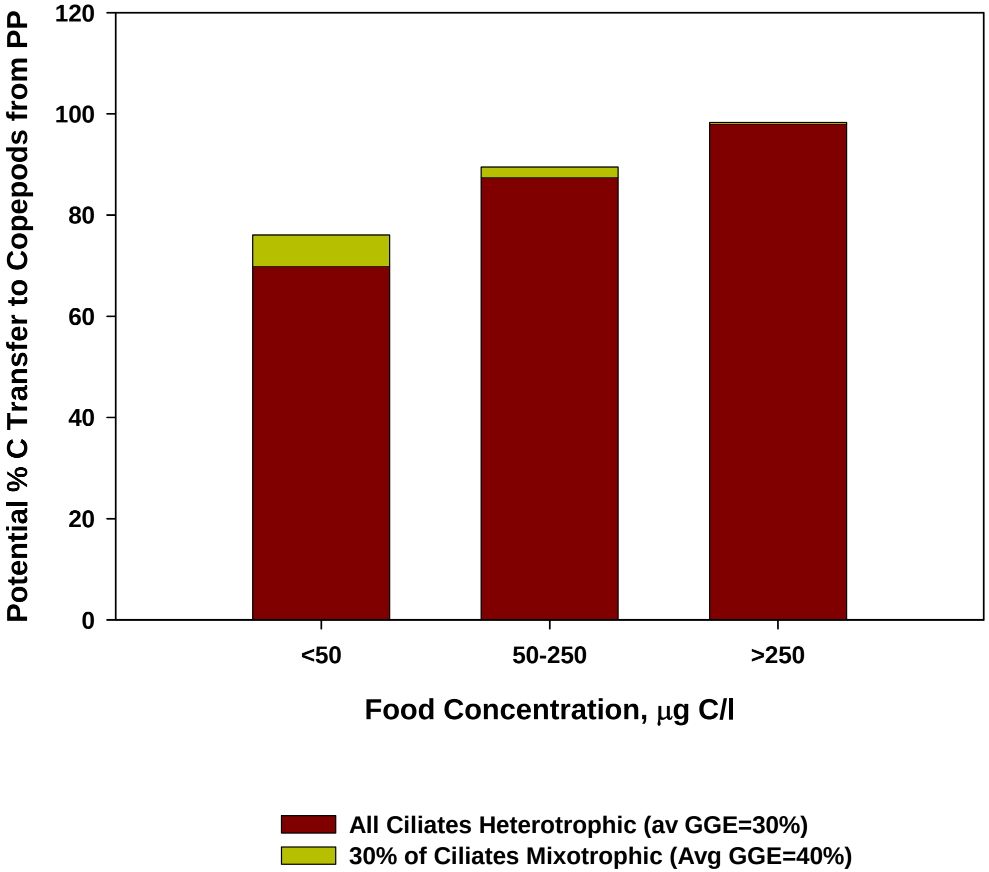
Calculated “boost” from mixotrophy in ciliates:

Low Food: 6%

Moderate Food: 2%

High Food: <1%

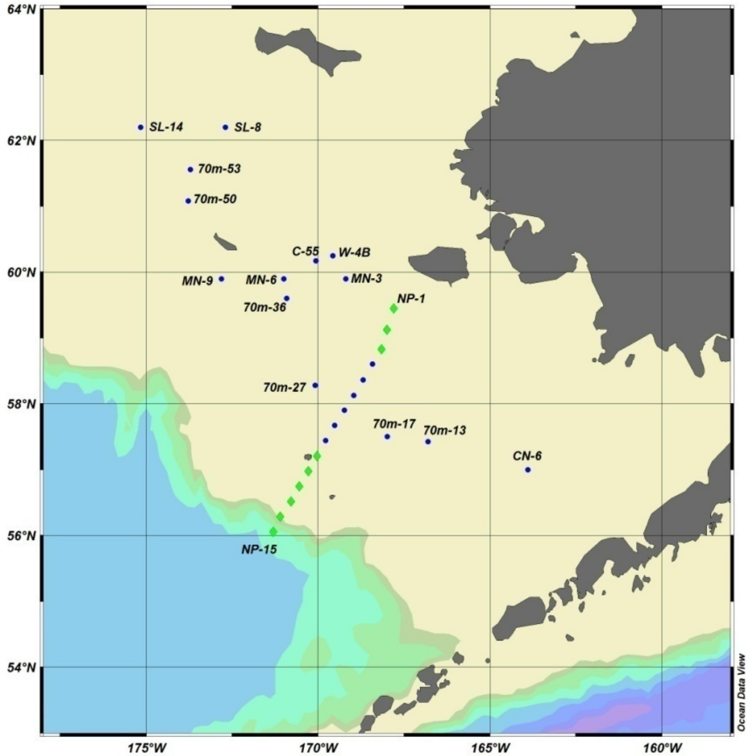
- Mixotrophy in ciliates has a very little effect on trophic transfer to copepods except at low food (chlorophyll) levels.
- In low food environments, total transfer is lower due to C losses in the MZ link, but mixotrophy can boost transfer by ~6%.
- In high food environments, total transfer is higher due to direct transfer of C from phytoplankton to copepods and mixotrophy has little effect on C transfer.



In arctic and sub-arctic seas in late spring and summer, mixotrophic ciliates can be particularly important as components of the microplankton

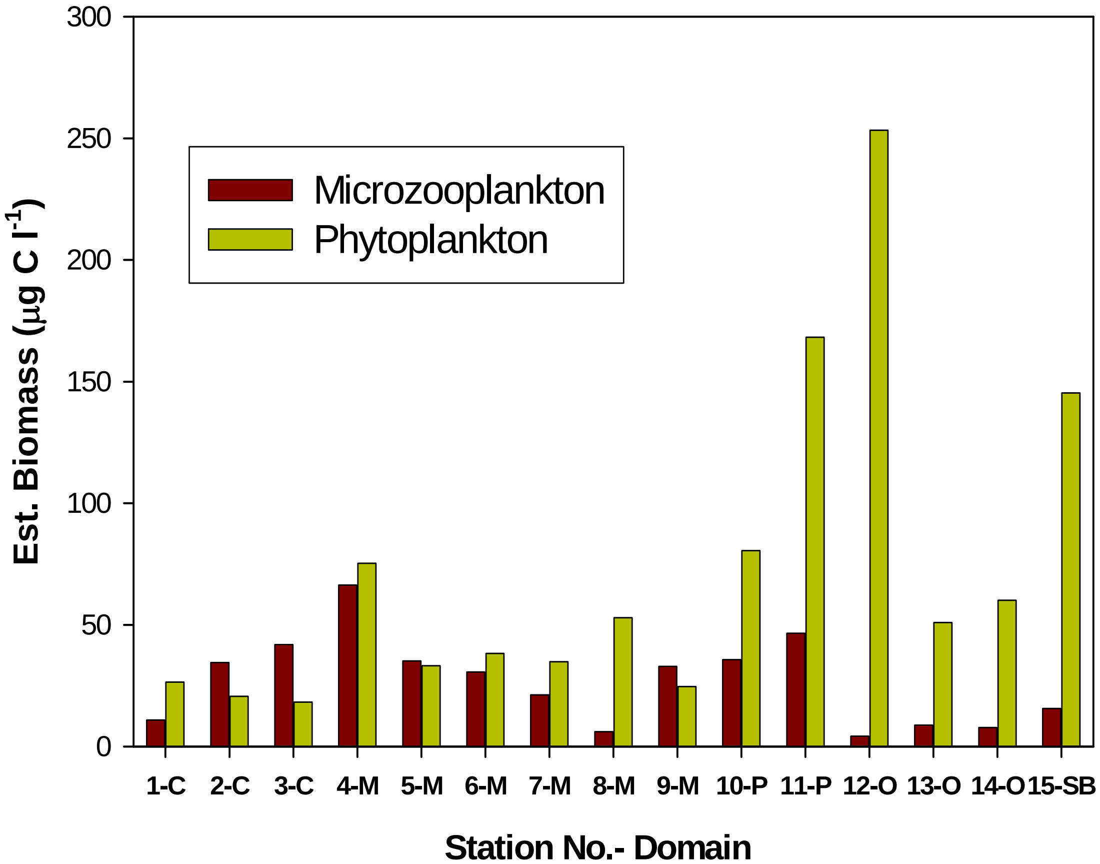
Region	Contribution to ciliate assemblage	Ref.
Iceland, Greenland & Barents Sea-summer, surface waters	58-65% abundance (4-15% total Chl.)	Putt (1990)
Disko Bay, coastal Greenland-summer, 0-28 m	13% abundance; 30% biomass	Levinsen et al. (1999, 2002)
Western Bering Sea, late spring-early summer	30-40% biomass	Sorokin et al. (1996)
Cobb Sea Mount, eastern subarctic Pacific, 0-24 m	Av. 40% biomass	Sime-Ngando et al. (1992)
Western subarctic Pacific, 0 m, spring	28% abundance, 48% biomass	Suzuki & Taniguchi (1998)
SE Bering Sea in Summer	?	

Abundance, biomass and grazing of MZ as part of BEST/BSIERP Program in SE Bering Sea. Data from July 3-31, 2008 summer cruise *(HLY0803)*-- Cross Shelf NP Transect and selected Middle Shelf Stations.



- **Transect included coastal (NP 1-3), middle shelf (NP 4-9), Pribilof Island domain (NP 10 & 11), outer shelf (NP 12-13) and shelf break (NP 15)**
- **Middle Shelf (50-100 m depth) Stations indicated by blue circles.**
- **Estimated phytoplankton biomass assuming C:Chl *a*=50.**

MZ and Phytoplankton Biomass (NP line, July 2008)



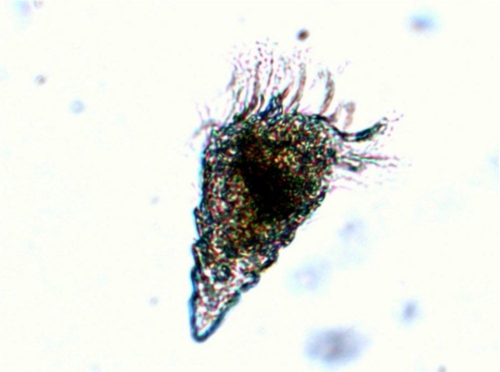
Food concentration low (usually <50 µg C/l) in coastal and middle shelf waters in summer. In middle domain, ~85% of chlorophyll *a* < 20 µm and MZ biomass equaled or exceeded biomass of phytoplankton, especially in > 20 µm size category.

The dominant microzooplankton in mixed layer were ciliates and heterotrophic dinoflagellates

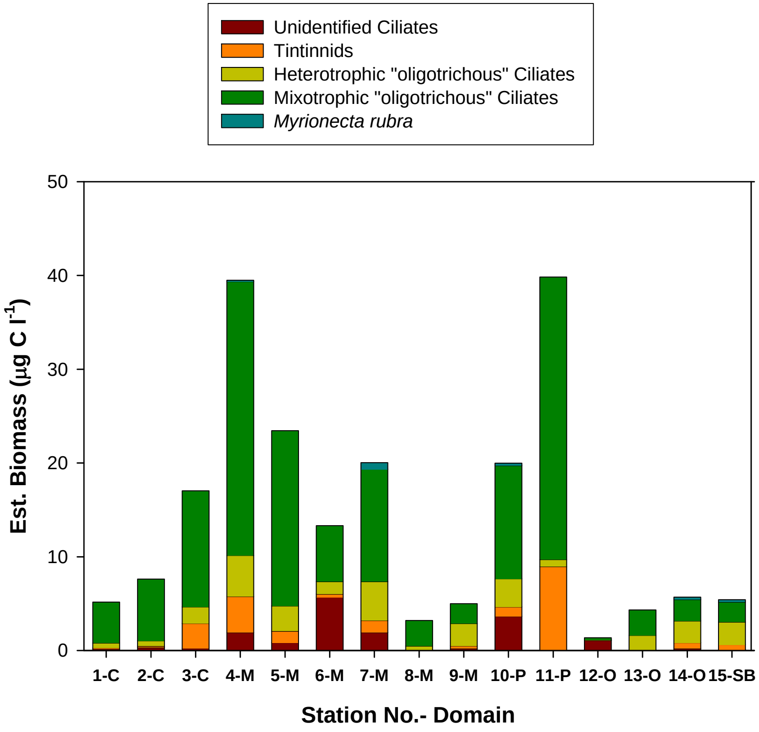
On NP line, ciliates accounted for 53% of MZ biomass

On NP line, dinoflagellates accounted for 46% of MZ biomass

Mixotrophic oligotrich ciliates dominated the ciliate biomass at coastal and middle domain stations

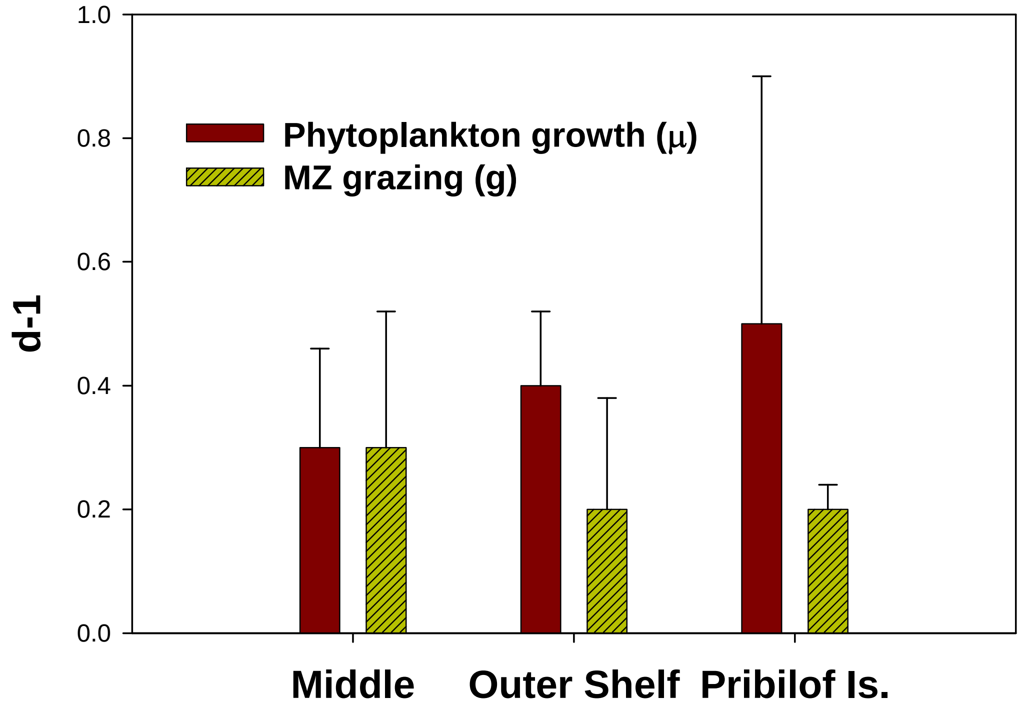


Composition Ciliate Biomass (NP line, July 2008)



C=Coastal, **M**=Middle Shelf, **P**=Pribilof, **O**=Outer Shelf, **SB**=Shelf Break

MZ grazing consumed >100% of daily phytoplankton growth on middle shelf, 56% on outer shelf, and ~41% near Pribilof Islands (July 2008, Mixed Layer, ~50% Io). The MZ link to higher trophic levels should have been very important on the middle shelf.

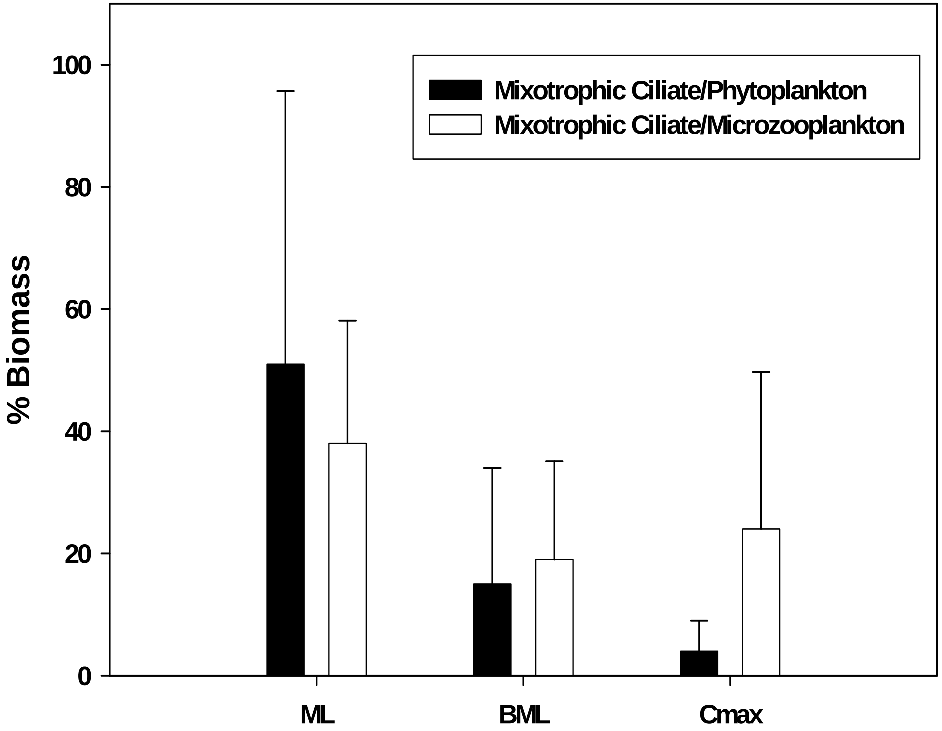


% Growth Grazed d-1: **131%** **56%** **41%**

MZ Sampling on the Middle Shelf, July 2008

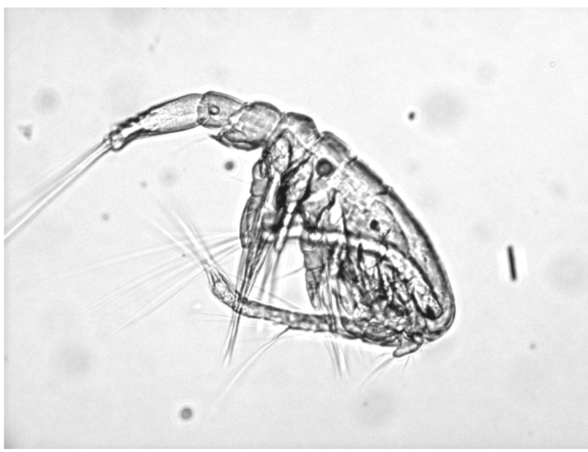
	Sample Depth (mean±STD)	**Temp. , °C (mean±STD)**	**Salinity (mean±STD)**	**Chl. a, µg/l (mean±STD)**	**Nitrate µM**
Mixed Layer (ML) (n=22)	6±2.3	5.6±0.97	31.3±0.42	0.3±0.18	0.5±1.82
Below Mixed Layer (BML) Chl. a <1 µg/l (n=8)	26±4.2	1.6±2.50	31.7±0.35	0.6±0.29	3.1±2.69
Chlorophyll Max (Cmax) Chl. a > 1 µg/l (n=9)	32±8.0	-0.3±2.53	31.9±0.22	4.1±4.04	3.7±3.58

Middle Shelf, July 2008: Contribution of mixotrophic ciliates to estimated phytoplankton and MZ biomass in mixed layer (ML), below mixed layer (BML), and in Chlorophyll max. (Cmax), if present.



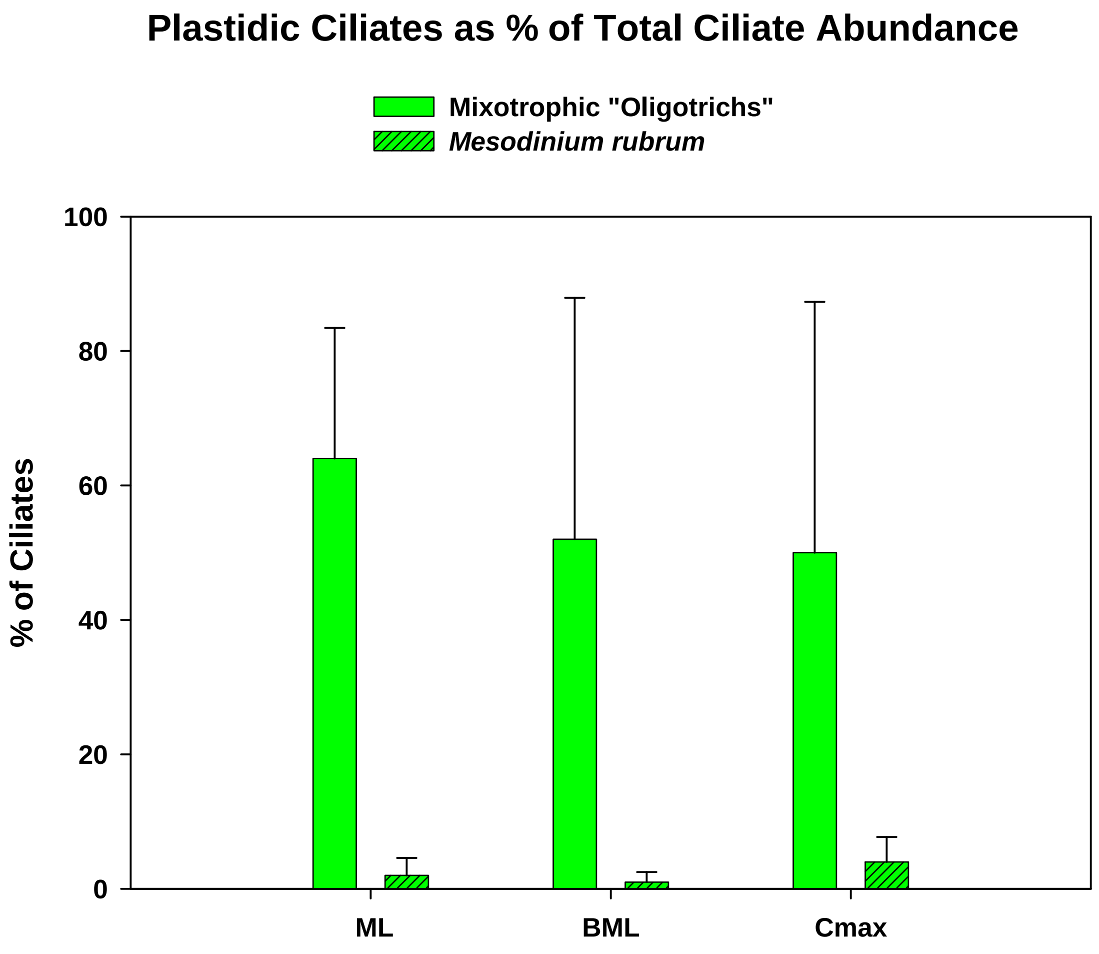
Mixotrophic ciliates were ~50% of phytoplankton biomass and ~38% of MZ biomass in the mixed layer.

Are mixotrophic ciliates important prey for zooplankton on the SE Bering Sea Shelf in summer?



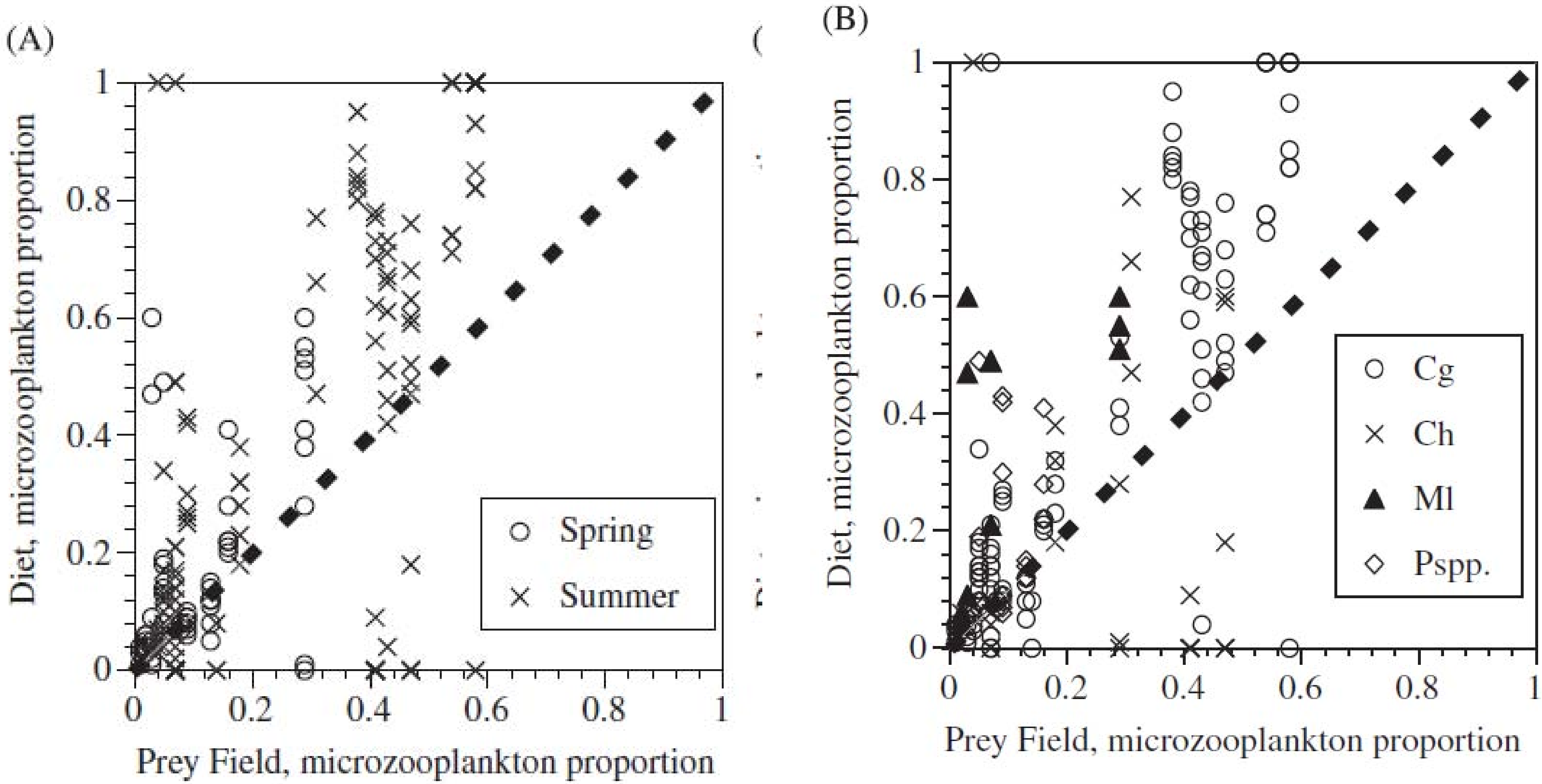
- No data available specific to mixotrophic ciliates and copepods on Middle Shelf.
- MZ, especially large mixotrophic ciliates, are preferred prey of copepods. When phytoplankton biomass is low, mixotrophic ciliates can comprise a high proportion of the daily ration of zooplankton (Christaki et al. 2009, Dutz & Peters 2008).
- Grazing experiments in nearby Arctic Seas have shown that MZ, including ciliates, are important components of the diet of copepods (Campbell et al. 2009).
- MZ , including ciliates, are also consumed by krill, larval fish and other types of zooplankton.

Middle Shelf, July 2008: Contribution of mixotrophic ciliates to total ciliate abundance in mixed layer (ML), below mixed layer (BML), and in chlorophyll max. (Cmax), if present.



≥ 50% of the ciliates were mixotrophic -- above and below the pycnocline

In Arctic Ocean, copepods have a strong preference for MZ prey, when MZ comprise 50% of more of prey field, the diet is 50% or more MZ (Campbell et al. 2009)

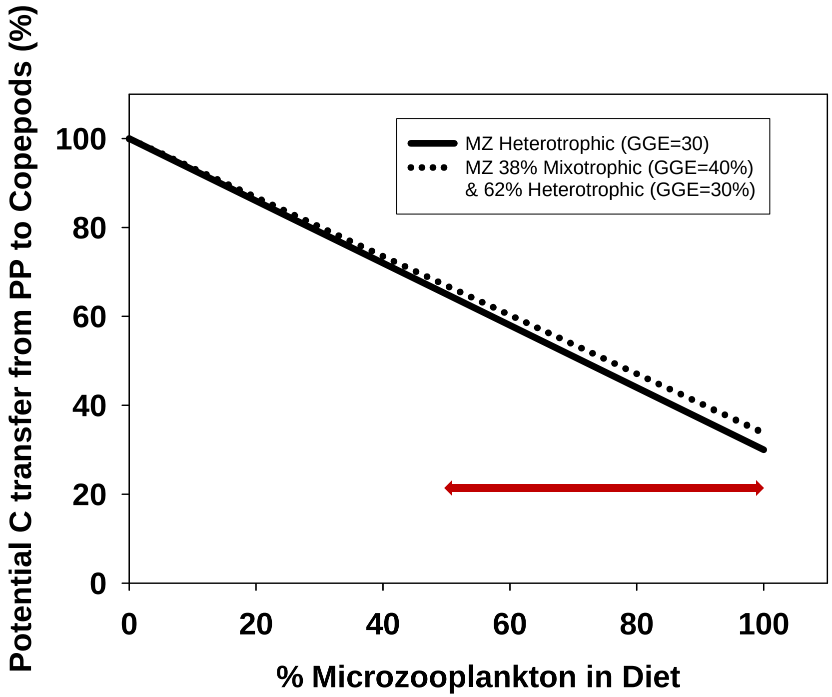


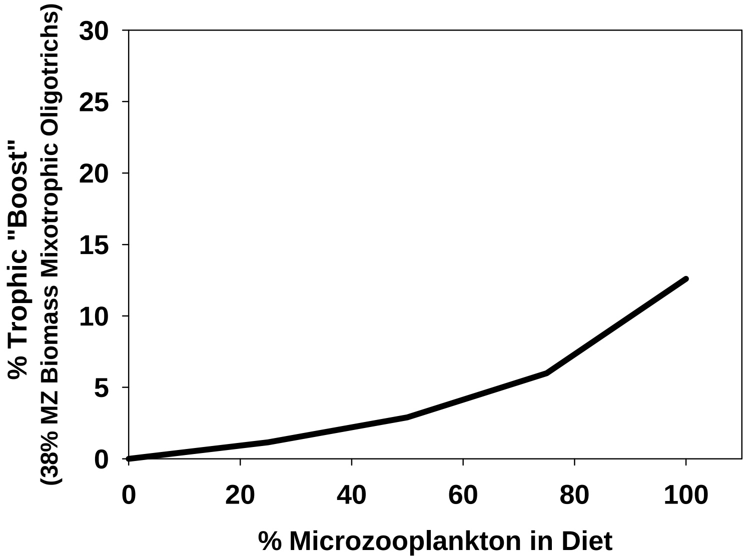
calanus spp. On Bering sea shelf *C. marshallae*, *Pseudocalanus* spp., *Acartia* spp. abundant (Napp et al. 2002) Cg= *C. glacialis*, Ch= *C. hypereus*, MI= *M. longa*, Pspp=*Pseudo*

Calculation of “trophic boost” to copepods based on summer Bering Sea Middle Shelf MZ and chlorophyll data

(ciliate and heterotrophic dinoflagellate biomass included in estimates of MZ)

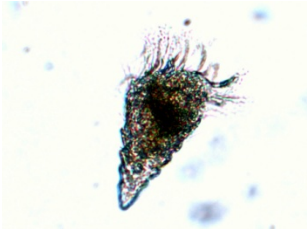
SE Bering Sea Middle Shelf-Summer
Potential impact of mixotrophy in ciliates on transfer of primary production to copepods. Mixotrophic ciliates are 38% of MZ biomass. Max. " trophic boost" ~12% with 100% of diet MZ.





Based on food concentration, ciliates should be av. 43% of diet (Saiz & Calbet 2010).
Based on MZ biomass and Chl. a, ~ 50% of prey field is MZ. Copepod diet should be >50% MZ (based on data of Campbell et al. 2009 for Arctic copepods)

Summary



- Microzooplankton (MZ) were abundant in the mixed layer in coastal and shelf waters of the Bering Sea in summer (July 2008) when phytoplankton biomass was very low. MZ had an estimated biomass ~ equal to phytoplankton.
- MZ grazed most of the phytoplankton. MZ dominated the prey field for copepods, especially in > 20 µm size range.
- Mixotrophic ciliates dominated the ciliate biomass and contributed about 38% of total MZ biomass.
- Photosynthesis in mixotrophic ciliates may have boosted transfer of primary production to copepods by as much as a 12% compared to estimate without acquired phototrophy in ciliates.
- In moderate to high food environments, acquired phototrophy has little impact on trophic transfer to copepods.