Feeding impacts of ontogenetically migrating copepods to the spring phytoplankton bloom in the Oyashio region

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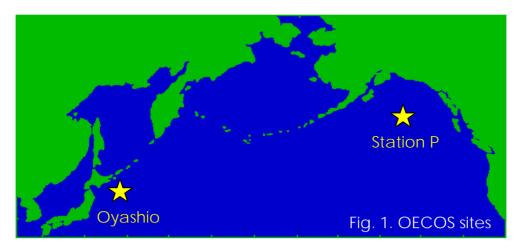
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East-West comparison



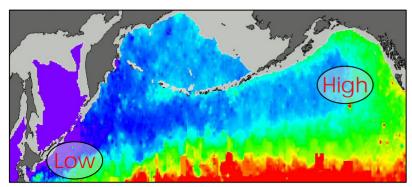


Fig. 2. Mean water temperature in 0-500 m determined with CTD (from Dr. K. Tadokoro).

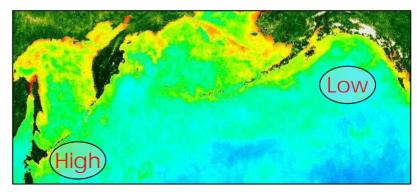


Fig. 3. Satellite image of sea surface chlorophyll *a* (from NASA).

Since 1980s, we have recognized that oceanographic conditions and plankton ecosystems are much different between the east and west of the PICES regions.

In the Gulf of Alaska, phytoplankton biomass is low when primary productivity is high and the ontogenetically migrating copepods appear abundantly.

This makes the hypothesis that the copepods create HNLC system by direct feeding on large phytoplankton cells. Thus, extensive efforts have been done for the life history and feeding ecology for the last three decades.

Mechanism of HNLC systems

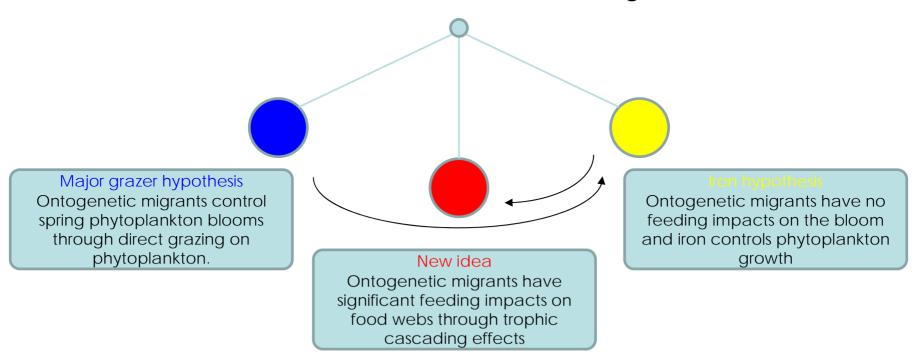


Fig. 4. The balance mechanism of oceanic HNLC ecosystems after PICES scientific report No.32.

According to our knowledge on the copepod feeding,

- The ontogenetically migrating copepods are feeding on flagellates, ciliates and sinking particles in HNLC systems.
- In phytoplankton-rich sites, major food items are changed from diatoms and dinoflagellates during the phytoplankton bloom to ciliates in the post bloom.
- On the other hand, there is increasing evidence that iron controls growth of large phytoplankton cells through *in situ* experiments.

These results have concluded that the copepod feeding does not control phytoplankton biomass.

However, OECOS group re-evaluates the ecumenical iron hypothesis and emphasizes that...

- They directly prevent the accumulation of large phytoplankton cells.
- They also stimulate the accumulation of the smaller phytoplankton by consumption of their major predators.

Objectives

In the present study, we investigated

- Feeding habits of the ontogenetically migrating copepods from in situ feeding experiments.
- Response of the copepod community feeding to the phytoplankton bloom from gut fluorescence analyses

From these results, we evaluate the feeding impacts on the phytoplankton bloom and food web

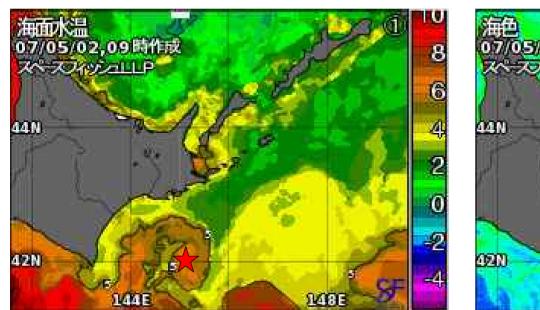
We established two working hypothesis (H_o).

- Major food resources of the ontogenetic migrants are larger phytoplankton dominating in the water column during the spring bloom.
- The copepod feeding does not have significant impacts on phytoplankton bloom.



Fig. 5. Objective copepods and their predators

Complexity of water masses



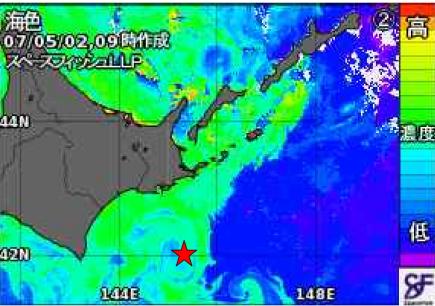


Fig. 6. Daily changes in satellite images of sea surface temperature and chlorophyll *a* concentrations during OECOS-West cruises in April 2007. Stars indicate sampling station.

- Large temporal and spatial fluctuations are evident for satellite images of SST and sea surface chlorophyll around the OECOS-WEST site.
- Sampling station is placed in the subarctic waters, but surface layers are covered with the warm and saline water mass during late April.
- High chlorophyll appear around the coastal areas in early April and spread toward offshore in late April.
- These results suggest that phytoplankton bloom are strongly associated with the coastal water mass.

Phytoplankton bloom

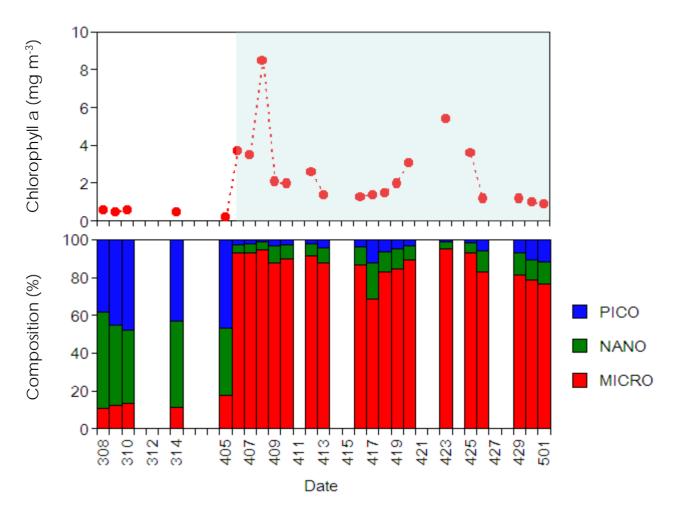


Fig. 7. Temporal changes in mean chlorophyll a concentration in 0-150 m layer and its size composition.

- Size-fractionated chlorophyll showed that the phytoplankton bloom was lasted from early April to early May and micro-sized phytoplankton was predominant.
- Chlorophyll a concentrations were temporally fluctuated due to the exchange of the different water masses as shown by the previous slide.

Copepod community

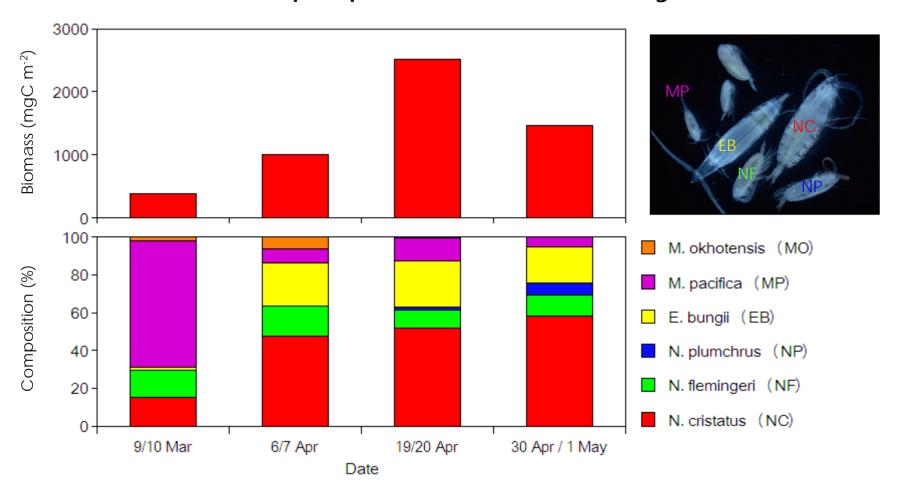
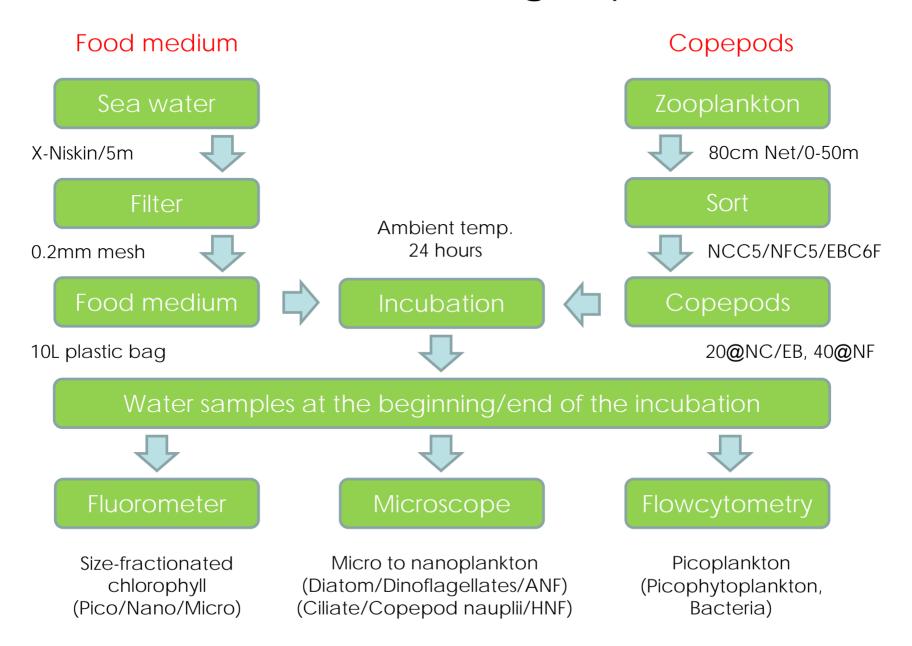


Fig. 8. Temporal changes in biomass of the ontogenetically migrating copepods in 0-150 m layer and the species composition.

- The copepod biomass were high during the phytoplankton bloom and reached a maximum in mid-April.
- *M. Pacifica* occurred abundantly in the pre-bloom.
- N. cristatus and E. bungii dominated the copepod biomass during the bloom and their late copepodites were
 responsible for the biomass increase.
- Especially, *N. cristatus* contributed to the temporal changes of the total biomass of the copepod community.

Protocol for feeding experiments



Ambient food items

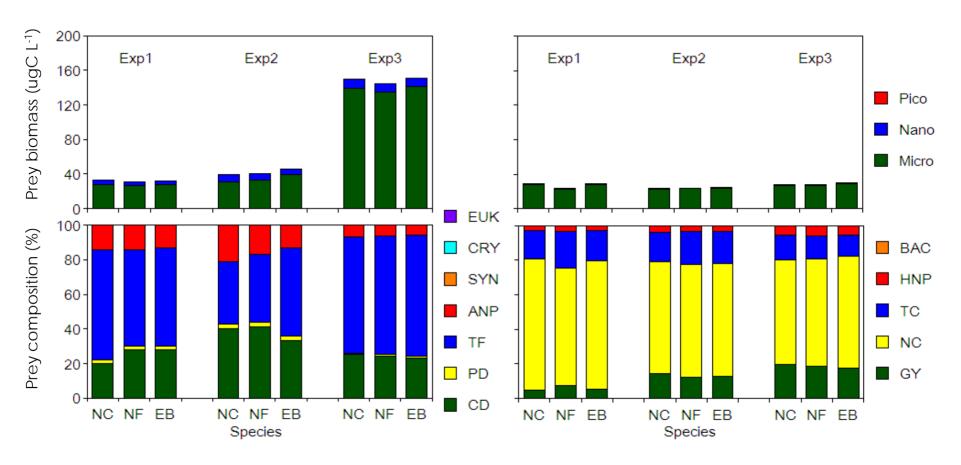


Fig. 9. Ambient prey biomass (upper panels) and its composition (lower panels) for 3 predominant copepods during the feeding experiments. Left panels are autotrophs and right panels are heterotrophs.

- Autotrophic prey biomass was increased by micro-sized phytoplankton in Exp3.
- Thecate flagellates and centric diatoms composed more than 80% of autotrophic prey biomass in each experiment series.
- Heterotrophic prey biomass showed no temporal change. Although heterotrophic preys composed half of the available food resources in Exp1 and Exp2, but much lower than autotrophic prey in Exp3.
- Naked ciliates were predominant among heterotrophic food resources.

Size selectivity

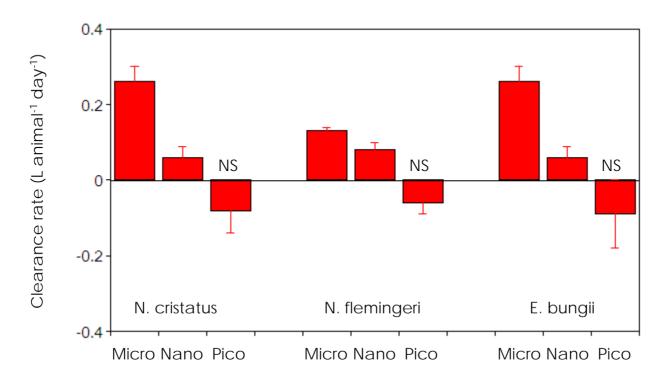


Fig. 10. Clearance rate on size-fractionated chlorophyll *a* for 3 predominant copepods. Bars show SE. NS: No significance to zero (p>0.05, t-test). Positive numbers mean the organisms are declined by the copepod feeding.

- Copepod clearance rates were the highest on micro-sized phytoplankton, indicating that they prefer larger particles as food items.
- Negative clearance rates on pico-sized chlorophyll were evident for some experiments, although these were not significantly different from zero.
- These results indicate that the small phytoplankton cells are sometimes increased through the copepod feeding.
- A part of the results can be explained by the trophic cascading effect, which the copepods stimulate the
 accumulation of the smaller phytoplankton cells by consumption of their major predators such as
 microzooplankton

Clearance rate

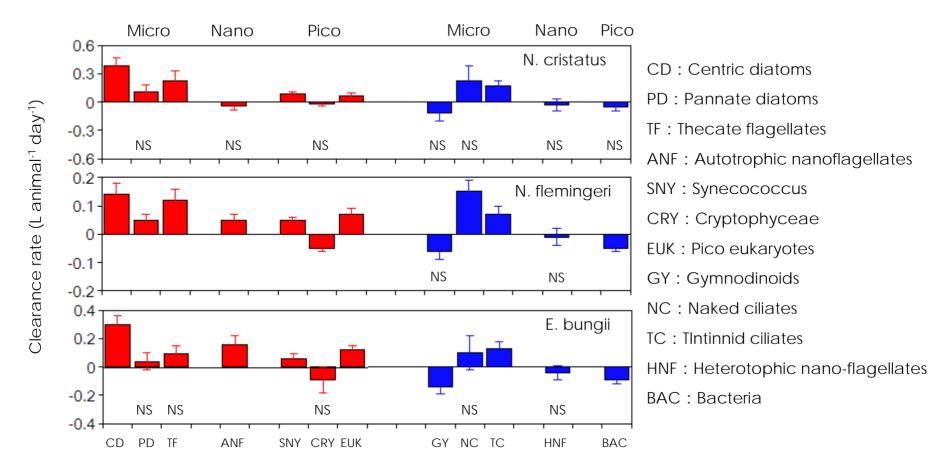


Fig. 11. Clearance rate on phytoplankton and zooplankton prey items for 3 predominant copepods. Red means autotrophic preys and blue is heterotrophic preys. Bars show SE. NS: No significance to zero (p>0.05, t-test).

- Positive clearance rates were evident for centric diatoms, thecate flagellates, autotrophic nano-flagellates and tintinnid ciliates, indicating that the copepods primarily feed on these preys.
- The copepod clearance rate was negative for bacteria, but positive for Synecococcus and pico-eukaryotes, although they belong same size categories.
- These results could not be explained by the simple trophic-cascading as shown in the previous slide, and suggest more complicate trophic interaction.

Ingested preys

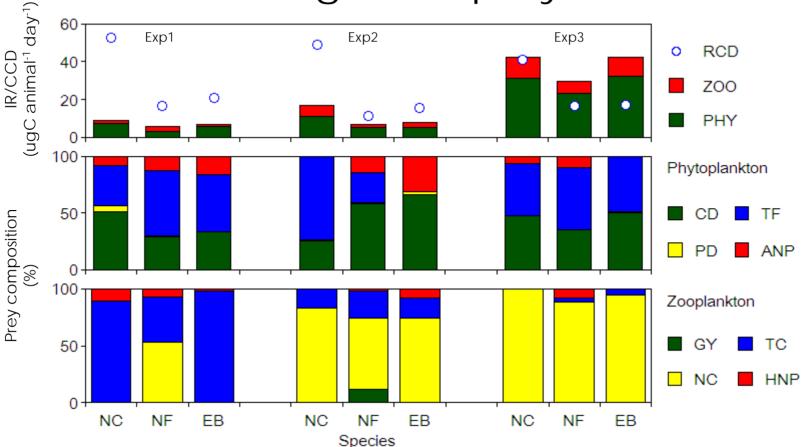


Fig. 12. Ingestion rate (IR), carbon demand (CCD) and the composition of ingested phytoplankton and zooplankton preys for 3 predominant copepods. CD: Centric diatom. PD: Pannate diatom. TF: Thecate flagellate. ANP: Autotrophic nanoplankton. GY: Gymnodinoids. NC: Naked ciliate. TC: Tintinnid ciliate. HNP: Heterotrophic nanoplankton

- In upper panel, you can see that these copepods consume more phytoplankton preys than zooplankton.
- Ingested carbon came from centric diatoms, thecate flagellates and naked ciliates.
- Tintinnids and autotrophic nanoflagellates were important for some species as supplement foods.
- Ingested carbon did not meet their carbon demands at Exp1 and Exp2 when ambient prey was low, suggesting that they feed on larger chain-forming diatoms, copepod eggs or nauplii, and sinking particles.

Protocols for gut pigment analyses

Zooplankton

Collect by 80cm ring net from 50-m depth



Concentrate

Anesthetized with soda and then concentrated with mesh



Preserve

Immediately frozen with LN₂ and preserved at deep freezing



Sort

Object species/stages are sorted from the thawed samples

C5: N. cristatus/N. flemingeri/N. plumchrus C6F: E. bungii/M. pacifca/M. okhotensis

Gaetanus spp./P. scutullata



Extract

Gut pigments are extracted with DMF



Gut pigment

Determined with the acidified method

Gut pigment contents

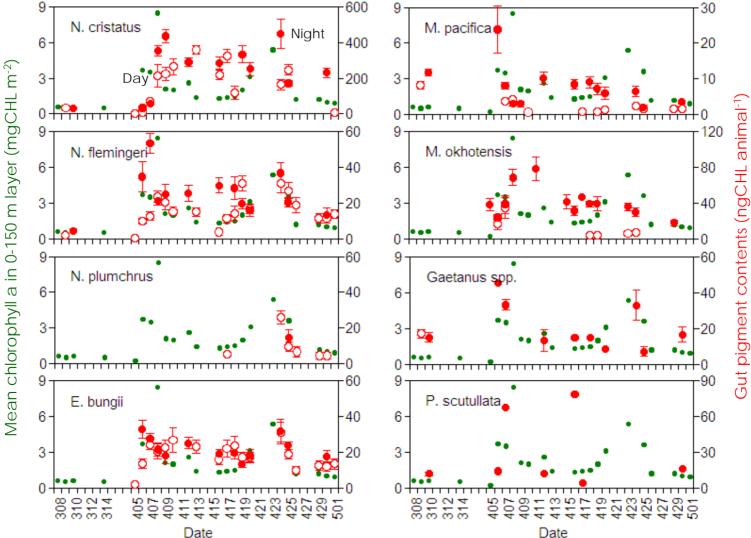


Fig. 13. Daily changes in gut pigment contents of surface residents (left) and day-night migrants (right). Green circles are mean chlorophyll *a* in the water column.

- Gut pigment contents of surface residents were well synchronized with chlorophyll a, indicating that the contribution of phytoplankton to the ingested preys is associated with food availability.
- Day-night migrants showed the higher gut fluorescence at night time rather than those at daytime.

Feeding impacts on phytoplankton bloom

Table 1. Feeding on phytoplankton community and relative importance of phytoplankton sources in the ingested carbon for the predominant copepod community in the layer above 150 m. C/CHL ratio is assumed to be 21. Feeding rate is estimated from respiratory demand (6.5% of biomass: Dagg et al. 1982), 0.6 of assimilation efficiency and 0.3 of gross growth efficiency. ND: No data. *: Isada et al. (in prep).

Parameter	Source	9 Mar.	6 Apr.	19 Apr.	30 Apr.
Primary production* (PP: gC m ⁻²)		-	3.6	1.7	1.2
Copepod biomass (gC m ⁻²)		0.4	1.0	2.3	1.4
Feeding rate (gC m ⁻² day ⁻¹)		0.2	0.4	1.2	0.7
Ratio ingested (%)	Phytoplankton	23.3	38.6	41.4	19.8
	Other POC	76.7	61.4	58.6	80.2
Ratio grazed on PP (%)		-	4.7	28.2	12.0
Carbon flux at 40 m (F ₄₀ : gC m ⁻² day ⁻¹)		-	0.4	0.5	0.7
Contribution of feces to F_{40} (%)		-	24.2	49.5	21.2

- Primary production is much higher during phytoplankton bloom and micro-sized phytoplankton contributes to it.
- In our observations, feeding rate of the copepod community reach up to 28% of primary production and it is responsible for the increase of late copepodites of *N. cristatus*.
- The copepod community feed on particles other than phytoplankton as food items even though phytoplankton bloom occurs.
- Moreover, the copepod fecal pellets reach up to half of the sinking POC flux at 40 m.
- These results indicate that the copepod community does not graze phytoplankton bloom down but often show significant impacts on large phytoplankton cells.
- Also, they are considered to have important roles to channel phytoplankton and other POC into vertical carbon flux through their actively feeding.

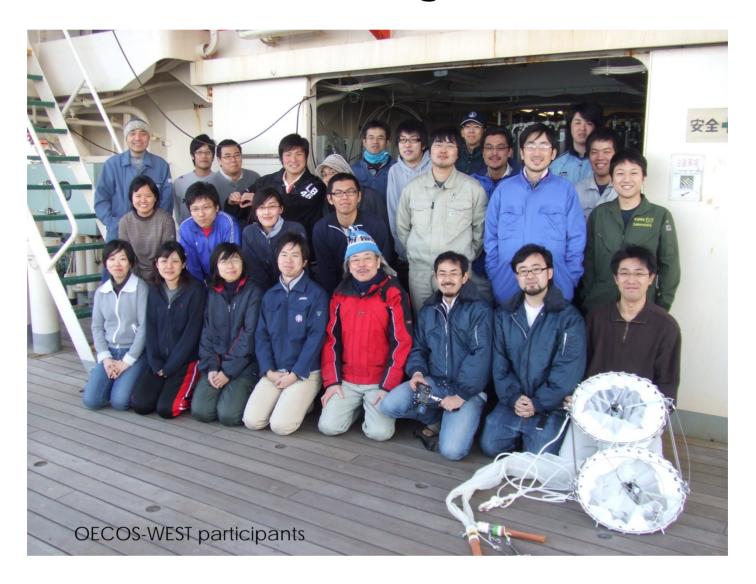
Conclusion

- Ontogenetically migrating copepods dominate zooplankton biomass during the phytoplankton bloom in the OECOS-WEST site.
- These copepods prefer larger particles.
- Major prey items are centric diatoms, thecate flagellates and naked ciliates which are predominant among the ambient preys during the phytoplankton bloom.
- The copepod community does not graze the phytoplankton bloom down, but often show significant impacts on large phytoplankton cells.
- The copepod feeding have important roles to transform larger phytoplankton cells to fast sinking POC during the phytoplankton bloom.

In terms of working hypothesis,

- Major food items of the copepod community are larger phytoplankton dominating ambient prey during the spring bloom?
 Partially YES, but they feed on particles other than phytoplankton even in the spring bloom.
- The copepod feeding does not have significant impacts on phytoplankton bloom?
 - Partially YES, the copepod feeding does not graze the phytoplankton bloom down but they have significant impacts on large phytoplankton cells.

Acknowledgement



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