Arctic zooplankton in a warming scenario: Metabolism, tipping points and stoichiometry of regenerated nutrients

Miquel Alcaraz1, Rodrigo Almeda1, Enric Saiz1, Albert Calbet1, Carlos M. Duarte2, Susana Agustí2, Rocio Santiago2, Juancho Movilla1, Alejandro Alonso1, Jorge Felipe1, Agata Weidmann3, Elena Arashkevich3, Ulrike Grote5

1 Institut de Ciències del Mar, CSIC. Barcelona (Spain).
e-mail: miquel@icm.csic.es
2 IMEDEA, CSIC. Esporles, Mallorca (Spain)
3 Institute of Oceanology PAS. Sopot, Poland
4 Shirshov Institute of Oceanology RAS. Moscow, Russia
5 Institute of Arctic and Marine Biology, University of Tromsø. Tromsø, (Norway)

I want to talk about some effects of global warming on zooplankton, and of their contribution to increase possible changes in Arctic pelagic ecosystems.
As everybody knows, IPCC predicts a significant rise in temperature that will be more important in high latitudes, and specially in the Arctic. And the temperature increase will result in a drastic reduction in the surface and thickness of Arctic ice in summer, with the corresponding problems related to the changes in intensity a quality of the light reaching marine systems, and the changes in the phenology of primary producers and consumers.
1. - The ecosystem response to quantitative or qualitative changes in environmental variables is usually non-linear and abrupt.

2. - These changes can start with weak modifications of the *functional response* (rate processes) followed by *structural changes* (variations in the taxonomy or size structure of primary producers or first consumer levels) that lead to non-linear alterations of the *Ecosystem Function* that lead to a new equilibrium state, when they reach a TIPPING POINT.

Changes on ecosystems can be or are frequently non-linear, leading to regime shifts. It could start with slight quantitative (metabolic rates) or qualitative structural changes like variations in the size structure of primary producers or first consumers levels that reach a point where the in the ecosystem function leads to a different equilibrium state when they reach a tipping point.
CONSEQUENCES OF CLIMATIC CHANGES FOR ARCTIC MARINE ECOSYSTEMS

INTENSIVE PROPERTIES
primary production, feeding rates and metabolism

STRUCTURAL PROPERTIES
abundance, taxonomic composition and size-spectrum of primary producers and consumers

SIGNIFICANT CHANGES IN THE PATHWAY OF MATTER AND ENERGY TRANSFER

In the case of the Arctic ocean, the warming and corresponding summer ice retreat will affect both the structural conditions of phyto- and zooplankton. The first effects will be observed in the intensive properties of ecosystems: Changes in the primary production, feeding rates and metabolism that will lead to structural properties, with the corresponding changes in the transfer pathway of matter and energy.
In marine systems, zooplankton plays a crucial role in marine biogeochemical cycles. By grazing reduce the POC; Change the downward flow of POC; enhance the PCO2 (respiration) and therefore the final fate of biogenic C. N and P cycles increase the per cell nutrient quota, both by grazing and excretion; modify the relative proportion of dissolved N and P (changes in the C:N:P metabolic ratios) and also the quality of the available nutrients for phytoplankton (ammonia, urea, Dissolved primary amines, etc.)
Metabolic indicators of zooplankton trophic status and nutrient regeneration

Specific metabolic rates

<table>
<thead>
<tr>
<th>C losses</th>
<th>N excretion</th>
<th>P excretion</th>
</tr>
</thead>
<tbody>
<tr>
<td>C:N</td>
<td>C:P</td>
<td>N:P</td>
</tr>
</tbody>
</table>

Budget of matter and energy

\[ P = I - (E + U + R) \]

So, the changes in zooplankton metabolism would be observed, first in the specific rates of respiration and excretion, and second in the metabolic ratios, indicators of their trophic status, that is, the quotients between the respiratory carbon losses and the N and P excreted, in one side,

Ad second, in the zooplankton metabolic budget, that is, in alterations in the balance between the terms of the equation relating production as the difference between the ingestion minus excretion, egestion and respiration.
Metabolic indicators of zooplankton trophic status and nutrient regeneration

Specific metabolic rates

C losses  N excretion  P excretion

C:N  C:P  N:P

Budget of material and energy

\[ P = I - (E + U + R) \]

Possible changes in relation to metabolic quotients....
...we studied the metabolism of zooplankton in the eastern Greenland Current and N of the Svalbard during the year of the record reduction of sea ice extension, in July 2007.
We studied the respiration and ammonia and phosphate excretion by incubation experiments in temperature-controlled baths at “in situ” conditions. Respiration was continuously monitored by Optodes, the ammonia excreted was analysed by fluorimetry, and phosphate according to Grasshoff.
• Identification and quantification

Parallel zooplankton aliquots allowed to obtain Biovolume - AFDW transform factor (mg AFDW = 0.134 mm³)...

...and the relationships between Zoolmage biovolumes and semi-automatic image analysis biovolumes* we calculated zooplankton C (mg C = 0.062 mm³).

*(Alcaraz et al., 2003)

The taxonomic composition, size-structure and individual volume of zooplankton were estimated with the Zoolmage method. The biomass as organic C, by the relationships between bivolume and AFDW and the relation between Zoolmage BV and semi-automatic method.
Average specific metabolic rates (* µmol C_{zoo}^{-1} \cdot day^{-1})

<table>
<thead>
<tr>
<th>µmol C/ind</th>
<th>spec-C</th>
<th>spec-</th>
<th>spec-P</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>58.04 (220.78)</td>
<td>0.0195 (0.0133)</td>
<td>0.0059 (0.0046)</td>
<td>0.0004 (0.0003)</td>
<td>1</td>
</tr>
<tr>
<td>61.06 (55.79)</td>
<td>0.0219 (0.0114)</td>
<td>0.0019 (0.0013)</td>
<td>0.0002 (0.0002)</td>
<td>2</td>
</tr>
<tr>
<td>----</td>
<td>0.0283 (0.0231)</td>
<td>0.0016*</td>
<td>----</td>
<td>3</td>
</tr>
</tbody>
</table>

1: This study
2: Ikeda et al. 2001
3: Conover and Gustavson (1999) **
Urea + NH_4-N

The results: The values obtained for specific respiration and excretion here differed from previous data from similar areas and season and similar individual biomass. During our cruise C losses were from 10 to 30 % lower than in previous reports, N excretion rates were higher for a factor of 3, and P excretion about twice. And it must be considered than Conover data for N excretion include both ammonia and urea, the main N-product excreted by large copepods (C. Hyperbore)
Average metabolic quotients (atoms)

<table>
<thead>
<tr>
<th></th>
<th>C/N</th>
<th>N/P</th>
<th>C/P</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>13.2</td>
<td>14.15</td>
<td>210</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>(3.5)</td>
<td>(7.2)</td>
<td>(150)</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>37.2**</td>
<td>-</td>
<td>-</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>(24.9)</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>4.23</td>
<td>16.91</td>
<td>75.07</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>(1.43)</td>
<td>(9.16)</td>
<td>(61.01)</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>5.62</td>
<td>16.0</td>
<td>90.0</td>
<td>4</td>
</tr>
</tbody>
</table>

1: Ikeda et al. (2001)
2: Conover and Gustavson (1999)
**: Urea + NH₃-N
3: This study
4: Rios & Fraga (1987)

Of course, the average atomic ratios of the metabolic products differed from previous data: Regarding C/N quotients, there was a significant reduction by a factor of 3; N/P ratios were slightly higher, and C/P ratios lower than previous reported values, that were quite similar to the stoichiometric values observed for phytoplankton by Rios and Fraga.
High (>12) metabolic C/N quotients suggest a metabolism based in the use of lipids, are generally attributed to herbivorous diets, and are typical of high-latitude zooplankton in summer.

Low C/N and C/P quotients indicate the use of N- and P-rich metabolic substrates (i.e., proteins and structural phospholipids), correspond to zooplankton from lower latitudes and suggest a carnivorous diet. Typical of Arctic zooplankton in winter.

The N/P metabolic ratios values determine the stoichiometry of regenerated nutrients available for primary producers.

What these changes mean? The metabolic quotients of zooplankton give useful indications about their trophic status or their metabolic substrate:

Higher than 12 C:N ratios suggest a metabolism based in the use of lipids, are generally attributed to herbivorous diets and are typical of arctic zooplankton in summer.

Lower C/N and C/P ratios indicate the use of metabolic substrates rich in nitrogen, like proteins, and phospholipids, are typical of zooplankton of low latitudes or Arctic zooplankton in winter.

And what is important, the excreted N/P values determine the stoichiometry of the regenerated nutrients and hence of the dissolved nutrient pool available for primary producers.
Protein-based metabolism?

Non-herbivorous diet (or at least very low phytoplankton ingestion rates, Saiz et al. this symposium).

Shift in the structure of phytoplankton (diatoms substituted by a bloom of *Phaeocystis pouchetti*), so other food sources (ciliates and heterotrophic dinoflagellates?) must have been used by zooplankton, or starving conditions required the use of their own N-rich substrata.

Why the changes observed? Everything points towards a protein-based metabolism,

1) either a shift in the diet (the ingestion rates on phytoplankton were very low, (see the poster by Saiz et al),

2) The early occurrence bloom of colonial Phaeocystis, almost non-edible by zooplankton, so other food items like ciliates could be used, or

3) Starving conditions that lead to the use of their own proteins as a metabolic substrate.
Temperature-C:N:P metabolic rates of Arctic zooplankton (in situ values)

There is a significant decrease of metabolic quotients as a function of temperature.

C:N -3.25 %  C:P -5.3 %  N:P -10.3 %

But even more important than the difference in the average values were the significant negative relations between temperature and metabolic quotients: The C:N ratio decreased more than 3% for every degree centigrade of temperature increase.

More than 5 % the C:P ratios, and more than 10 % N:P ratios,
Metabolic indicators of zooplankton trophic status and nutrient regeneration

\[
\begin{array}{ccc}
C: N & C: P & N: P \\
\end{array}
\]

Zooplankton matter and energy Budget

\[
P = I - (E + U + R)
\]

Now we will go towards the balance between the rate processes that could be modified by changes in temperature: the matter and energy balance.
We concentrated in two terms of the balance: Ingestion and Respiration
The study took place in June 2009 around the Svalbard Islands, on board the Jan Mayen, during the project Arctic Tipping Points.
Respiration: Incubation of *Calanus* and aliquots of mixed zooplankton with FSW in temperature-controlled baths at 0, 3, 6 and 10 ºC above “in situ”.

Ingestion: Incubation of *Calanus* with *in situ* phytoplankton community in temperature-controlled baths at 0, 2.5, 5, 7.5 and 10 ºC above “in situ”.

The objective was to study the effects of sudden temperature rises and the possible existence of non-linear responses and tippig points in the feeding and metabolic response of zooplankton, specifically *Calanus glacialis*. The study consisted in incubation experiments at 0, 3, 6 and 10 ºC above “in situ”, both for respiration and for feeding experiments using the in situ phytoplankton community.
Ingestion rates (µg pig/ind/day)

Those were the responses observed in different stations with different phytoplankton concentrations, or when enriching with a culture of Thalassiosira gravida. The responses were also different for different species.
As average, Carbon Specific ingestion rates increased with temperature rise until reaching the maximum around 2 °C, and afterward significantly decreased. While respiration increased until 6 °C and afterwards decreased. Those were the typical response, with an increase for temperatures below the optimum, a maximum, and a further decrease. But what happens when both processes have their optimum at different temperature? In the case of ingestion and respiration, the two main terms of the matter and energy balance, the temperature at which both variables intersect is the equilibrium point where growth (or production) will be zero, and at higher temperature it will be negative.
When considering the effects of temperature rise on Arctic plankton systems, we see that the metabolic balance (the balance between C gains and losses) reduces and even becomes negative; the metabolic C:N:P ratios also reduce, thus contributing to change the dissolved pool of nutrients for phytoplankton; the receding ice cover changes the irradiance conditions, both the quality and quantity of radiation reaching the water surface, thus changing the C:NP: composition of phytoplankton and contributing to the shifts in the community structure, both regarding the size and the taxonomic composition, which changes the metabolic substrate and reinforces the temperature effects alone; is affected back that reinforces and contributes to change the shifts in zooplankton taxonomic composition and size structure, and from here affect the higher consumer levels and probably the whole ecosystem.