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Preface

"Arctic ocean acidification: pelagic ecosystem and biogeochemical responses during a mesocosm study"

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The growing evidence of potential biological impacts of ocean acidification affirms that this global change phenomenon may pose a serious threat to marine organisms and ecosystems. Whilst ocean acidification will occur everywhere, it will happen more rapidly in some regions than in others. Due to the high CO_2 solubility in the cold surface waters of high-latitude seas, these areas are expected to experience the strongest changes in seawater chemistry due to ocean acidification. This will be most pronounced in the Arctic Ocean. If atmospheric pCO_2 levels continue to rise at current rates, about 10 % of the Arctic surface waters will be corrosive for aragonite by 2018 (Steinacher et al., 2009). By 2050 one-half of the Arctic Ocean will be sub-saturated with respect to aragonite. By the end of this century corrosive conditions are projected to have spread over the entire Arctic Ocean (Steinacher et al., 2009). In view of these rapid changes in seawater chemistry, marine organisms and ecosystems in the Arctic are considered particularly vulnerable to ocean acidification. With this in mind, the European Project on Ocean Acidification (EPOCA) chose the Arctic Ocean as one of its focal areas of research.

With the majority of studies conducted in the laboratory and most of them investigating the responses of single species, we presently know little about how organism responses scale up to the community and ecosystem level and what the consequences are for marine food webs and biogeochemical cycles. To help close this critical gap in our knowledge on ocean acidification impacts, EPOCA put an emphasis on community-level experimentation. This, in combination with EPOCA's focus on Artic waters, paved the way for a multidisciplinary mesocosm CO_2 perturbation experiment off the northwest coast of Svalbard in 2010. With a total of 35 participants from 9 EPOCA partner institutes and 4 non-EPOCA partners, this was the project's largest joint activity (Fig. 1).

Nine units of the Kiel Off-Shore Mesocosms for Ocean Simulations (KOSMOS) were deployed in Kongsfjorden about 1.5 nautical miles north-west of the Ny-Ålesund research base on 31 May. Each unit enclosed ca. 50 m^3 in a 17 m-long, 2 m in diameter polyurethane bag (Fig. 1; see Riebesell et al., 2013 and Schulz et al., 2013 for details on the experimental design). The plankton community at the start of the experiment was characteristic for a post-bloom situation and a retention-type food web with high bacterial production, high abundance of mixotrophic phytoplankton, and comparatively low mesozooplankton grazing. After closing the mesocosms and completing the CO_2 manipulation, the enclosed plankton community passed through three distinct phases, each characterized by a peak in phytoplankton biomass dominated by different species assemblages: phase 1 – end of CO_2 manipulation until nutrient addition ($t4$ to $t13$); phase 2 – inorganic nutrient addition until the second chlorophyll *a* minimum ($t13$ to $t21$); phase 3 – the second chlorophyll *a* minimum until the end of this study ($t21$ to $t30$).

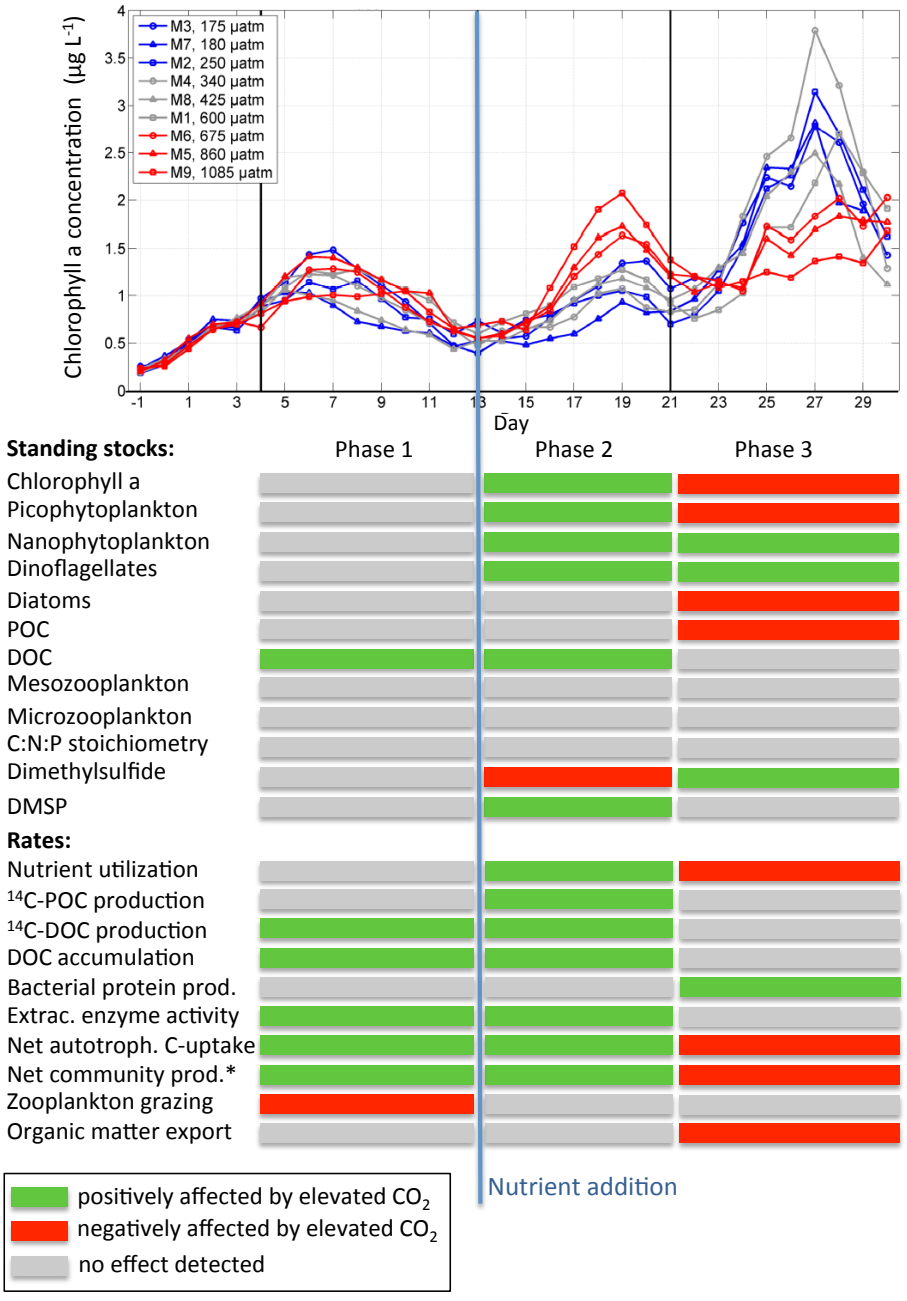
In total over 50 parameters were measured daily during the experimental period. This unique and comprehensive data set, available at Pangaea doi:10.1594/PANGAEA.769833, lends itself for in-depth analyses and well-grounded interpretations of the observed trends, both in terms of the unperturbed plankton community succession and

Fig. 1. Top – KOSMOS mesocosms deployed in Kongsfjord, Svalbard. **Bottom** – participants of the mesocosm study (from left to right - front row: Eva Leu, Ulf Riebesell, Rui Zhang, Anna de Kluijver, Chiaki Motegi, Michael Meyerhöfer, Signe Koch-Klavsen, Sarah Romac, Andrea Ludwig, Corinna Borchard, Richard Bellerby; back row: John Stephens, Tsuneo Tanaka, Kai Schulz, Jan Czerny, Nicole Händel, Matthias Fischer, Martin Sperling, Anja Engel, Judith Piontek, Tor Einar de Lange, Merel Collenteur, Tim Boxhammer, Anna Silyakova, Michael Sswat, Jozef Nissimov, Frances Hopkins, Kerstin Nachtigall, Susan Kimmance, Corina Brussaard, Jean-Pierre Gattuso, Anna Noordeloos, Sebastian Krug, Lucie Bittner, Harry Witte)

biogeochemical cycling as well as their modifications in response to ocean acidification. Integrating the broad spectrum of observations allows for a synoptic view of pelagic ecosystem sensitivities to ocean change in Arctic waters. Here we summarize some of the major results of this study (see also Box 1):

Autotrophic standing stocks, composition, and activities:

1. Autotrophic biomass was similar in all CO_2 treatments during phase 1 prior to nutrient addition, was higher at elevated pCO_2 during phase 2 after nutrient addition, and lower at elevated pCO_2 during phase 3 (Schulz et al., 2013).
2. The rate of nutrient utilization after nutrient addition was higher at elevated pCO_2 (Schulz et al., 2013).
3. ^{14}C fixation was higher at elevated pCO_2; for POC production this trend was significant after nutrient addition, for DOC production it was significant both before and after nutrient addition (Engel et al., 2013). DOC accumulation during phases 1 and 2 correlated positively with pCO_2 (Czerny et al., 2013).
4. Following nutrient addition, elevated pCO_2 stimulated picoeukaryotic photoautotrophs and to a lesser degree nanophytoplankton, leading to stronger nutrient drawdown in the high CO_2 treatments during phase 2; as a result of this, growth and biomass of the diatom community developing during phase 3 was negatively correlated with pCO_2 (Brussaard et al., 2013; Schulz et al., 2013).



Box 1. Upper panel: Chlorophyll *a* concentration (µg L^{-1}) in the nine mesocosms over time. Colours and symbols represent the different CO_2 treatments; blue – low pCO_2 (175–250 µatm), grey – intermediate pCO_2 (340–600 µatm), red – high pCO_2 (675–1085 µatm). **Bottom panel:** effects of elevated CO_2 on measured standing stocks and rates; phase 1 – end of CO_2 manipulation until nutrient addition ($t4$ to $t13$); phase 2 – inorganic nutrient addition until the second chlorophyll *a* minimum ($t13$ to $t21$); phase 3 – the second chlorophyll *a* minimum until the end of this study ($t21$ to $t30$). * Net community production estimated from carbonate chemistry measurements.

5. Growth of dinoflagellates, developing during phase 2 and into phase 3, was positively affected by elevated pCO_2 (Schulz et al., 2013; Leu et al., 2013).

6. CO_2-related changes in phytoplankton taxonomic composition during phases 2 and 3 were mirrored in the fatty acid composition of suspended matter: the contribution of poly-unsaturated fatty acids (PUFA) correlated positively with pCO_2 (Leu et al., 2013); an exception to this is 20:5n3 eicosapentaenoic acid (EPA), an important diatom marker, which was negatively correlated with pCO_2 during phase 3 (Leu et al., 2013).

7. No indications were found for a generally detrimental effect of ocean acidification on the planktonic food quality in terms of essential fatty acids (Leu et al., 2013).

Microbial heterotrophic diversity and activities

1. The bacterial community attached to particles was more diverse at high compared to medium and low pCO_2 (Sperling et al., 2013).

2. The maximum apparent diversity of bacterioplankton differed significantly between CO_2 treatments; the relative abundance of *Bacteroidetes* correlated negatively with pCO_2 at the end of the experiment; in general bacterial diversity, taxonomic richness and community structure were influenced primarily by variation in primary production (Zhang et al., 2013).

3. Fifteen rare bacterial taxa correlated significantly with the pCO_2 treatment, most of which increased in abundance with higher CO_2 (Roy et al., 2013).

4. Time-integrated primary production and bacterial protein production were positively correlated, suggesting that higher amounts of phytoplankton-derived organic matter were assimilated by heterotrophic bacteria at increased primary production (Piontek et al., 2013).

5. Extracellular enzyme activity of β-glucosidase and leucine-aminopeptidase increased with increasing pCO_2 (Piontek et al., 2013).

6. Higher rates of viral lysis at elevated pCO_2 led to lower bacterial abundances in phase 3 (Brussaard et al., 2013). Bacterial protein production (BPP) was higher in high CO_2 treatments during phase 3 despite lower total bacterial cell numbers (Piontek et al., 2012).

7. No CO_2 effect was observed for bacterial respiration, carbon demand, and growth efficiency (Motegi et al., 2013).

Zooplankton abundance and composition

1. Meroplanktonic larvae (cirripedia, polychaeta, bivalvia, gastropoda, and decapoda) dominated the mesozooplankton community while copepods (*Calanus* spp., *Oithona similis*, *Acartia longiremis* and *Microsetella norvegica*) were found in lower abundances (Niehoff et al., 2013).

2. Mesozooplankton abundance and taxonomic composition developed similarly in all mesocosms with no pCO_2 effect on the abundance of single taxa and the overall community structure (Niehoff et al., 2013).

3. Microzooplankton composition and diversity was similar in all CO_2 treatments, indicating that neither direct pCO_2/pH effects nor indirect effects through changes in food composition impacted microzooplankton carrying capacity and phenology (Aberle et al., 2013).

4. Zooplankton grazing decreased with increasing pCO_2 during phase 1 (de Kluijver et al., 2013).

Community structure, production, and respiration

1. The planktonic community developed from a post-bloom retention-type system at the start of the experiment to a new production system after nutrient addition; the nutrient-induced increase in primary production and phytoplankton biomass was initially dominated by pico- and nanophytoplankton (phase 2) before it shifted towards microphytoplankton, predominantly diatoms and dinoflagellates (phase 3) (Schulz et al., 2013; Brussaard et al., 2013).

2. Elevated pCO_2 enhanced net autotrophic community carbon uptake during phases 1 and 2; the opposite trend was observed during phase 3 (Czerny et al., 2013; de Kluijver et al., 2013).

3. Net community production obtained from carbonate chemistry measurements increased with increasing pCO_2 during phases 1 and 2 and decreased with pCO_2 during phase 3 (Silyakova et al., 2013).

4. Significantly lower gross and net community production at elevated pCO_2 during phase 3 was also obtained from changes in dissolved oxygen during incubations (Tanaka et al., 2013).

5. Community respiration remained relatively constant throughout the experimental period, with no significant differences between CO_2 treatments (Tanaka et al., 2013).

Biogeochemical processes and production of trace gases

1. Following inorganic nutrient addition, the carbon to nutrient uptake ratios were lower than Redfield proportions during phase 2 and higher than Redfield during phase 3, with no detectable effect of pCO_2 on uptake stoichiometry (Silyakova et al., 2013); for the total post-nutrient period (phases 2 and 3) ratios were close to Redfield proportions.

2. pCO_2 had no significant effect on the elemental composition of particulate organic matter (Czerny et al., 2013).

3. Budget calculations revealed that CO_2-stimulated carbon consumption resulted in higher accumulation of

dissolved organic carbon in high compared to low pCO_2 treatments (Czerny et al., 2013).

4. Export of fresh organic matter increased with increasing pCO_2 before nutrient addition (de Kluijver et al., 2013), but overall carbon export decreased with increasing pCO_2 during the export event thereafter (Czerny et al., 2013).

5. Concentrations of dimethylsulfide (DMS) were reduced by 35 % at intermediate and by 60 % at high pCO_2 levels relative to ambient pCO_2; in contrast, concentrations of dimethylsulphoniopropionate (DMSP), the precursor of DMS, were elevated by 30 % and 50 % at intermediate and high pCO_2, respectively. Elevated DMSP production at high pCO_2 correlates positively with higher dinoflagellate biomass (Archer et al., 2013).

6. The response of halocarbons to pCO_2 was subtle or undetectable: despite strong significant correlations with biological parameters, iodomethane (CH_3I) dynamics were unaffected by pCO_2. In contrast, a significant positive response to pCO_2 was obtained for diiodomethane (CH_2I_2) with respect to concentration, the rate of net production and the sea-to-air flux; there was no clear effect of pCO_2 on bromocarbon concentrations or dynamics (Hopkins et al., 2013).

Taken together, these results indicate a considerable resilience of the enclosed plankton communities to ocean acidification, but also some notable sensitivities which – if representative for plankton communities in high latitudes – point towards substantial restructuring of pelagic ecosystems and biogeochemical cycling under future ocean conditions. Distinctly different responses thereby occurred before and after nutrient addition (Box 1). In the absence of inorganic nutrients CO_2-stimulated photosynthetic carbon fixation did not translate into phytoplankton biomass production, but resulted in increased DOC exudation at elevated CO_2 (Fig. 2, upper panel). At this stage excess DOC accumulating in high CO_2 treatments did not stimulate the microbial loop, indicating limitation of bacterial growth by inorganic nutrients. Viral lysis and microzooplankton grazing were the dominant loss processes for phytoplankton biomass, with the latter correlating negatively with pCO_2. Sinking of particulate organic matter was of minor importance during this phase. Due to the lack of data on transparent exopolymeric particles (TEP) it is unclear to what extent rising DOC concentrations led to increased TEP formation, which may have contributed to the observed higher particle sinking of fresh organic matter at elevated CO_2. The latter response to elevated CO_2, i.e. increased DOC release followed by enhanced TEP formation and particle sinking, was in fact described in Arrigo (2007) based on observations reported in Riebesell et al. (2007) and Bellerby et al. (2008).

Following nutrient addition (phase 2), growth of phytoplankton was stimulated by elevated CO_2 in the pico- and nanoplankton size fractions, leading to enhanced nutrient uptake and higher biomass build-up in these groups (Box 1, Fig. 2, lower panel). DOC production and accumulation continued to be higher under elevated CO_2 during phase 2. Contrary to the previous phase, under nutrient-replete conditions the microbial loop now responded to the CO_2-stimulated DOC production with higher turn-over under elevated CO_2. CO_2 stimulation of the microbial loop may also partly explain the higher grazing rates, predominantly by microzooplankton, in high CO_2 treatments (Box 1, Fig. 2, lower panel). In the microphytoplankton size range growth of dinoflagellates, which started to increase during phase 2, was also stimulated by elevated CO_2. CO_2-enhanced nutrient utilization by pico- and nanophytoplankton occurred at the expense of diatoms (Fig. 3), which increased in biomass only during phase 3. The impact of a CO_2-induced stimulation of pico- and nanophytoplankton growth at the expense of diatoms on biogeochemical cycling was visible in sedimentation fluxes, which were lower at elevated pCO_2. With more of the available nutrients utilized by pico- and nanoplankton and channelled into the microbial loop, less of the primary produced organic matter is available for transfer to higher trophic levels (Fig. 3). While this can be expected to also impact growth and reproduction of mesozooplankton, this study was too short to resolve this kind of indirect response, particularly because the difference in diatom production occurred towards the end of the study. In summary, under nutrient-replete conditions, the combination of CO_2-stimulated growth in the pico- and nanoplankton size range, CO_2-stimulated DOC production, enhanced microbial degradation, and reduced diatom production resulted in a reduced strength of the biological pump at the expense of heterotrophic consumption in a retention-type food web (Fig. 2, lower panel).

In the seasonal succession of pelagic systems nutrient-replete conditions supporting export production are typically followed by nutrient-limiting conditions favouring a retention-type community. Due to the risk of sea ice formation in the study area early in the year, our mesocosm experiment only started after the winter/spring bloom had terminated and inorganic nutrients were exhausted. Because nutrients were added only half way through the experiment, the community succession induced in the mesocosms was therefore in reverse order. To what extent this has influenced the observed responses is presently unclear. Obviously, future experiments of this kind should avoid employing nutrient additions at times when the plankton community is not naturally expecting inorganic nutrient supply. Notwithstanding the reversed order of nutrient-limited versus nutrient-replete conditions, our results demonstrate that the impacts of elevated CO_2 on pelagic systems are strongly modified by nutrient availability. The effect sizes for the different phases during the seasonal succession and their relative contributions to the annual primary production and organic matter turn-over will ultimately determine the net impact on an annual basis.

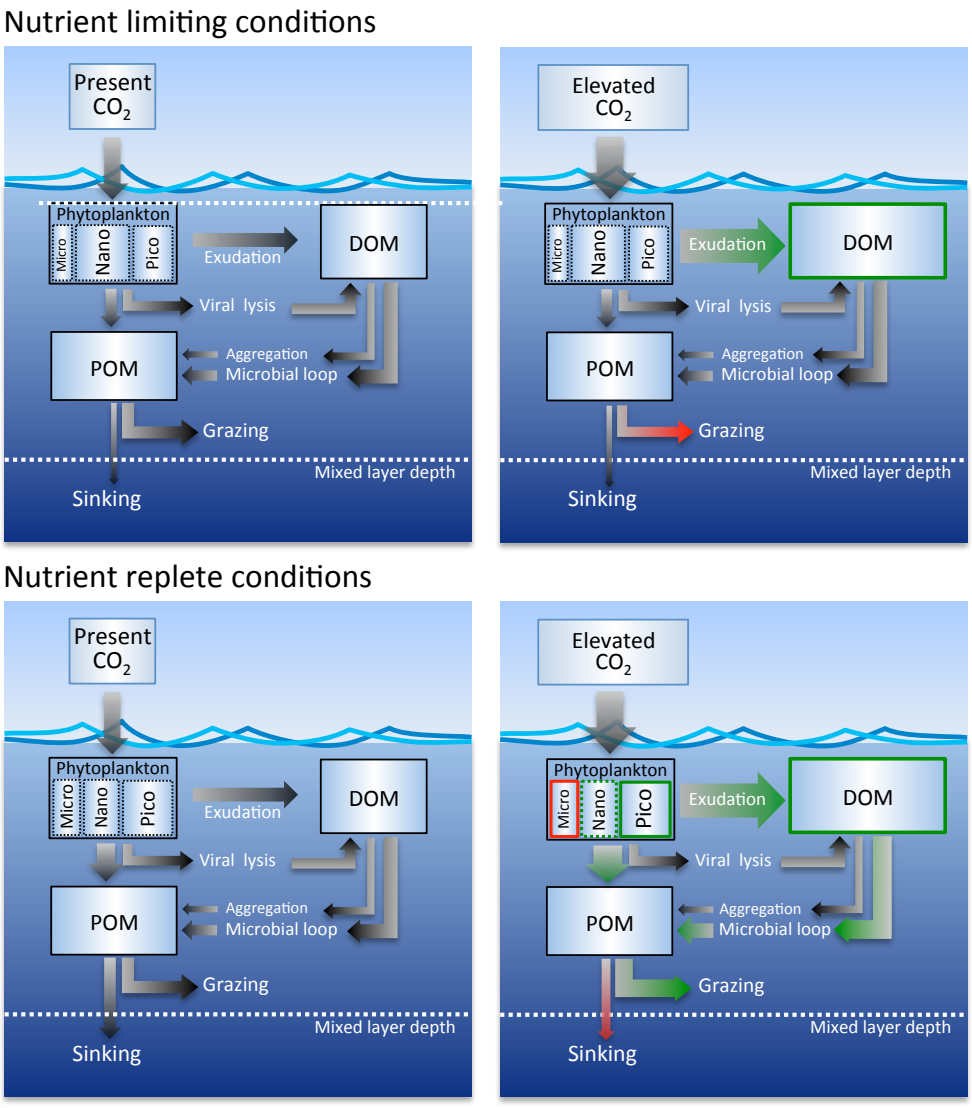


Fig. 2. Sketch of carbon pools and fluxes at present day (**left panels**) and elevated CO_2 levels (**right panels**) under nutrient-limiting (**upper panels**) and nutrient-replete conditions (**lower panels**). The sizes of the boxes represent pool sizes, the thickness of the arrows represent the magnitude of the fluxes between pools; green arrows indicate fluxes stimulated by elevated CO_2, red arrows fluxes which are reduced at elevated CO_2. POM, particulate organic matter, DOM, dissolved organic matter. With a depth of 17 m, the water body enclosed in the mesocosms was entirely in the euphotic zone. Note that some of the fluxes were not measured directly but calculated or inferred from other measured parameters. Modified from Arrigo (2007) according to the outcome of this study.

While it is too early to conclude what the net impact will be, it is obvious from these results that substantial changes in ecosystem dynamics and biogeochemical cycling will occur in a future high CO_2 Arctic Ocean.

The results of this study demonstrate the high potential of community-level field experimentation to better understand the complex interactions triggered by both direct and indirect responses to environmental changes. They emphasize the importance of accurately replicating the environmental conditions and covering the natural community succession. In this context, the mesocosm methodology provides an ideal platform for a systemic approach, integrating across scientific disciplines and thus providing a holistic view of the sensitivities of marine biota to ocean change. The use of a mobile experimental platform, such as the KOSMOS system, opens up the opportunity to test for impacts of ocean changes on ecosystems and in regions deemed most vulnerable to environmental perturbations. Future studies using this or similar approaches in other oceanographic settings and covering different periods of the seasonal plankton succession are urgently needed to evaluate the representativeness of the findings obtained in the EPOCA 2010 mesocosm study off Svalbard.

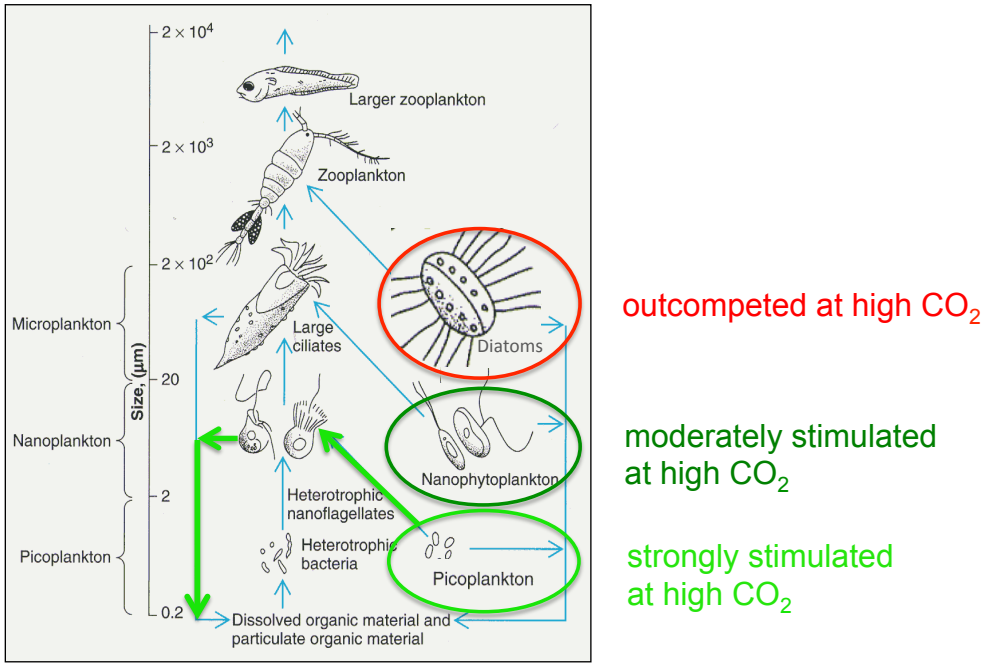


Fig. 3. Sketch of plankton groups and size classes represented in the mesocosms; blue arrows indicate trophic linkages; green circles and arrows indicate groups and processes stimulated by elevated CO_2, red circle indicates diatoms being negatively impacted through CO_2-stimulated effects in the smaller size classes (graph copyright 2001 by Benjamin Cummings).

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