Ratios Matter

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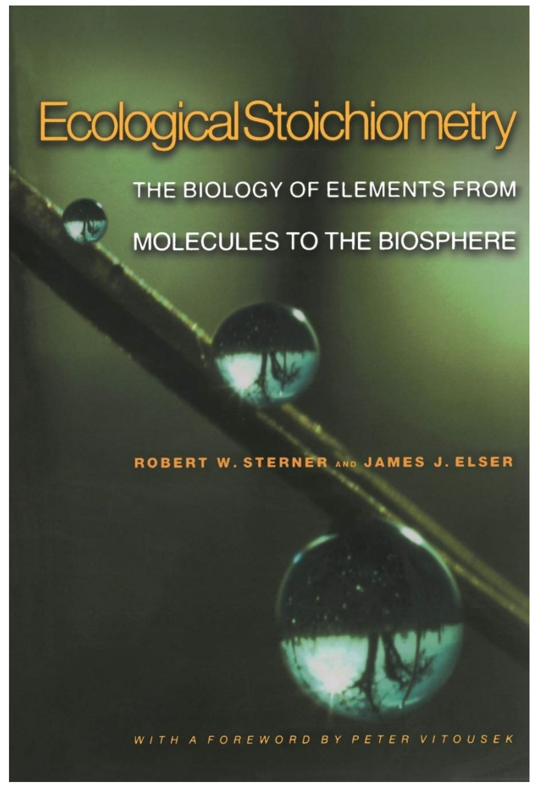
Happy 20th Birthday!

Can you believe it's been twenty years since *Ecological Stoichiometry* was published? It is safe to say that this book has had an important and lasting influence on the study of ratios in ecology. One reason for this lasting legacy is that the book brought together many keystone concepts that laid the foundation for many future research developments. Reflecting its synthetic and comprehensive treatment of a relatively new field, the book has accumulated more than 5000 citations (according to Google Scholar) from papers that cover topics too diverse to fully catalogue here. The book has been the first introduction of many ecologists and others to the fascinating world of elemental constraints and how they affect ecology.



As with all good milestones, we can't help but think rhetorically about the future. What exciting and groundbreaking new stoichiometry will Ecological Stoichiometry inspire? What will future generations think of a book that has been held so closely by so many of us. Are we alone in wondering if there is a revised version in the works?

Reviews from the time of its release may have sounded overstated at the time but are quite prophetic now.

"Few, if any, details of stoichiometry seem to have been overlooked by Sterner and Elser, and their book will be a useful reference to me for many years to come. . . . The hundreds of references in the bibliography are worth the price of the book alone."---David W. Schindler, Nature

"A truly outstanding book. Sterner and Elser provide extremely convincing evidence in support of their hypothesis that elemental stoichiometry is a key to many central issues in ecology."—Val H. Smith, University of Kansas

"Sterner and Elser provide the definitive text on ecological stoichiometry. This is a fundamental advance in unifying ecology across levels of organization." — Simon Levin, Princeton University

"A book founded on the hypothesis of the importance of the N/P ratios in biology. Either you believe or you don't but there is a lot of useful information present." —Reasonable, Amazon.com reviewer

Share Your Stoichiometry with *Ratios Matter*

Ratios Matter is dedicated to sharing news and stories about ecological stoichiometry. This includes material sent to us by our readers. You could share a summary of your newest **stoichiometry** article, a photo of **stoichiometry** research, or possibly some commentary on an emerging **stoichiometric** topic. Or maybe you have news to share on upcoming conference sessions or a new collaborative project that would be of interest to **ratio**-oriented researchers. We welcome all stoichiometric submissions. These are screened for relevance and may be lightly edited. Or in other words,

we will publish almost anything (as long as its stoichiometry).

Ecological stoichiometry has a very long history

Ever since Redfield published that first paper in the 1930's, ecological stoichiometrists have worked from the assumption that marine phytoplankton have a fixed C:N:P ratio of 106:16:1 that hasn't changed over evolutionary time. However, a new paper from Sharoni and Halevy (2022) suggests that this may not in fact be the case. The authors used a model of long-timescale biogeochemical cycles with nutrient- and temperature-dependent phytoplankton C:N:P ($C:N:P_{org}$) parameterizations to calculate $C:N:P_{org}$ through the Phanerozoic Eon, the geological time period from formation of complex life in the early Cambrian Period to the present day.

Sharoni and Halevy's model suggests that during the Paleozoic, organismal C:P and N:P ratios were much higher than the present day with the model giving estimates of C:P 300-400 for Pre-Cambrian phytoplankton. These ratios decreased during the Paleozoic Era as a result of decreasing global temperatures and increasing marine phosphate availability, driven by several large-scale events throughout this era and the first period of the Mesozoic era. In particular, the expansion of land plants in the mid-to-late Paleozoic and the break-up of Pangea in the early Triassic may have increased weathering at a continental scale and fluxes of weathering-derived phosphates into the oceans.

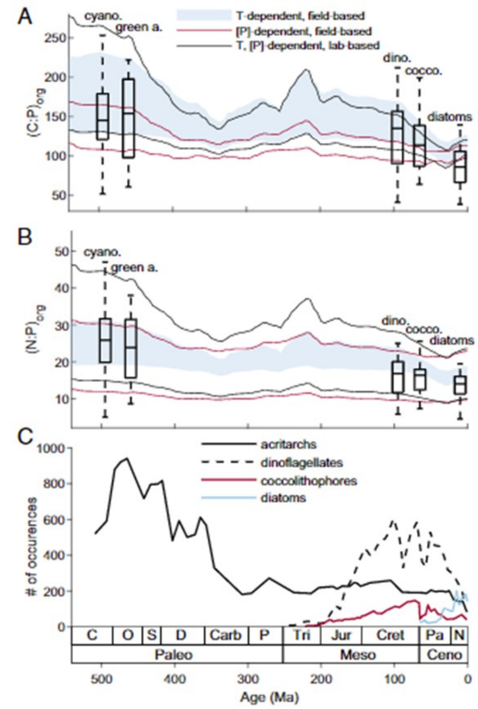


Figure 1. The evolution of phytoplankton $C:P_{org}$ (A), and $N:P_{org}$ (B) (molar ratio) calculated from ~106 model simulations (5th to 95th percentiles of the results). Boxplots show the $C:P_{org}$ and $N:P_{org}$ of modern major phytoplankton groups (boxes, 25th, 50th, and 75th percentiles; whiskers, 99.3% of the data) growing under nutrient-replete conditions, plotted against their time of peak occurrence in the fossil record.(C) Occurrence of the different phytoplankton groups in the geologic record.

As phosphate availability in the oceans increased, so did the "energetics" (i.e., biomass, metabolic rate, motility) of marine fauna, potentially indicating the point at which phytoplankton food quality started to increase. Around the same time, marine phytoplankton communities started to change and diversify, away from the cyanobacteria which had previously dominated and towards other algal taxa such as diatoms, coccolithophores, and dinoflagellates. Mapping this evolutionary journey onto oceanic stoichiometry (Fig. 1) suggests that cyanobacteria did not evolve in nutrient-rich waters. In fact, cyanobacteria may always have been suited to the low nutrient levels that they evolved in and now still occupy waters similar to those they evolved in and which cannot be exploited by more modern, nutrient-rich taxa.

From the paper: "*Our…[research]…suggests that the elemental composition of these phytoplankton groups is a conserved trait, which is constrained by genetics and evolutionary history, and not an acquired trait.*"

Contributed by Catriona Jones

Sharoni, S. and I. Halevy. 2022. Geologic controls on phytoplankton elemental composition. Proceedings of the National Academy of Sciences of the United States of America 119.

How a single shrub mediates stream nutrient status in the tundra

In the tundra, climate change is expanding shrubland. If we understand effects of these shrubs on nutrient availability, we may be able to use physical landscape features that limit their expansion to anticipate the nutrient status of streams in sub-arctic watersheds. Alder (*Alnus* spp.) is a dominant species that heavily subsidizes N availability in adjacent ecosystems because it contains nitrogen (N)-fixing symbionts. The impacts of alder on phosphorus (P) availability are less clear. In some systems, increased P mineralization rates within the rhizosphere of alder elevate soil P. Elsewhere, high P demand by N-fixing enzymes can reduce soil P beneath alder. Moreover, physical watershed features and seasonal changes in meteorological conditions can modulate the quantities of alder-derived nutrients that adjacent ecosystems receive.

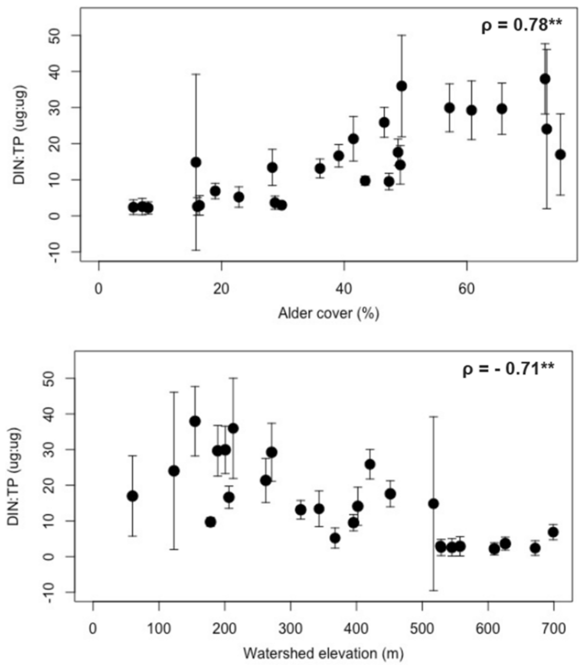


Figure 1. Relationships between alder cover and watershed elevation, and stream DIN:TP ratios (by mass). Circles are mean DIN:TP values and bars are standard deviations.

To better understand the influence of alder on both N and P, and determine how the physical landscape drives this influence, Devotta et al. (2021) examined the relative effects of watershed alder coverage, physiographic variables, and weather on N and P dynamics in 26 streams in southwestern Alaska over four years. We installed soil resin lysimeters in soils beneath alder and non-alder vegetation to assess contributions of alder-derived N and P to streams.

Soils under alder leached almost three times more N, and two times more P than under non-alder vegetation on an annual basis. Although this extra alder-derived N reached the streams, the extra alder-derived P did not, likely due to biotic uptake. Because alder contributed significantly more N relative to P to streams, and more alder cover occurred at lower elevations, stream N:P increased with alder cover and decreased with elevation (Figure 1). Regarding the impacts of weather on stream nutrient levels, snowmelt-associated nutrient pulses and hydrology increased stream N and P in the spring, compared to the summer. However, weather parameters only impacted stream N via their interaction with alder. Taken together, these results suggest that alder intensified P-limitation and elevation was the ultimate driver of stream nutrient status in these watersheds.

From the Paper: "*Based on this rationale, elevation can be considered a generator and proxy indicator of stream nutrient status, potentially even functioning as a predeterminant of aquatic nutrient status in watersheds where alder is abundant.*"

Contributed by: Denise Devotta **Communicated by: Charlotte Narr**

Devotta, D.A., J.M. Fraterrigo, P.B. Walsh, S. Lowe, D.K. Sewell, D.E. Schindler and F.S. Hu. 2021. Watershed *Alnus* cover alters N: P stoichiometry and intensifies P limitation in subarctic streams. Biogeochemistry 153: 155-176.

Can herbivory tilt the scales of competitive outcomes between cyanobacteria and green algae?

Cyanobacteria that can fix atmospheric nitrogen (N_2) are predicted to be better competitors at low N:P ratios because they have an unlimited supply of N compared to non-N-fixing phytoplankton. Many freshwater N-fixing cyanobacteria make heterocysts to protect the N-fixing enzyme, nitrogenase, from oxygen. The formation of non-dividing heterocysts incurs a demographic cost to population growth. However, this demographic cost has never been examined in resource competition theory with and without the presence of herbivory. In this paper, Grover et al. (2022) use mathematical simulations to determine the competitive outcome of N-fixing cyanobacteria and green algae in the presence or absence of a zooplankton grazer. As predicted by resource competition theory, cyanobacteria dominate at low N:P ratios while green algae dominate at high N:P ratios in the absence of herbivory and at low mortality rates (Figure 1). Slightly increasing the mortality rate resulted in co-existence at low N:P and green algae domination at high N:P ratios. Adding herbivory to the demographic costs of producing heterocysts caused surprising competitive outcomes that are not predicted based on resource competition theory. The presence of herbivores with a low attack rate on cyanobacteria resulted in green algae dominating at low and high N:P ratios and cyanobacteria co-existing or dominating at intermediate N:P ratios (Figure 1). Lowering the P or N quotas of the herbivore widens the cyanobacteria dominance or promotes co-existence across the N:P range.

From the paper: "*With herbivores present, high loss rates due to ingestion are predicted to reduce the fitness value of N-fixation to cyanobacteria, and to sharpen apparent competition with non-N-fixing competitors.*"

Contributed by Nicole Wagner

Grover J.P., J.T. Scott, D.L. Roelke and B.W. Brooks. 2022 Competitive superiority of N-fixing cyanobacteria when fixed N is scarce: Reconsiderations based on a model with heterocyst differentiation. Ecological Modelling 466: 109904. (doi:10.1016/j.ecolmodel.2022.109904)

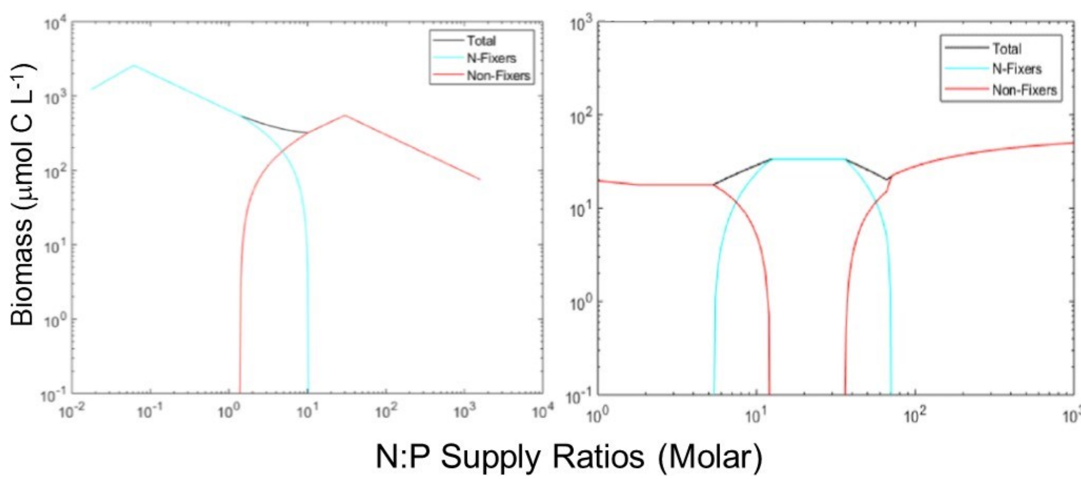


Figure 1. Left: At low loss rates and in the absence of herbivores, the biomass of cyanobacteria (cyan) dominate at low N:P ratios and green algae (red) dominate at high N:P ratios. Right: In the presence of herbivores, the biomass of cyanobacteria (cyan) dominate at intermediate N:P ratios and green algae (red) dominate at both low and high N:P ratios. Figure panels from Grover et al. 2022- left, Figure 4b and right, Figure 6b.

Stoich-apalooza 2022 at the JASM

In May, nearly 2,500 aquatic scientists descended upon Grand Rapids, Michigan for the 2022 Joint Aquatic Sciences Meeting. And, to no one's surprise, all of them tried to attend the stoichiometry symposium, "Stoichiometry in a Changing World: Assessing Elemental Ratios from Organisms/Ecosystems." Well that second part isn't exactly true, but to those of us competing for space in our cramped session room, it certainly felt that way! So, if you were one of those waiting in the mosh pit at the doorway (Figure 1) or were not able to attend the conference but are still keen to hear what happened, fear not; we have you covered!

Figure 1. The line to see Bob and Jim's talk, which later morphed to an autograph line…really! (Photo from Audrey Huff)

Jim Elser and Bob Sterner launched the session with an invited talk, "Stoichiometry: 20 years after," which detailed their scientific adventures after publication of The Book*. Since then, both have had extraordinary careers that were in many cases eerily synchronous. For example both currently serve as directors of large lake research programs at Flathead Lake and Lake Superior, respectively. During their talk, they taught us a bit about these lakes and shared their newest exploits. This includes Bob becoming a movie star (https://freshwater.org/2022/01/27/freshwater-film/) and expanding his stoichiometric reach across the Great Lakes. Jim is once again scaling mountains, this time to study the stoichiometry of snow algae.

After that, the STOICH project highlighted efforts to improve stoichiometric data visualization (Eric Moody), develop an aquatic stoichiometry database (Casey Brucker), and dive deeper into our understanding of the biogeochemical relationship between nitrate and organic carbon concentrations in aquatic ecosystems (Reilly Farrell). Results from Rules of Life project were also presented by Jana Isanta-Navarro, Logan Peoples, and Clay Prater who discussed integrative insights into growth and stoichiometric coupling across the tree of life. Other research groups also presented in the session. The Hawaiian Shirt Mafia from Baylor (Figure 2) presented experimental results of N:P supplies on N dynamics in eutrophic lakes (Isabelle Andersen, Alexa Hoke) and on tradeoffs between growth, resource acquisition, and toxin production of cyanobacteria (Nicole Wagner).

As for session awards, the "World Traveler" award went to Kauan Fonseca who flew in from Rio de Janeiro to present his work studying the effects of *Corbicula* on lake stoichiometry. Former *Ratios Matter* AE Casey Godwin took home the award for "Most Eyebrow Raising Research Question" by asking: "Is P special?" Don't worry, he reassured us that it is while also highlighting the tight relationships between phytoplankton growth and content of other elements including a suite of lesser studied essential elements including Si and Fe. Current *Ratios Matter* AE Charlotte Narr won the award for "Coolest Measurements" after presenting scanning electron microscopy- energy dispersive spectroscopy (SEM-EDS) data documenting *in vivo* variation in individual parasite stoichiometry for the first time.

Figure 2. The Scott Lab from Baylor University. (Photo from Mark McCarthey)

The most coveted award of "Mass Balance Master" went to Kaitlin Bush for her impressive research documenting the effects of diet composition on C, N, and P assimilation, egestion, and excretion rates of largemouth bass. Finally, we were ultimately deadlocked on the best student oral presentation award, so we would like to split the award among: Tyler Butts, Isabella Sadler, Stephanie Shousha, Nate Tomczyk, Audrey Huff, and all of the students mentioned above for their excellent presentations!

The very last talk, given by Eugenia Zandona, was particularly memorable for two reasons. First, it was an excellent comparison of the predictions of the metabolic theory of ecology with those of ecological stoichiometry using tropical fish nutrient excretion estimates. And more somberly, it was dedicated to Zandona's PhD advisor, Sue Kilham, who recently passed away. The godmother of stoichiometry, Sue's work was foundational in establishing the importance of resource ratio supplies for freshwater phytoplankton growth and diversity. She was also a mentor and an inspiration to many early career women scientists, having herself persevered in a profession not always welcoming to women. Thanks Sue for paving the way for so many of us and for setting a high bar for excellence and enthusiasm as we carry on your legacy of biological research using elemental ratios.

We would also like to thank our session co-organizers, particularly Jana Isanta-Navarro and Nicole Wagner (pictured with the dynamic duo in Figure 3), as well as the other members of our team Patrick Kelly, Felicia Osburn, and Libin Zhou.

Contributed by Jessica Corman and Clay Prater

Figure 3. Some of the organizers and stars of the show, just prior to heading off for the stoichiometry happy hour/all-nighter at Founder's Brewery. From left: Clay Prater, Jana Isanta-Navarro, Nicole Wagner, Jessica Corman, Jim Elser, and Bob Sterner.

*The Book = Sterner and Elser. 2002. Ecological Stoichiometry. Princeton University Press

Warming and the stoichiometry of the spring bloom

What comes to your mind when you think of spring? Warmer temperatures? Newborn animals? Cleaning out your closet? For limnologists (in temperate regions), spring is associated with one important event, a bloom of phytoplankton. As temperatures increase, the bloom is followed by an increase in grazing zooplankton which then consume the algae and the lake enters a "clear water" phase. This seasonal transition from spring bloom to clearwater phase has been documented in many lakes for many years. This pattern is partly attributed to the ability of phytoplankton to grow fast at low temperatures, which allows them to temporarily outgrow their grazers. New research from Diehl *et al.* 2022 suggests that warming and its effect on autotroph stoichiometery may disrupt this well-known pattern.

Mesocosms and simulation experiments revealed that elevated spring temperatures (of about 3.6°C) increased phytoplankton C:P ratios in comparison to ambient conditions (see Figure 1 on next page). The total amount of phosphorus in both the empirical and model system was fixed. Thus after the initial uptake of the mineral phosphorus, the fast growth of algae observed in the warmed treatment was fueled by internal cellular P stores leading to a dramatic increase in C:P content and reduction in quality as a food resource.

The *Daphnia* population in the warmed treatment initially benefited from the higher temperatures, reaching higher densities than ambient populations early in spring. However, as phytoplankton quality decreased over time, these populations experienced a greater imbalance between their stoichiometric requirements and what was provided by their food. As such, grazer populations began to crash due to the inability to obtain enough of the nutrients which limit growth (despite an abundance of carbon), eventually reaching levels below detection capacities. The first (that we know off) larger-scale, empirical demonstration of the "paradox of enrichment"!

In warmed treatments, the spring bloom never ended. In the absence of grazers, algal abundance remained high until the termination of the 3-month experiment. Although follow-up research needs to be done, this study demonstrates the alarming possibility of dramatic change in aquatic ecosystems – resulting from temperature-induced changes in stoichiometry!

From the paper: "*… warming increases food abundance but decreases food quality, promoting the existence of an alternative Daphnia extinction equilibrium at higher temperatures*"

Contributed by Kimberley Lemmen

Diehl, S., S.A. Berger, W. Uszko, and H. Stibor. 2022. "Stoichiometric Mismatch Causes a Warming-Induced Regime Shift in Experimental Plankton Communities." Ecology 103(5): e3674. https://doi.org/10.1002/ecy.3674

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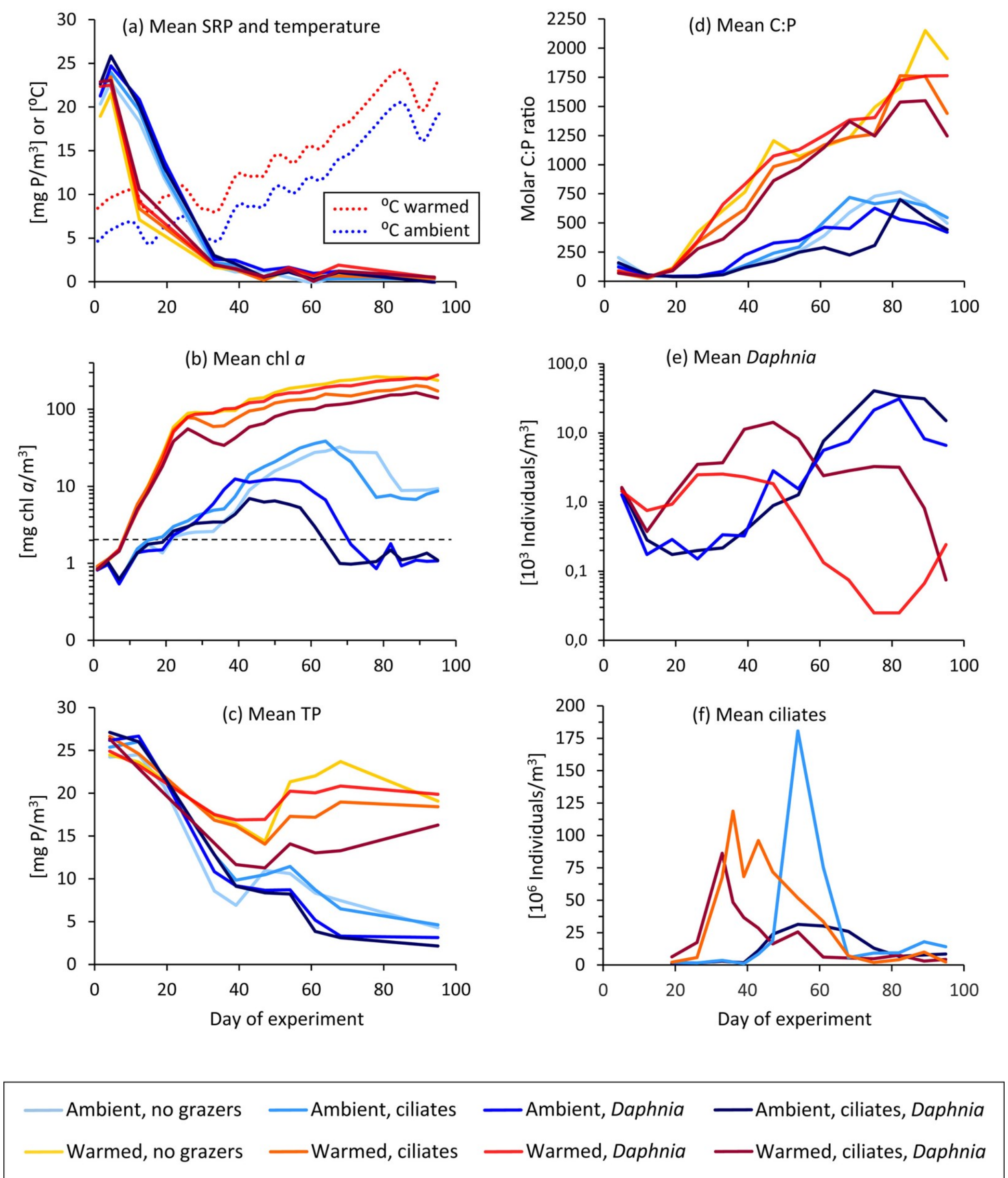

Figure 1. Changes in temperature, water chemistry, algae, and grazers in mesocosms.