CM 2008/A:03

Transformation of dissolved organic matter and its diverse effect on higher trophic level

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Abstract

A considerable amount of primary production by marine phytoplankton is released to seawater as dissolved organic matter (DOM) via exudation and leakage processes. The labile fraction of DOM can either directly serve as a source of energy and nutrients, or is transformed to particulate matter by abiotic gel particle formation. Principally, both pathways induce diverse effects on higher trophic levels, as they: a) affect the growth of bacteria and photo-autotrophic nanoplankton, which directly affects the microbial food-web, and b) enhance the formation of aggregates, which provide pelagic microhabitats but also accelerate the export of organic matter to benthic ecosystems. Reliable biogeochemical flux estimates of these distinct pathways will crucially depend on our understanding of small-scale processes. Here, we show examples that address the microbial turnover of organic matter and how it is related to primary and secondary production in the North Atlantic and at sites in shelf regions. Recent findings on the sensitivity of microbial processes to changes in temperature and pH will be incorporated. Ecosystems in coastal- and shelf regions are most sensitive to anthropogenic impacts, as they are not only susceptible to global but to regional changes. We will therefore give an outlook on how to improve monitoring, experimental, and modeling strategies to better account for microbial food-web dynamics when assessing climate change effects on ecosystems in coastal- and shelf regions.

1. Introduction

Our present understanding of individual processes involved in marine biogeochemical cycling and food web dynamics, has reached a degree of complexity that exceeds our perception of how all processes actually act together. The synthesis and assessment of complex process interactions are tasks that are often assigned to biogeochemical-, and ecosystem modelers, mainly in order to derive estimates of mass fluxes of carbon, nitrogen and phosphorus within open ocean-, shelf-, and coastal regions. Apart from residual errors in simulating ocean circulation, model estimates remain highly uncertain, in particular if the number of biological processes resolved is high. Given our prior knowledge about the variety of processes within an ecosystem does not automatically imply better state estimates of the biogeochemistry or of the food web. The prevailing problem is to constrain the relative separation between different organic matter losses of phytoplankton: a) cell lysis and exudation of dissolved organic matter (DOM), b) aggregation and sinking, and c) grazing by higher trophic levels. Each of these processes listed is a possible sink for phytoplankton biomass and, in turn, exhibits different interpretations of sustaining regenerated production. As a consequence, ecosystem models may resolve equally well the total amount of regenerated and total production, but the pathways may differ, depending on prior assumptions made for the model configuration (along with the choice of parameter values).

In many marine ecosystems, the microbial community controls the balance between regenerated and new production and has therefore been incorporated into a series of ecosystem models (e.g. Fasham et al., 1990; Pahlow et al., 2008). Most studies impose a single sink of DOM, namely hydrolysis by bacteria, and interpret changes of measured bulk dissolved organic carbon and nitrogen (DOC and DON) concentrations solely based on this premise. If more details were known about quality changes in the dissolved organic pool it would not only unravel sources and sinks of DOM, but could help to constrain the separation between pathways outlined before. For example, the alternative sink of DOM to coagulate and form larger colloidal particles is mainly associated with acidic polysaccharides (PCHO). This pathway is hardly considered, but is actually an important connection between DOM exudation by phytoplankton and particle aggregation (Engel et al., 2004; Schartau et al., 2007). Shelf- and coastal regions, in particular, are subject to allochtonous particulate material transport but also to DOM input from rivers. Thus, to differentiate between major pathways of organic matter flux (as well as their interdependency) is challenging but is of great importance for reliable biogeochemical state estimation in such regions.

Figure 1 illustrates the separation of different pathways that can affect the accumulation and demise of phytoplankton biomass. The uptake of dissolved inorganic nutrients by phytoplankton is drawn as an influx sustaining primary production, whereas fluxes leaving the system indicate particle export via sinking and net loss to higher trophic levels. A central role is assigned to DOM. Depending on its chemical quality DOM either promotes particle export or supports the microbial activity. This reflects the idea that the quality of DOM is linked to the predominant ecosystem functioning (Azam and Malfatti, 2007). In the following, we will outline some of the future challenges of biogeochemical modeling in open ocean, shelf- and coastal regions. The proposed modeling tasks are rather generalized and confined to the production and fate of DOM, postulating that a better representation of the microbial community is essential for a better understanding of ecosystem functioning. Due to the complexity of this issue, we will primarily focus on those aspects that are associated with organic carbon exuded by phytoplankton and abiotic particle formation, including the potential sensitivity to variations in carbon dioxide (CO_2) concentration and temperature. Furthermore, the topics addressed are discussed and related to the microbial food web. Finally, we will propose ideas on how to complement monitoring strategies with intermittent observations that include information on DOM quality and plankton community structure in coastal regions.

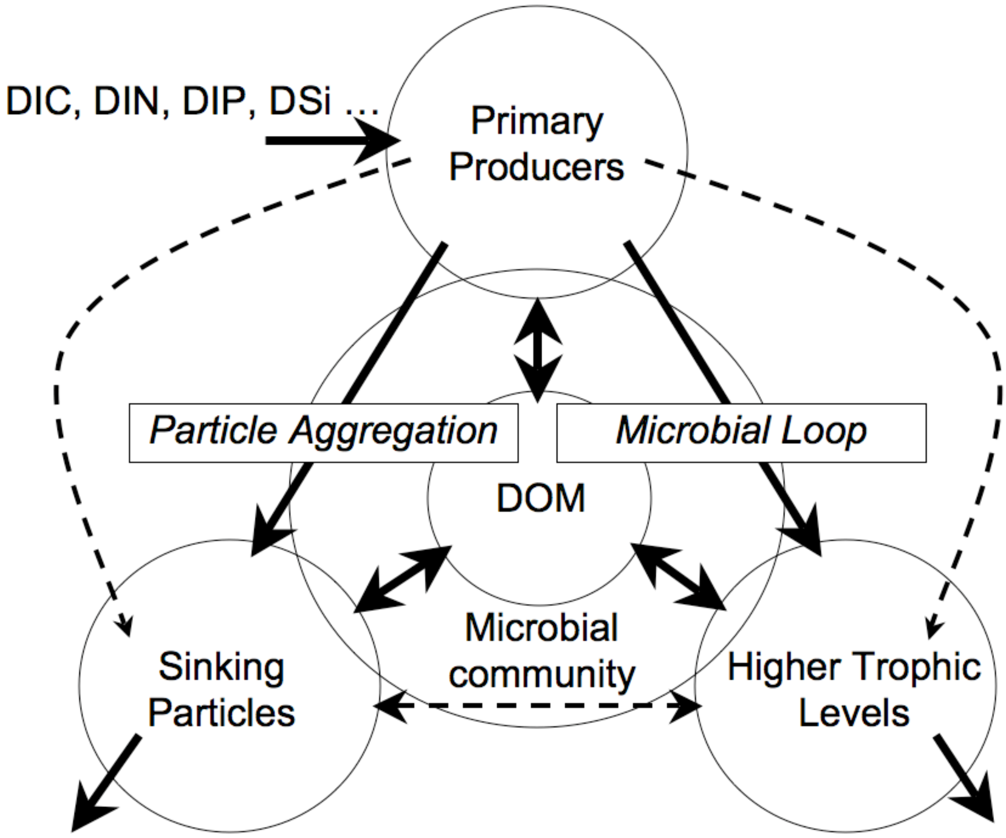

Figure 1: The upper influx arrow represents new production (with dissolved inorganic- carbon, DIC; nitrogen, DIN; phosphorus, DIP and silica, DSi), whereas the two arrows leaving the system indicate the different organic matter pathways that are associated with the net loss of phytoplankton biomass: Export of particulate organic matter and transfer of organic matter to higher trophic levels. The centered position of DOM and microbial community expresses that it mediates between the two pathways. Lysis, leakage, and exudation of DOM by phytoplankton is not regarded as an obvious net loss term, but contribute to either of the two net sinks, by supporting hydrolysis or by enhancing particle formation.

2. On the limitation of typical bulk data to constrain ecosystem models

Great effort is spent on process studies at local sites, where it is possible to come up with measurement strategies that can cover certain periods, e.g. the development and decay of a spring bloom, or that allow frequent sampling over many years. Local studies have their own value but become particularly precious if one can extrapolate their important findings to larger scales and assess their overall consequences for biogeochemical flux estimates in the ocean. The importance of extrapolating in space and interpolating in time has been stressed during the Joint Global Ocean Flux Study (JGOFS) and during the study of Global Ocean Ecosystem Dynamics (GLOBEC). Since then, the number of different ecosystem- and biogeochemical models has increased immensely. Simultaneously, the variety of solutions has increased in terms of ecological functioning, although different models may simulate identical observations equally well (Friedrichs et al., 2007). In spite of now having more biological data available then 30 years ago, one question remains: How much unambiguous information about ecosystem functioning can we infer from fitting current models to those observations?

Productivity under oligotrophic conditions, as found in the subtropical gyre region in the North Atlantic, is discussed to largely depend on physical transport of inorganic and organic nutrients. Recent findings suggest that it is mainly the meridional transport of DON that is responsible for sustaining primary production in the North Atlantic's subtropical gyre (Williams and Follows, 1998; Roussenov et al, 2006; Charria et al., 2008). Although being conclusive in terms of DON transport, the biological origin of the DON transported is not well constrained, and similar results can explain the same pattern in productivity. For example, Oschlies and Schartau (2005) applied a coupled physical-biological model, whose ecosystem module was optimized at local sites in the North Atlantic simultaneously (Schartau and Oschlies, 2003). Their data-assimilative approach yielded results that point towards an efficient recycling loop of organic matter in the subtropical oligotrophic regions, with primary producers being the primary source of the DON that is almost instantaneously hydrolysed. In Charria et al. (2008) DON is explicitly resolved and the subtropical primary production is sustained by the hydrolysis of DON. The difference is that DON is transported over larger distances and comes from northern, more productive regions where the modeled zooplankton becomes the primary source of DON. Advection of DON requires low turnover rates by bacteria (semi-labile DON), whereas Oschlies and Schartau (2005) can only explain their model results in terms of rapid microbial turnover of nitrogen. Given this as an example, different implicit assumptions about the quality of DON (labile versus semi-labile fraction) can produce similar productivity and chlorophyll *a* patterns. Because of different prior information entering both models, their results remain inconclusive with respect to ecosystem functioning. Additional information about bacterial activity and the lability of DON is required. Thus, to resolve quality changes of DOM can be crucial for constraining biogeochemical model results.

The simplest classification of organic substances in the ocean separates dissolved from particulate matter (DOM, POM), along with the carbon, nitrogen, and phosphorus content. The precise distinction between the two partitions is somewhat arbitrary and derived from the application of filters with pore size of 0.45 µm. However, modelers use this definition in order to specify modeled POM as being exclusively cellular biomass: the sum of detritus, phytoplankton, zooplankton, and bacteria. Azam and Malfatti (2007) recall that seawater was found to be replete with colloids that can form larger, gel-like macromolecules. Gel formation is primarily described as a physical-chemical interaction, covering particles in the size range from 10 nm to >100 µm that can either be dissolved or particulate, according to the filter definition. It means that the interaction of colloids induces another sink of DOM, in addition to enzymatic hydrolysis. For example, an increase in transparent exopolymer particles (TEP) can be explained by means of coagulation dynamics (Mari and Burd, 1998). In its simplest form, the mathematical description of the coagulation dynamics for TEP can be reduced to a two-class model, resolving the coagulation of the high-molecular weight fraction of DOM, such as PCHO, to form TEP (Engel et al., 2004), this transition corresponds to an organic matter flux from DOM to POM. The simplified representation of the PCHO-TEP coagulation dynamics has been successfully applied in Schartau et al. (2007), in conjunction with an explicit phytoplankton growth model with variable carbon and nitrogen stoichiometry. With their data-assimilative approach they found that a substantial fraction (64±20%) of DOC must have been exuded as acidic PCHO during the experiment. Eventually, 30% of the POC was attributed to the carbon content of TEP. Their study clarified that great care must be taken when it comes to the interpretation of POC data, in particular during post-bloom periods when phytoplankton growth is either nitrogen- or phosphorus limited.

To date, the modeled counterparts to POC data are interpreted as cellular biomass and extra-cellular POC formation from PCHO (a fraction of the DOC pool) is largely ignored. This is surprising since the coagulation of PCHO and TEP is recognized as being an important link to marine snow formation and thus to carbon export (Jackson and Burd, 1998). From our current knowledge about colloidal dynamics (at the transition between DOM and POM) we may infer from PCHO and TEP fractions of the DOM and POM pools whether the formation of marine snow is promoted (e.g. when PCHO fraction of DOM is exceedingly high) or microbial activity is stimulated such that it diminishes the entire labile pool of DOC, DON, and dissolve organic phosphorus (DOP).

3. Sensitivity of DOC production to climate change

Carbohydrates are the largest fraction of characterized organic matter in seawater, followed by amino acids (Pakulski & Benner, 1994). Given an estimated net oceanic uptake of carbon dioxide (CO_2) of approximately 2.2 Gt C per year (Takahashi et al., 2002) and an globally integrated ocean pool of 685 Gt DOC, it is likely that even small variations in the turnover of DOC can affect the balance between oceanic and atmospheric CO_2.

To date, the exudation of PCHO by phytoplankton is regarded as a "carbon overflow" mechanism, depending on the current rate of photosynthesis under nutrient depleted conditions (e.g. Obernosterer and Herndl, 1995; Søndergaard et al., 2000). Increasing CO_2 concentrations affect rates of photosynthesis (Rost et al., 2003) and therefore the exudation of PCHO is expected to be sensitive to variations in CO_2 concentration as well. In Engel (2002) an increase of TEP was observed with increasing CO_2 concentration accordingly. Such response is hypothesized to affect particle formation in a way that more carbon is sequestered to the deeper ocean under a future raise in atmospheric CO_2 concentration and the concomitant ocean acidification (e.g. Riebesell et al., 2007; Arrigo, 2007). A causal link between atmospheric CO_2 concentration, ocean acidification, production of DOM, and particle dynamics, must be anticipated to affect the space-time distribution of the microbial community, especially within shelf- and coastal regions with a significant riverine input of suspended particulate matter and DOM.

In addition to the suggested sensitivity of photosynthesis and DOC exudation to variations in CO_2, biological processes are known to be highly sensitive to temperature changes. Ocean warming, as best apparent in shelf- and coastal regions (e.g. Wiltshire and Manly, 2004), is likely to enhance metabolic rates of organisms. The temperature dependence is commonly expressed by the Q_{10} factor that is defined as the factorial increase of a physiological rate if temperature is raised by 10^{O} Celsius. Photosynthesis and algal growth is primarily controlled by incident light and resource availability and therefore exhibit only moderate temperature sensitivities, with $1<Q_{10}<2$ (Eppley, 1972). On the other hand, bacterial heterotrophic activity is known to be more sensitive to temperature variations, usually between $2<Q_{10}<3$ (Pomeroy and Wiebe, 2001). This raises the interesting question on how the microbial community will respond to an increase of the resource DOC (e.g. due to ocean acidification) along with enhanced heterotrophic activity (due to raise in mean temperature) (Hoppe et al., 2008). Yet, the correlation of temperature and CO_2 effects on the production and utilisation of DOM is poorly understood.

4. Resolving effects of environmental changes on size density distribution

The concept of the microbial food web stands for the major pathway of energy/mass flux from picoplankton to mesozooplankton based upon utilization of DOM (Pomeroy, 1974; Azam et al., 1983). Mesozooplankton is then consumed by higher trophic levels. In addition to the aspects of quality and origin of DOM, as mentioned before, it is the trophic size-structure of the microbial community that reflects the functioning of the microbial food web. Therefore, a sophisticated analysis of the size-community structure is required (Ducklow, 1994). The complicated link between DOM (or resource) quality, bacterial activity, and trophic interaction can be viewed as a trade-off between resource uptake and predation defense (e.g. Thingstad et al., 2005). Accordingly, we can expect to find a response in the community size-structure along with variations of the quantity or quality of DOM. However, even if significant changes in size-density distributions were observed, it remains a difficult task to resolve such trade-off and distinguish between possible benefits in resource uptake versus predator defense. For example, CO_2 perturbations during a mesocosm experiment induced changes in plankton community structure that were apparent from shifts in the size-density distribution (Engel et al., 2008). High CO_2 concentrations reduced the abundance of small cells (< 3 µm) whereas a significant increase in abundance was observed within the size range between 4 and 6 µm. The authors discuss the potential effect of diffusive CO_2 supply to the cells in relation to their surface-to-volume ratio and the efficiency of the carbon concentrating mechanism. The response seen cannot be explained with a generalized allometric scaling law for carbon supply for algal growth alone, in particular since the response is mainly restricted to a narrow size range. Thus, an increase in mean CO_2 concentration does not automatically imply that more carbon will be channeled through the microbial food web but will depend on the trade-off between the phytoplankton's species-specific efficiency of the carbon concentrating mechanism and predation defense. This further complicates the picture and a generic model that is able to resolve the effect of climate change on the microbial food web will probably need to account for different functional phytoplankton types (with their predominant differences in carbon concentrating mechanisms), such as silicifying, calcifying, and nitrogen fixing algae.

One of the best aggregated representation of the marine ecosystem, including aspects of the microbial loop, was provided with the model of Fasham et al. (1990). The reason for reducing the complexity of the Fasham et al. (1990) model in subsequent studies was solely motivated by the fact that their model could not be well constrained with data available. Contrariwise, extensions of their model were introduced in order to better simulate distinct pattern seen in well-resolved time-series data. To date, we can resort to a series of non-aggregated, size-based models that have been suggested to describe the predator prey interaction within the microbial food web and beyond. Armstrong (1999) analyzed common models with multiple size classes, such as Moloney and Field (1991) and Gin et al. (1998). The stability analyses of Amstrong (1999) explain why size-based models, where larger size classes exclusively feed on the closest smaller size fraction, can come up with aggravating oscillations. Unless quadratic mortality closure terms are included to such models, as suggested by Steele and Henderson (1992), the oscillatory behaviour can hardly be avoided, which makes these sorts of models impractical. An alternative approach is to describe grazing on smaller plankton with a size-distribution function that is convolved with individual size distributions of different plankton species (Armstrong, 1999; Armstrong, 2003). Models with distributed grazing should be insensitive to the chosen number of size classes and their individual widths, but will require good information on characteristic size density distributions of predominant species. Apparently, theoretical considerations (modelling approaches) are advanced but data on plankton size density distributions are scarce and extensive statistical analyses of plankton size structure are still needed. Given the current modeling approaches, the explicit demand for plankton size-structure analyses, as emphasized by Ducklow (1994), has become even more important then ten years ago.

5. Future strategies and data requirements

We consider the dynamics of the microbial community as an important mediator between major pathways that differ in ecosystem functioning. In order to better constrain organic matter flux we need to infer information about DOM quality and lability in conjunction with the plankton community structure (size-density distributions). At best, future experiments should be designed to obtain this information simultaneously. A distinction between DOM affecting physical-chemical particle dynamics and its transformation within the microbial loop is particularly relevant for coastal regions, when assessing anthropogenic impacts on the ecosystem functioning. For example, Sobczak et al. (2002) have shown how an assessment of the bioavailability of organic matter within the San Francisco Estuary can help to characterize trophic pathways (detrital versus algal resource), providing recommendations on how to sustain the planktonic food web. In terms of modeling, progress has been made in how to account for quality changes of DOM and microbial activity, either by explicitly resolving energy requirements for the variety of hydrolytic reactions (Vallino et al., 1996) or by describing the lability of DOM as an explicit property state variable, which affects the ecosystem functioning (Pahlow et al., 2008). Yet, a simple but ideal combination of modeling DOM quality changes along with particle aggregation and distributed grazing has to be worked out, as it would become a good modeling counterpart to observations of DOM and plankton community structure. A successful research strategy must support a simultaneous, iterative process of data acquisition, model improvement, and data analysis.

Currently, worldwide initiatives are developed to improve substantially our possibilities to make high temporal and spatial online observations (e.g. Liverpool Bay, Gulf of Maine, German Bight). Such observational systems are often a combination of different techniques, using ships-of-opportunity, land based radar stations for currents and waves, buoys to make continuous vertical observations of water related parameters. Also the Continuous Plankton Recorder fits into this concept. A nearby coastal station may be used as a long-term reference station (e.g. Helgoland Time Series since 1964, with daily observations). These days, high quality observations can be made of temperature (spatial scale by Remote Sensing), salinity, pH, turbidity, chlorophyll (by fluorescence), primary production, oxygen and pCO_2. More complicated and laborious are measurements of size spectra and species composition of the plankton (for example with FlowCam and CoulterCounter), dominant algal species by molecular techniques based on genomics, and the underwater 3-D structure by a scan-fish. No direct measurements are possible of higher trophic levels, such as jellyfish, fishes and fish larvae, seabirds and marine mammals. Future challenges not only relate to these groups but also to further develop methods to determine rates of important processes, such as microbial uptake mechanisms. The combination of remote sensing and FerryBox transects in the southern Bight of the North sea shows several important characteristics: algal blooms sometimes occur during seasons when they are not expected; extension of algal blooms can only be examined by using remote sensing pictures covering the whole of the southern North Sea; pH, oxygen and chlorophyll measurements show very good spatial agreements; occurrence and transport of blooms as well as their wane can be clearly identified by the temporal combination of the transects.

Despite the fact that the quality of DOC is recognized as being crucial in specifying the organic matter flux and elemental cycling, the molecular composition and compound specific quantities of DOM in seawater are largely unknown (Benner, 2002). Part of the problems is the high salt concentration of seawater that interferes with the chemical analysis of several organic moieties, and limits the application of standard analytical protocols. For example, the quantification of carbohydrates or amino acids, the two most abundant characterized compound classes in DOM, is restricted to the determination of a few standard molecules, despite technical advances being made in ion chromatography and high pressure liquid chromatography techniques. The quantification of dissolved and aggregated acidic sugars, i.e. TEP, or of gel particles in general is still at its infancy. In order to achieve major advancements in unraveling the intrinsic relationships between organic matter chemical quality and its reactivity in biological and aggregation processes, a closer interdisciplinary approach between marine ecology, chemistry and technical engineering will be inevitable.

Acknowledgements:

The presentation includes data and figures from Judith Piontek, Nicole Haendel, and Corinna Borchert from the Alfred Wegener Institute for Polar- and Marine Research, Bremerhaven. Their contributions are gratefully acknowledged.

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