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Microbial traits

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1 Executive Summary

This deliverable presents the conclusions and recommendation from a workshop on Microbial Traits held at DTU in September 2021. The terms of reference were to ensure that the unicellular modelling component in the NUM model (D3.1) covered sufficient detail to ensure it fulfills the requirements of ECOTIP. This work is a direct output from Task 3.1 *Generalized trait-based model of plankton* and it supports the scientific basis of the model framework. The general recommendations are that diazotrophy, while important on a global scale, is not of immediate importance for the diversity and ecology of the subpolar North Atlantic. Of more direct importance are the microbial traits that lend directly to the coagulation and sinking of organic carbon, addressing one of the most immediate unresolved issues of the biological carbon pump; how export flux is related to the community structure of primary producers and their consumers in the surface ocean.

2 Deliverable description from DoA

Report compiling and documenting a critical review of mechanistic trait modeling (Workshop M3.1) associated with microbial processes in the marine environment (following from M3.1). Key traits to be examined are those associated with diazotrophy, particle remineralization, and deep water productivity.

3 Contribution to ECOTIP tasks

This deliverable is a follow up from deliverable D3.1 and provides an assessment of trait coverage of the unicellular components of the NUM marine ecosystem model. This deliverable integrates across several tasks. It is a direct product of Task 3.1 (Generalized trait-based model of plankton) and feeds directly into Task 3.2 (Mechanistic size-based fish community model) and Task 3.3 (Bayesian Network to visualize stressors and vulnerabilities).

With regards Task 3.1, important outcomes for biodiversity and potential regime shifts are net productivity, community size structure, community transfer efficiency and export flux. These aspects will be verified against the output of Task 2.2 (Understanding the pelagic and benthic processes and their alteration due to environmental change) and Task 2.3 (Evidence of altered ecosystems due to changes in biodiversity distribution, invasions and trophic interactions) when the full model is completed (MS18). The ultimate ambition of this task is to include a trait-based approach into biogeochemical models as a component to Earth System Models.

Table 1. Contribution of D3.1 (Mechanistic trait.-based model for unicellular plankton) to addressing the knowledge gaps identified by ECOTIP

Knowledge gaps to be investigated in ECOTIP	Contribution by deliverable D3.1
Biodiversity in terms of functional (trait) diversity is rarely quantified in general and in the Arctic, despite its demonstrated value in relating changes in biodiversity to changes in ecosystem functions and services	Assesses the coverage of unicellular traits to ensure the major components and functions of the plankton community are considered.
Mechanisms behind responses of Arctic biodiversity to multiple stressors are mostly unknown which hampers predictions	
The interaction of multiple environmental stressors, functional (trait) diversity and ecosystem vulnerability is unknown which hampers upscaling and extrapolation of the effects	
Non-linear changes and potential ecosystem tipping cascades in Arctic marine ecosystem can result from changes in composition of natural community, but have not yet been demonstrated, nor have their tipping potential estimated.	Improves confidence in numerical experiments and sensitivity analysis of tipping thresholds and their safe operating space.
The Arctic Ocean is not uniform and the geographic variation both in biodiversity and anthropogenic stressors is unknown and likely to be high – we lack both long-term data series, and pre-historical baseline data.	
Lack of optimized monitoring strategies and significant gaps in knowledge on (particularly) microbial and plankton diversity and across trophic levels, hamper accurate Arctic biodiversity estimates.	Will help identify knowledge gaps where targeted observations and monitoring would be invaluable.
Phenology is poorly resolved. There are a few examples of a changing phenology in the Arctic marine environment, such as earlier spring bloom following from an early ice melt. However, we do not know how that affects trophic linkages and food webs.	Well posed microbe trade-offs provide a mechanistic link to changing phenology.
Socio-economic changes following from the biodiversity change have not been resolved, although the change in fish communities and production will have large consequences for industry, infrastructure, local economy and life-style of indigenous people.	Provides input to the Bayesian Network model that is seen as an important management tool for socio-economic planning, conservation and sustainable development.
Adequate adaptation strategies have not been proposed to facilitate informed decision-making on local to regional scales regarding biodiversity conservation and sustainable development	

4 Microbial traits; function performance and trade-off

In September 2021, an ECOTIP workshop on Microbial Traits was held at DTU, Denmark. This deliverable is a report arising out of that workshop. The workshop was conducted to help outline an appropriate modelling strategy to achieve the aims of ECOTIP. Specifically, to investigate any shortfalls or unresolved issues in the unicellular component of the NUM model described in deliverable D3.1 that would be required to address knowledge gaps and optimize the impacts outlined in the work program.

Trait-based approaches are fast becoming a central concept in functional ecology (McGill et al. 2006, Litchman et al. 2007, 2013, Kiørboe et al. 2018), not only as a means of quantifying functional diversity in marine communities, but also as a tractable means of modelling the complex processes that shape community structure and their impact on ecosystem function. A central task of ECOTIP is to investigate precisely how functional diversity of marine communities respond to anthropogenic stressors, climate change included, with potential precipitous impacts on ecosystem services.

As a unifying theme, processes involved in the biological carbon pump are of most immediate relevance for ECOTIP. Indeed, it is well worth reminding ourselves of the central concept of ECOTIP illustrated in Figure 1 where anticipated increased stratification will fundamentally alter the vertical connectivity of surface, pelagic and benthic ecosystems of the subpolar Arctic and North Atlantic. It is hypothesised that these changes will (1) reduce seasonal variations in production (2) reduce export flux and carbon sequestration, (3) reduce benthic pelagic coupling, (4) increase microbial recycling in surface waters and (5) reduce the populations of large overwintering copepods and the lipid pump.

It was with these considerations in mind that the scope of the workshop on microbial traits was defined.

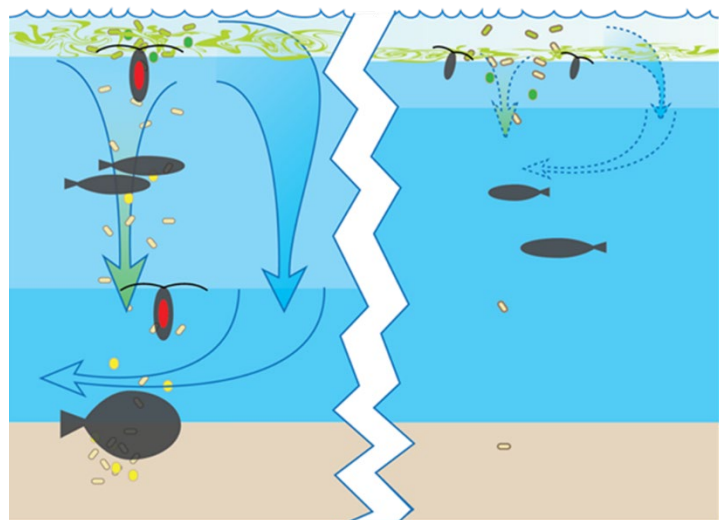


Figure 1. The hypothesized switch of the marine ecosystem under climate change. Current state left with high vertical connectivity, and future state with reduced vertical connectivity. These changes will cascade into the structure and function of marine ecosystems producing a regime shift in plankton communities, leading to changes in the major ecosystem services of carbon sequestration through the biological pump (including microbial carbon pump) and of fisheries production. Reduced vertical connectivity will push the system from a seasonally pulsed high production - high export system dominated by large primary producers and large vertically migrating copepods with a strong

benthic-pelagic coupling (left) toward a system where production by small phytoplankton is more evenly distributed over the season, recycling by microbial loop is enhanced and vertical export is dominated by refractory carbon (right). Migratory species (e.g. forage fish) as well as species depending on benthic production (e.g. benthic invertebrates, cod) will be impaired due to the changed magnitude, timing and size distribution of primary production. Further, altering the ratio of carbon export to recycling will decrease the efficiency of the biological carbon pump and its feedback to the climate-carbon cycle through the reduced CO₂ uptake of the ocean. The basic food web related functions - sedimentation, production and remineralisation - will thus be different in b) and c), with the new food web resulting in changed (lower) fisheries production and carbon sequestration. Irrespective if the change is gradual or abrupt, it will be critical for both local societies and (global) climate.

The overriding aim of the workshop was to ensure various microbial cell processes are properly incorporated into a predictive model of ocean ecosystem functioning; specifically within the context of ECOTIP and ecosystem tipping processes in the Arctic Ocean and the subpolar North Atlantic.

As a starting point, and within the context of ECOTIP goals, the workshop was framed around processes that have a significant impact on the biogeochemistry (e.g. biological pump, carbon sequestration, deoxygenation) that occur in association with the production, export and remineralization of sinking organic material. Specific topics to be explored were listed as:

- Flux and flux attenuation: how well can our current trait-based approach describe the link between surface productivity, community structure and the subsequent export and attenuation characteristics of organic matter in the ocean's interior. Currents status exemplified in (Serra-Pompei et al. In review).
- Differential remineralization: the Redfield ratio of organic material changes under remineralization, often times with nitrogen and phosphorus components being solubilized more rapidly than carbon (e.g. (Koeve 2006)). While clearly important, is this a process we know sufficiently well to be included in our simulations?
- Electron acceptor: Remineralization of sinking organic material draws down O₂, and is associated with the global distribution of Oxygen Minimum Zones (OMZ), (Oschlies et al. 2008, Schmidtko et al. 2017, Oschlies 2021). Under anoxic conditions, other electron acceptors (e.g. NO₃⁻, SO₄²⁻) are available for remineralization (Bianchi et al. 2018, Chakraborty et al. 2021)
- By-products: Remineralization of detrital material produces a rich mixture of byproducts that (1) feed the microbial loop and (2) release dissolved nutrients back to the environment (Hansell et al. 2012).
- Quantify biodiversity in a microbial community: Biodiversity of microbial communities, particularly their prokaryote components, is difficult to quantify, both in terms of α and β diversity. Are there useful metrics that can be used (Haegeman et al. 2013).
- Genomics to functional traits: Genomics represents an important tool that can be potentially used to describe plankton communities (Stec et al. 2017). eDNA for instance is being used in ECOTIP to map aspects of biodiversity. There is also an idea that genomic analysis of sediment trap samples can help illuminate the relationship between surface community structure and export flux. How much do we know of the link between these metrics and functional diversity?
- Trade-offs: While traits are useful descriptors of communities, their real utility lies in that functional trait values invariably are constrained by trade-offs. The more functional, the stronger the trade-off. In this, mechanistically identifying trade-offs is a fundamental criterion for trait inclusion in our trait-based approach (Andersen et al. 2015, Kiørboe et al. 2018).
- Accessible to modelling framework: The point was made, that while the topics to be explored represent significant knowledge gaps in marine microbial processes, we should remain mindful of the types of processes that have a significant impact on ecosystem function in terms of net productivity and carbon

sequestration. Further, if these processes are deemed important, the ultimate goal of ECOTIP is to describe them mechanistically with a view to include them in our trait-based modelling approach.

While this list of topics represented the starting point for discussion, not all talking points received the same consideration. Indeed, some issues not on this list were felt to be of more importance. The following presents an overview of the recommendations that came out of the workshop together with appropriate background.

5 The NUM model

The unicellular component of the NUM model has been described in detail in D3.1 and several of its components have appeared in the literature (Chakraborty et al. 2017, Hansen & Visser 2019, Serra-Pompei et al. 2020, Cadier et al. 2020). Briefly, this model considers most of the major classes of unicellular organisms in the marine environment - from bacteria to microzooplankton. It uses size as a master trait. Trophic function is plastic and is determined by the cell's investments in light harvesting, nutrient uptake, and phagotrophy. It inherently allows for mixed trophic strategies, *i.e.* mixotrophy to emerge as an optimal strategy. The organisms that occupy this trait axis we term generalists spanning from pure autotrophs to pure heterotrophs with mixotrophs inbetween. These include a broad class unicellular organisms that include representations corresponding to cyanobacteria (e.g. *Prochlorococcus*), algal cells (*Chlorarachniophyte* etc.), phytoflagellates, dinoflagellates, and ciliates. Because of their importance in temperate and high latitude oceans, the model also includes a trait axis representing diatoms – where the main trait axes are cell size and vacuole volume both of which determine their mass of the silicate shell together with investment in light harvesting. Finally, there is a representation of osmotrophic bacteria feeding on dissolved organic matter. The microbial loop has a relatively simple representation with a constant turn over time, and detrital material, both dissolved and particulate serving as a nutrition source for heterotrophic microorganisms.

5.1 Photosynthesis

A universal model for photosynthesis is adopted (Raven 1984, Cullen 1990, Hansen & Visser 2019) using a fixed carbon to chlorophyll ratio, a fixed quantum yield, and a fixed cost-benefit relationship for investment in light harvesting (Raven 1984). This model is calibrated against measured light affinities across a large range of photosynthetic plankton including diatoms (Edwards et al. 2015). Details of the photosynthesis model are presented in deliverable D3.1. There is no specific representation of photo acclimation or different pigment classes. Photosynthetic production is partially down regulated under nutrient limitation with unutilized carbon being released as dissolved organic matter.

5.2 Nutrient uptake

The model tracks two nutrients, nitrate, and silicate. Both are taken up with the same general form of size dependent specific affinity; for cells greater than about 2 μm , affinity is essentially controlled by the rate at which molecules diffuse towards the cell while for cells less than 2 μm , affinity is controlled

by the rate at which nutrients are processed (either by porters on the cell surface or internally in biosynthesis). There is a correction for diatoms in that their physical size and carbon mass scale differently depending on their vacuole size. We do not provide cells with the ability to store nutrients, so growth is controlled by Liebig's law of the minimum rather than the Droop model (Droop 1974, Flynn 2008).

At the moment, the NUM model does not track iron (Fe).

Several studies have hypothesized trade-offs regarding nutrient acquisition (Aksnes & Egge 1991, Armstrong 2008, Fiksen et al. 2013) in terms of the number of nutrient porter sites (Berg & Purcell 1977), their packing on the cell's surface (Zwanzig 1990) and uptake kinetics associated with porter handling times (Pasciak & Gavis 1974). Unfortunately, these have not been able to resolve the issue satisfactorily. For the purposes of the NUM model, we defer to a mechanistically derived functional form fitted to observational data (Edwards et al. 2012). A validation of this aspect of the model has been conducted.

5.3 Phagotrophy & mixotrophy

Heterotrophic capture of particulate matter, living and dead, is modelled as a size (predator-prey ratio) dependent consumption of encountered prey. In essence this simulates phagotrophy; the complete engulfment of a prey particle in a feeding vacuole. There are other forms of prey capture in the unicellular arena that operate on a more size symmetric fashion, such as swarm attacks, parasitic infestation or scavenging of much larger prey items. Having said that, direct ingestion into a feeding vacuole appears the dominant mode for most mixotrophs (Stoecker et al. 2016). One of the distinctions that the NUM models does not make is the various taxonomic classifications (e.g. constitutive, nonconstitutive (Mitra et al. 2016)) of mixotrophy that seem to occupy the attention of marine ecologists. Such distinctions would be lost in the general framework of the NUM model.

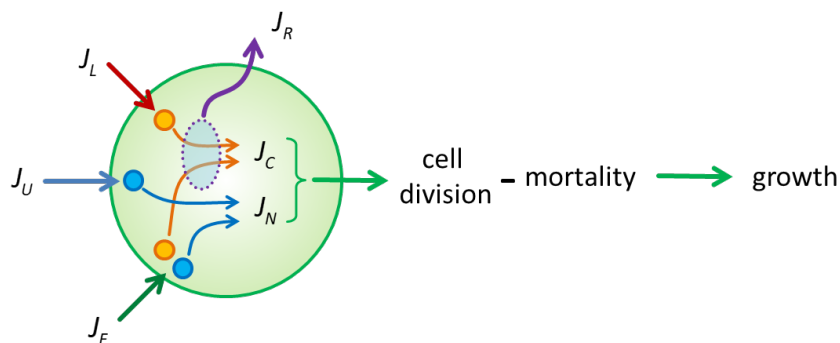


Figure 2. Conceptual pathways of carbon and energy for a generalist mixotroph. Nutrients (blue) are taken up either as dissolved mineral species (J_U), or through phagotrophy (particulate) or osmotrophy (dissolved) as organic nitrogen (J_F). Fixed carbon (orange) enters the cell either by light harvesting (J_L) or heterotrophic uptake (J_F). Carbon is also lost by the cell through basal respiration plus other metabolic costs involved in light, nutrient, and food uptakes. Stoichiometric balance between net carbon (J_C) and nutrient (J_N) as dictated by Liebig's law of the minimum determines cell division rate. Growth rate is division rate minus mortality loss rate – in part determined by larger mixotrophs. All fluxes (J_s) are determined by geometry (mainly cell size) and how the cell allocates its carbon mass to the various tasks of light, nutrient, and food uptake. In essence the cell's allocation schedule and size constitute its functional traits.

One intriguing aspect of mixotrophic strategies is that of photoheterotrophic bacteria (e.g. *Roseobacter*, *Erythrobacter*) that use photon capture to produce ATP but not fix carbon.

Prey ingestion is simply modelled as a maximum clearance rate multiplied by the sum total of all available prey items within a size preference. This formulation thus does not distinguish between the wide variety of movement patterns that bring about encounters – whether turbulent stirring, passive sinking, motile prey, motile predators, or both (Prowe et al. 2019).

5.4 Diazotrophy

There is currently no representation of nitrogen fixation in the model. A key question for discussion is whether such a trait axis should be incorporated in the NUM model for the purpose of ECOTIP.

Nitrogen fixation, or diazotrophy, is the ability of marine phytoplankton to acquire nitrogenous nutrients directly from N_2 gas, a highly inert form of nitrogen that is plentiful and constitutes about 80% of the atmosphere. Diazotrophy is an important component of the ocean's biogeochemistry and productivity (Falkowski et al. 1998, Gruber & Galloway 2008), and counterbalances nitrate losses due to denitrification (Gruber & Sarmiento 1997) and anammox (Devol 2003). It is conducted largely by cyanobacteria, either free-living (e.g. *Cyanothece*) or colony forming filamentous types (e.g. *Trichodesmium*) and is quantified not so much by taxonomy as by *nifH* gene sequencing [Foster and Zehr, 2006]. There is some evidence that diazotrophy can also be conducted by diatoms (Carpenter et al. 1999) as well as by heterotrophic bacteria on sinking marine snow aggregates (Chakraborty et al. 2021).

In large part, diazotrophy fuels primary production in regions of the world's oceans where nitrates are limiting, but phosphates and light are still plentiful. This strategy clearly carries the benefit that diazotrophs can flourish where their non-nitrogen-fixing competitors cannot. There are, however, costs involved. Firstly, converting N_2 to biologically accessible NH_3 is energetically costly. Specifically, the cost is about 8 moles of ATP and 4 moles of electrons per mole of NH_3 produced. Secondly, the enzyme responsible, nitrogenase, is highly sensitive to oxygen. This places quite a strong constraint on the

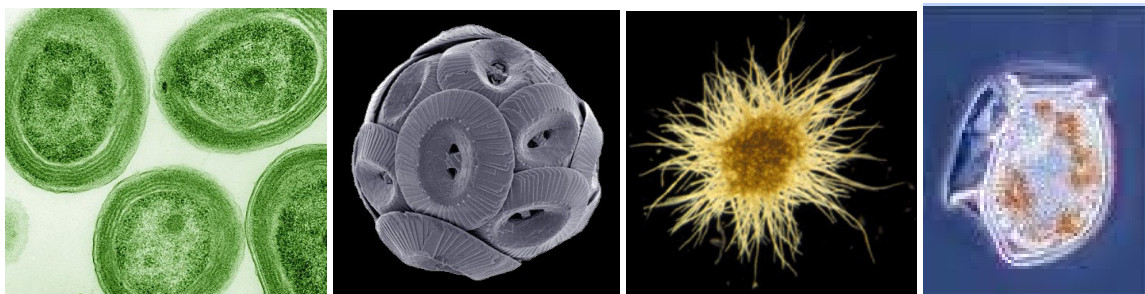


Figure 3. (a) *Prochlorococcus*, a small (0.6. μm diameter) but very abundant cyanobacteria responsible for a large percentage of primary production in the oceans. (b) The calcifying phytoplankton *Coccolithus pelagicus* (10 μm in diameter). (c) The colony-forming filamentous nitrogen fixing cyanobacteria *Trichodesmium*. Filaments are typically composed of about 100 cells, and colonies measure up to 1 mm in diameter. (d) The mixotrophic dinoflagellate *Dinophysis acuta* containing captured chloroplasts (organelle spots) from its cryptophyte prey.

biochemistry of diazotrophs as they have to manage O₂ an unavoidable byproduct for oxygenic photosynthesizers. This is either done by confining diazotrophy to adjacent “service” cell as in the filamentous cyanobacterium *Trichodesmium*, or placing the function within heterocysts, or by conducting diazotrophy during hours of darkness, and “burning-off” excess O₂ metabolically. Finally, diazotrophy competes with photosynthesis in that both rely on Fe, an often limiting micronutrient (Berman-Frank et al. 2007).

Existing mechanistic models of diazotrophy span a range from those seeking to understand biogeographic distributions to more detailed descriptions of cellular processes. The biogeographical models utilize the general paradigm that diazotrophs flourish where sunlight and phosphates are plentiful while nitrogen is limiting. The costs are largely modelled as a reduced growth rate reflecting the energetic expenditure involved in N fixation. With size as a master trait, (affecting photosynthesis, nutrient uptake, metabolic rate etc) this provides a well-founded trade-off landscape for mapping biogeography (Monteiro et al. 2010). At the other extreme are cellular level models that seek to understand in more detail the physiological and biochemical tradeoffs involved (Pahlow et al. 2013), as well as the micro-environments surrounding active diazotrophs (Bianchi et al. 2018, Chakraborty et al. 2021).

While clearly a global implementation of NUM should require some representation of diazotrophy, the immediate need in ECOTIP remains tangential. Diazotrophy is not a major process in subpolar and arctic seas. If such a capacity is required, the biogeography approach seems best suited and has been successfully validated (at least phenomenologically) in a variety of studies.

5.5 Cyanobacteria

As a follow on from the above, while cyanobacteria constitute an important diazotrophic taxon in marine ecosystems, not all cyanobacteria are diazotrophs. Notable cyanobacteria in this class are the globally important marine taxa *Prochlorococcus* and *Synechococcus*. Ostensibly, these species occupy the smaller size classes of the generalist trait axis in the NUM model. There is however, a transition between these smaller and larger taxa, namely the transition from prokaryotes to eukaryotes. While there are considerable physiological and biochemical differences between these cell types, the most approachable for the NUM model has to do with the proportion of the cell’s carbon content that is allocated to cell walls and membranes. In particular, as eukaryotes decrease in size, they lose functional capacity as an increasing percentage of their carbon mass must be devoted to cell walls and the membranes of organelles (hence less for light harvesting, nutrient uptake and biosynthesis). Prokaryotes do not suffer these restrictions to the same degree; they have no organelles, and their cell walls are generally thinner. While it would be feasible to “hard wire” these constraints into the NUM model, they would introduce an alternate problem; namely what would limit the upper size of prokaryotes? We have looked into implementing a trade off based on leaked production (*i.e.* dissolved organic material) as a penalty for having thinner cell walls. Another potentially important consideration is the very small genome (and hence nitrogen requirements) of prokaryotic cyanobacteria compared to eukaryotes; providing a competitive edge for small prokaryotes. Unfortunately, these trade-offs remain

speculative and largely unresolved. Thus, given that cyanobacteria do not play a dominant role in Arctic and subpolar marine ecosystems, we have not pursued this issue in ECOTIP.

5.6 Diatoms

Diatoms are represented in the NUM model and have their own orthogonal trait axis. The key trade-off is between vacuolation – increasing specific nutrient affinity – and lowered mortality risk – the so-called Winnie-the-pooh strategy. The NUM model does not give diatoms higher growth rates as is usually the case in functional type models of marine ecosystems.

One aspect that should be noted is that the NUM model assumes diatoms are solitary cells, and does not provide a specific consideration of chain formation. Benefits of

Diatoms are arguably the most important primary producers in the world's oceans, contributing with about 40% of marine primary production (Mann 1999). They are arguably responsible for as much as 20% of global carbon export flux (Nelson et al. 1995, Behrenfeld & Falkowski 1997, Falkowski et al. 1998) (but see (Buesseler et al. 2020)), with explicit dominance after seasonal bloom events (Smetacek 2000, Sarthou et al. 2005).

Diatoms differ from other marine pelagic protists by having hard silicate frustules and large central vacuoles filled primarily with water. This physical construct brings benefits, costs and restrictions to diatoms that are not relevant to other members of the unicellular plankton community (Raven 1987, Hansen & Visser 2019). A large vacuole for instance, apart from many other potential benefits, first and foremost provides diatoms with larger physical size than non-vacuolated cells of the same biomass (cytoplasm volume). This Winnie-the-pooh strategy (large, yet small) provides diatoms with increased diffusive nutrient uptake capability as well as lowered predation risk (Thingstad et al. 2005, Winter et al. 2010), even without factoring in the mechanical protection potentially provided by the frustule (Hamm & Smetacek 2007, Pančić & Kiørboe 2018). There are, of course, trade-offs: the frustule requires an additional nutrient – silicon – which can become limiting from time to time. The frustule also increases cell's density and hence, potentially the sinking rate. In this context, the vacuole is thought to regulate the cell's buoyancy. With a few exceptions (Wener, 1977), the frustule precludes the ability of diatoms to engage in phagotrophy as practiced by many of their mixotrophic competitors/ consumers. In effect, this delineates a dichotomy in the nutrient acquisition strategies of planktonic primary producers between enhanced dissolved nitrogen uptake for diatoms compared to access to particulate organic nitrogen for mixotrophs¹.

The sinking speed of diatom cells remains a bit of a quandary. Observations suggest that when in a positive growth phase, diatoms of nearly any size remain nearly neutrally buoyant. Yet, these self-same cells when stressed or dead, sink rapidly in accordance with Stokes' law. The mechanism by which diatoms maintain their buoyancy was long thought to be associated with the portioning of "light" (e.g. Na^+ , NH_4^+) and "heavy" (e.g. Ca^+ SO_4^{2-}) in the vacuole sap (Boyd & Gradmann 2002). However, more

¹ The third nutrient management strategy is diazotrophy (listed above): the fixing of dinitrogen gas into biologically accessible nutrient molecules.

recent observations indicate that diatoms can manipulate their buoyancy from neutrally buoyant to negatively buoyant and back again in the space of a few milli seconds (Gemmell et al. 2016, Du Clos et al. 2019). Pumping ions both in and out of the vacuole on these time scales is exceedingly expensive (about 1 mole ATP per mole ion) and therefore likely not to be a feasible mechanism. Unfortunately, no other mechanism has been identified so this issue remains unresolved.

Diatoms (e.g. *Chaetoceros* spp) are particularly prolific in the production of TEP (transparent exopolymer particles), particularly during the senescent phase of blooms. As well as being a nutrition source for heterotrophic bacteria, TEP also plays an important role in carbon export. Specifically, TEP is highly sticky, and promotes the coagulation of marine detritus into larger, and hence more rapidly sinking aggregates. Indeed, TEP and coagulation is thought to play an important role in the termination of diatom blooms leading to a rapid and massive sedimentation when nutrients (nitrogen or silicate) become limiting, or when cells become infected by pathogens (Raven & Waite 2004). The NUM model carries some semblance of this process through the leakage of dissolved organic matter when production outstrips the availability of nutrients. The role of TEP in aggregation is yet to be fully incorporated (but see section 6).

5.7 Calcifying plankton

Despite their important role in ocean carbon budgets (Brownlee & Taylor 2002, Iglesias-Rodriguez et al. 2008, Grigoratou et al. 2019), there is currently no specific representation of calcifying phytoplankton (e.g. coccolithophores) in the NUM model. The primary reason for this is that it is difficult to ascribe a trade-offs e.g. coccolith shells as a mean of grazer protection (Pančić & Kiørboe 2018). This difficulty notwithstanding, coccolithophores are an important component of boreal and subpolar ecosystems contributing typically 1-10% of phytoplankton biomass and reaching up to 40% during spring bloom conditions (Monteiro et al. 2016). Their role is particularly important in the carbon export flux from the surface ocean, in terms of their biomass (Balch 2018), the ballasting of their carbonate shells (Ziveri et al. 2007), and their direct role in the oceans' calcium carbonate pump (Elderfield 2002, Iglesias-Rodriguez et al. 2002, Tyrrell 2008).

Within the context of the NUM model and its use in ECOTIP, there is a case to be made to incorporate some representation of calcifying phytoplankton.

The basic trade-offs involved in calcification are costs—generally thought of as energetic requirements in managing calcium and carbonate acquisition as well as sinking losses – balanced against benefits – protection against grazers and pathogens and perhaps in light acquisition (Monteiro et al. 2016).

The basic ingredients of calcite Ca^{2+} and CO_3^{2-} are relatively plentiful in marine environments and unlike silicate used by diatoms, are not likely to become limiting nutrients. Unlike silicate however, the utilization of these ions is relatively expensive; not so much in the direct uptake of material, but rather in managing the relative concentrations of Ca^{2+} , HCO_3^- and H^+ that allows for calcification to take place.

Specifically in addition to the uptake of Ca^{2+} and HCO_3^- , the cell also needs to deal with the expulsion of surplus protons H^+ (Raven & Crawford 2012, Holtz et al. 2013). Estimates for two common coccolithophores (*E. huxleyi* and *Coccolithus pelagicus*) indicate that between 25% to 30% of the cells energy income from photosynthesis is required for managing the biochemistry of calcification. Up to an additional 5% can be associated with the generation of polysaccharides associated with the formation and transport of calcite plates from the cell's interior to its surface.

Calcite is quite dense compared to seawater (about 2800 kg m^{-3} compared to 1027 kg m^{-3} for seawater). As such, coccolithophores and other calcifying phytoplankton are heavily ballasted – on a par with diatoms. The small size of typical coccolithophores (e.g. *E. huxleyi* 5 to 10 μm in diameter), however, means that individual cells sink relatively slowly, on the order of 5 to 10 m day^{-1} , although larger cell will sink faster. Unlike diatoms, coccolithophores do not have vesicles to offset their negative buoyancy, and losses due to sinking may well be significant. More importantly, their mineral content is likely to be an important ballasting ingredient in marine snow aggregates making coccolithophores a potentially important contributor to carbon export.

In terms of benefits, calcification has been postulated as an up concentrating mechanism for CO_2 that increases photosynthetic rates. This comes about as calcification reduces alkalinity (specifically, the expulsion of the H^+ byproduct of calcification) in the vicinity of the cell thus increasing CO_2 partial pressure (CO_2 is the species in the carbonate buffering system that is taken up by RuBisCO and transferred to the photo system). While stimulating considerable research, observations indicate that this is only a minor effect at best (Anning et al. 1996). The scattering of light has also been postulated as a mechanism increasing photosynthesis (Balch et al. 1996). Specifically, the presence of calcite increases diffuse light conditions and thus reduces the “self-shading” effect that can impact other phototrophs. Finally, calcification might serve to protect the cell from intense radiation and/or harmful wavelengths (Paasche 1968). Similar hypotheses have been posited to the opal shell of diatoms.

Perhaps the most likely – at least the most compelling – benefit derived from calcification is as protection against grazers and pathogens. There is little evidence one way or the other regarding viral resistance of coccolithophore. Microzooplankton on the other hand pose a significant predation risk. While the presence of a calcite shell is by no means fool-proof against ingestion, it can potentially lower the profitability (Visser & Fiksen 2013) of coccolithophores to selective grazers and hence their ingestion rate. Indeed observations suggest that grazers discriminate against coccolithophores when other prey are available (Huskin et al. 2000). Prey selectivity can be simulated in the NUM model as a decreased “palatability” of certain trait combinations and is currently implemented for diatoms (Hansen & Visser 2019, Cadier et al. 2020).

6 Export flux and community structure

One of the key aims of ECOTIP is to link changes in the biodiversity of the plankton community in the sunlit surface ocean, to the export of organic material into the ocean interior, and its impact on the

biological carbon pump and pelagic-benthic coupling. In this context, perhaps the greatest hurdle is the incomplete description of the sinking speeds of particulate matter. In the current implementation of the NUM model, sinking speed for detrital aggregates (marine snow) is set as a size independent constant. Sinking speed of fecal pellets is represented a bit more mechanistically derived based on a constant density and a size proportional to the size of the copepod that produced it. This has at least come some way in unraveling the relationship between primary production and export flux (Serra-Pompei et al. In Review). While this approach represents state-of-the-art, it is far from satisfactory as witnessed by the many appeals to improved knowledge on the link between export flux and plankton community structure. This is a research area where ECOTIP can make a real impact, by providing a size and trait resolved estimate of the sinking speed of detrital aggregates emerging from a plankton community.

6.1 Sinking speeds, size, excess density and aggregation.

How fast organic matter sinks is a fundamental issue for key aspects of the biological carbon pump, not only export flux (Ducklow et al. 2001, Mouw et al. 2016) and dependence on plankton community structure (Boyd & Newton 1995, Henson et al. 2012), but also remineralization depth (Marsay et al. 2015, Cavan et al. 2017), impact on carbon sequestration (Kwon et al. 2009), consumption of oxygen (Suess 1980, Bopp et al. 2002), nutrient recycling (Tréguer & Jacques 1992, Buesseler et al. 2007), and organic supply to sediments and benthic communities (Gooday 2002, Cael et al. 2021a). However, despite years of observations from laboratory and field, sinking speeds of natural aggregate particles remain as enigmatic as ever; aggregates of any size from microns to centimeters seemingly sink at any speeds from practically zero to several 1000s of meters per day (Iversen & Lampitt 2020, Laurenceau-Cornec et al. 2020, Cael et al. 2021b). Yet the physics of sinking speed is unequivocal. Sinking speed is set by a balance between buoyancy forces and drag (Stokes 1845, Clift et al. 1978), and while the precise formulation may not be as neat as Stokes' law (Oseen 1910, Loth 2008) the following principle must hold: sinking speed is a monotonically increasing function of aggregate size and excess density *ceteris paribus*.

We are currently exploring a novel means to simulate the production of detrital aggregates as a self-similar process. This arises out of the concept that marine aggregates are fractal entities (Alldredge & Gotschalk 1989, Logan & Wilkinson 1990, Jackson 1995) – they certainly exhibit fractal properties in the convoluted structure and their mass and porosity vary with size. In departure from previous works, we contend that it is only the process of aggregation that is self-similar, and not the aggregates themselves. The reason for aggregates not displaying universal fractal properties is the homogenous nature of the primary particles from which they are formed. Further, aggregates are under continual dynamical change as they are subject to degradation, dissolution, and fragmentation (Figure 4).

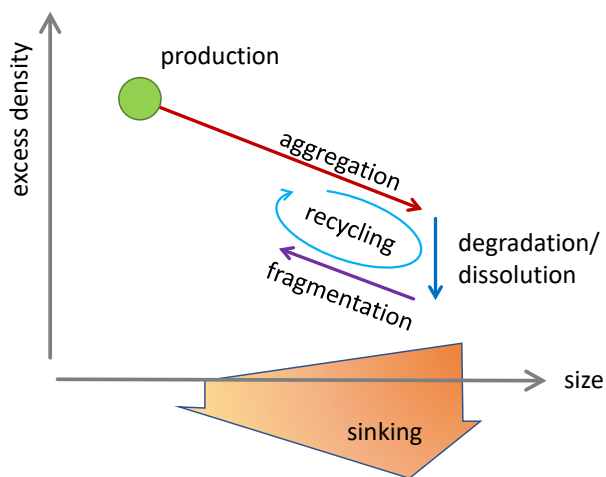


Figure 4. Aggregate dynamics depicted in 2 dimensional state space. Dynamics are driven by 3 processes; aggregation producing larger less dense aggregates, degradation/dissolution which reduces the solid mass (and hence excess density) of aggregates, and fragmentation. Primary particles (e.g. diatoms, coccolithophores) are produced in a specific size and density range. The production of other material such as dust and TEP can also be specified. The distribution of aggregates in this state space eventually reaches steady state when the rate of supply is balanced by the sinking losses particularly of large dense aggregates.

Preliminary work suggests that the variance in observed sinking speeds of marine aggregates (collated in (Cael et al. 2021b)) collapses when excess density is accounted for (Figure 5). Indeed, analyzing a subsection of the same observations (Engel & Schartau 1999, Engel et al. 2009, Iversen & Ploug 2010, Laurenceau-Cornec et al. 2015) – those that are conducted on relatively fresh, monocultures and preclude manipulations with extraneous material like TEP and dust – provide a means of constraining the self-similarity process. Finally, macroscopic properties of aggregate communities such as routinely measured aggregate size spectra can be used to validate the model.

To this end, the NUM model should extend its trait considerations to issues regarding excess density, both in terms of the cells themselves but also the material that they produce. The rationale for this lies in the practical issue of solving the sinking speed problems, but also in cementing a more robust description of aggregation in the marine environment.

Specifically, much of the literature concerning the fractal dimensions of aggregates has been built on the restrictive assumptions of irreversibility and uniform primary particles (Meakin 1987) which leads to the rather handy definition that the fractal dimension of aggregates is the slope of their $\log(\text{mass})$ versus $\log(\text{size})$ relationship (Burd & Jackson 2009). At the same time, aggregates found in the marine environment have been deemed to be fractal objects in that they display fractal type properties (Alldredge & Gotschalk 1989, Logan & Wilkinson 1990); an increase in porosity and a decrease in excess density as a function of size for instance. There is however a disconnect between these two concepts, namely that aggregation in the marine environment is not irreversible; aggregates degrade and fragment, and they are not composed of identical primary particles. All kinds of primary particles are introduced into the surface ocean by primary producers, sloppy feeding, fecal matter and aeolian

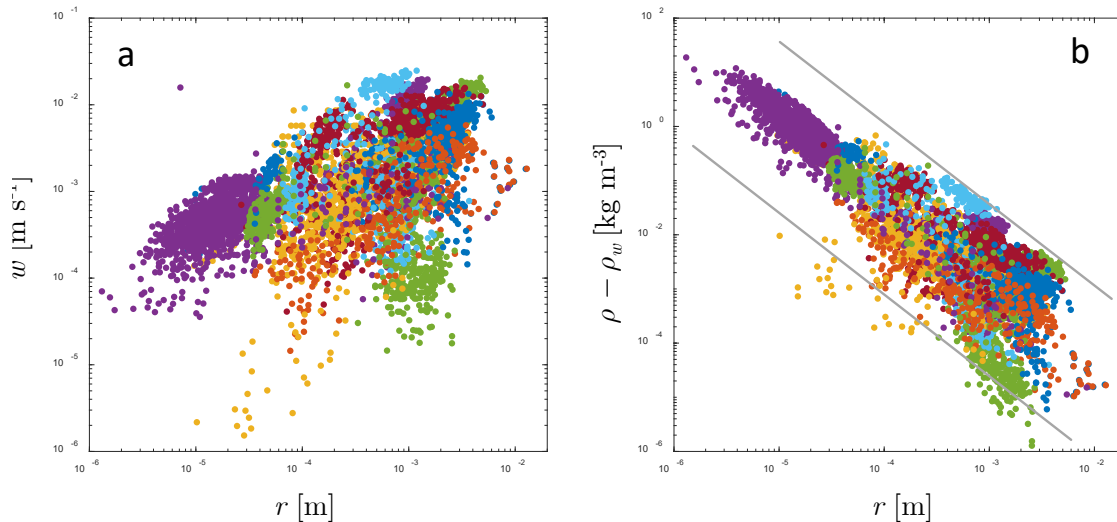


Figure 5. a) Over 7000 observations of aggregate sinking speeds reported in a large number of studies as a function of estimated spherical radius. (b) The excess density calculated from observed sinking speeds using a modified Stokes law. Colors represent different studies. The grey lines in panel (b) indicate a log-log slope of -1.4 and can be used to constrain the description of the underlying self-similarity process by which aggregates grow.

dust deposits. Further, the constituent components of detritus vary significantly in excess density (relative to seawater 1027 kg m⁻³) ranging from positively buoyant e.g. TEP in the range -200 to -300 kg m⁻³ (Azetsu-Scott & Passow 2004) and lipids around -300 kg m⁻³ (Visser & Jónasdóttir 1999) to near neutrally buoyant e.g. cytoplasm 3 to 70 kg m⁻³ (Miklasz & Denny 2010), to very much negatively buoyant, e.g. coccoliths 1700 to 1900 kg m⁻³, diatom frustules 1600 kg m⁻³ (Miklasz & Denny 2010) and atmospheric dust (quartz, feldspar, calcite) approximately 1700 kg m⁻³.

It is no surprise that neither a well constrained fractal dimension nor a size dependent sinking speed for marine aggregates have been found. More importantly, failure to recognize the variability in the density of primary material and how this propagates through an aggregate community confounds efforts to estimate fluxes and attenuation length scales of particulate matter in the oceans.

7 Conclusion

While there are a number of features of the NUM model that would be “nice to have” there are a few that can be deemed essential in order for ECOTIP to maximize its impact and contribution to knowledge gaps. For instance, alternative electron acceptors for the degradation of detrital material, and including Fe as a nutrient pool, while significant within the context of global biogeochemistry, are not of immediate importance for ECOTIP goals. The inclusion of Fe has already been raised for global simulations particularly with regards simulations including the Southern Ocean.

One aspect that can be improved is the distinction between prokaryotes and eukaryotes. In the model's current implementation, there is no distinction, and as a result small cells (1 μ m and less) are poorly represented; a general shortfall of the model given the importance of these size classes in both primary production and recycling of dissolved organic material. A relatively simple mechanistic trade-off involves the carbon mass of the cell wall; specifically thickness versus permeability.

One trait axis that should be resolved is that for calcifying phytoplankton. These constitute an important component of Arctic and subpolar marine ecosystems, both in their contribution to over all production, but also importantly on the control they exert on carbon export. While the precise trade-offs involved remain somewhat elusive, a working assumption is that it involves balance between reduced growth rates and reduce predation risk. Given their small size, they would thus remain competitive against diatoms, particularly when the latter have depleted their silicate supply.

The other important trait to be included is cell density; specifically the contribution to the sinking speed of detrital aggregates. In this, both diatoms and coccolithophores play a major role in that their mineral content serves as ballast for both marine snow aggregates and fecal pellets. For diatoms this is relatively straight forward as the volume of the frustule is already used in the simulation as a means of estimating the silicate demand of the cell. It is not currently used in the context of sinking speed as healthy cells appear to off-set the negative buoyancy of the shell with positive buoyancy in their vacuoles.

Of the trait issues that the NUM modelling framework fails to adequately address, excess density of cells and their constituent parts appear to be the most pressing. This speaks directly to the unresolved question as to how changing functional diversity of the plankton community impacts the export flux of carbon into the ocean's interior. This is a question that is primarily governed by the sinking speed of detrital material – a function of particle size and density – and while size is well resolved by the NUM model, excess density is not. Resolving this is well within the scope of the ECOTIP and is likely to be a lasting legacy.

8 References

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