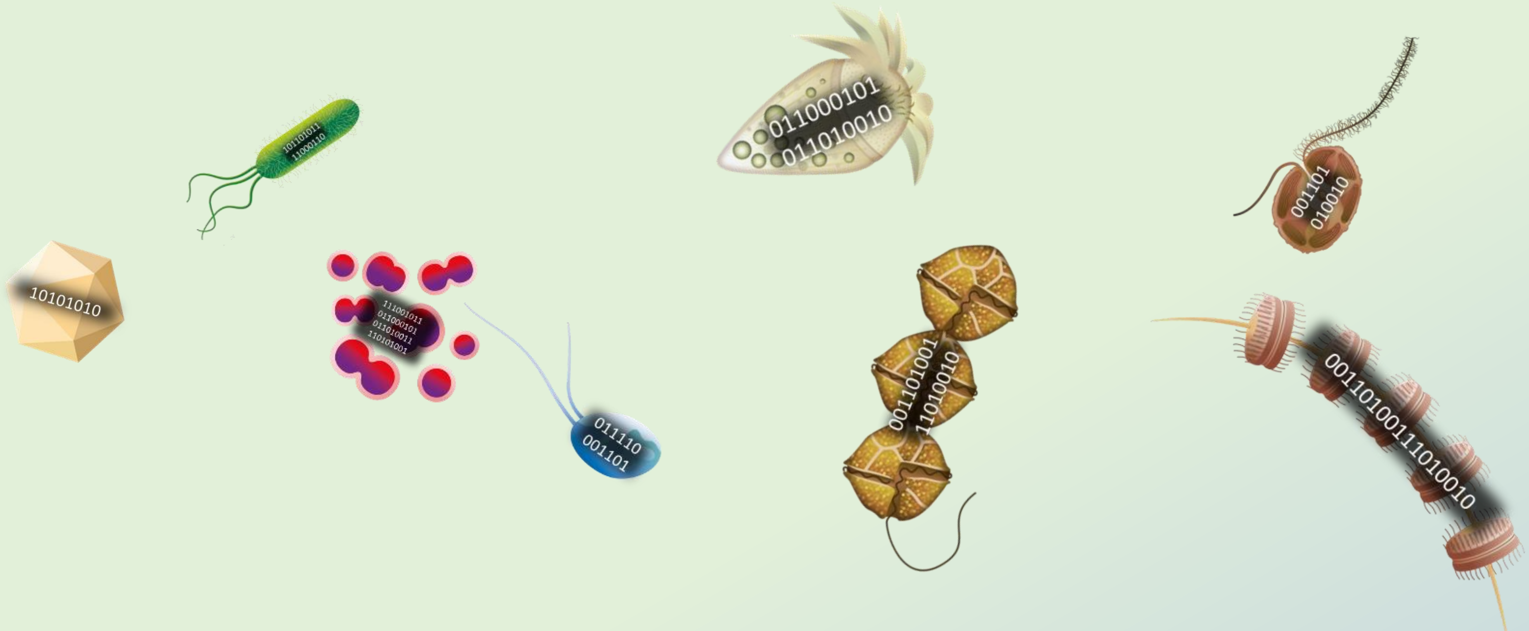

Simulating Plankton - getting it right in the era of Digital Twins of The Ocean

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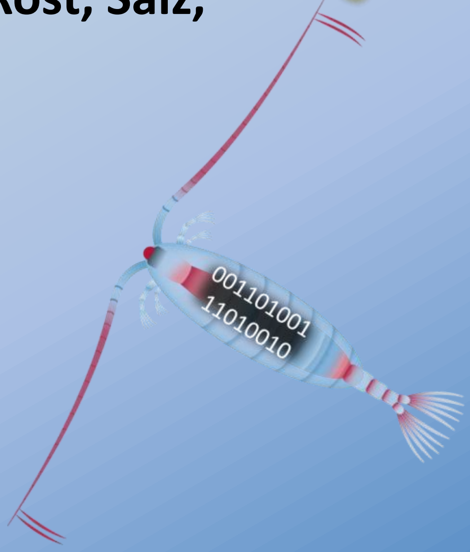

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Simulating Plankton - getting it right in the era of Digital Twins of The Ocean

Building and challenging perceptions

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Author Contributions

Flynn designed the project and task. Others, notably Sherr, helped to improve the task description. All, except Flynn, undertook the task described in Methods, working individually. Flynn undertook the initial analysis of the Results and drafted the Discussion. All contributed to finalising the report.

Executive Summary

This work describes the outcomes from a subcomponent of a project funded by the NERC (UK) during 2023, with the overarching aim of facilitating the construction of the next generation of plankton simulation models by engaging with experts in real plankton physiology and ecology. Over 30 experts, covering plankton from viruses to krill, contributed to various facets of the project. They were selected specifically for their empirical interests; modellers per se were not included. This component had 24 contributors.

Contributors were requested to respond to a series of plankton-specific (33) and general (34) statements and questions relating to the description of plankton in models as might be required for building digital twins. Although not directly emphasised, many of these matters may also be interpreted in the context of traditional extant plankton models. The format of the statements and questions varied, including provocative styles akin to those in a media (TV, radio) interview. For the bulk of the responses, contributors were in agreement.

Complexity in depth is of greater interest than complexity in breadth. Accordingly, digital twins describing rather few plankton types with physiological/behavioural detail were of more interest than models in which many plankton types are described each with little detail. This interest also aligns with that for multi-stressor environments and factors that potentially affect changes in plankton biodiversity. The construction of aspirational plankton digital twins which push the boundaries of empirical understanding are encouraged; examples included interests in dissolved organic matter (DOM) production and exploitation, and the subject of stability in food web dynamics. To deliver to such interests will require significant effort to not only design the simulation engine for the plankton but also the functionality of the graphic user interface.

Failures of aspirational digital twin models due to insufficient detail (as distinct to errors in detail) are not unwelcome, as they flag where more science effort is required. Failures due to simplicity for the sake of simplicity (to minimise computational loads) are considered counterproductive, and arguably dangerous, especially if the user of such information is unaware of the problems because model functionality is described inadequately. The underlying functionality of plankton models needs to be clear. Appropriate use of infographics to explain model functionality to empiricists, rather than relying on mathematical or computer language, is highly desirable. Opportunities to educate empirical plankton scientists in simulation modelling is also required.

Responses to the questions/statements cast doubts upon the functionality of core parts of extant plankton models. By inference (although only raised explicitly in 1 of the 77 questions/statements), doubts are also cast upon the deployment of those plankton simulation models for applied use in, for example, fisheries and biogeochemical circulation models. Having simple plankton models with biodiversity-like descriptors (i.e., species or taxon names) for organisms that are not actually matched by the models functionality give an unjustified level of confidence in simulation projections.

The failure to adequately integrate plankton simulation modelling with empirical plankton research over the last 50 years has resulted in miss-communication and a loss of opportunity for further understanding of plankton communities. The availability of plankton digital twins, available in some form of in silico laboratory, would help promote bi-directional interactions between empiricists and modellers.

Contents

1. Introduction

Simulation models of plankton activity have a long history with conceptual cores stemming from the 1960's (e.g., Monod 1949; Holling 1965; Droop 1968). Over that time the technology available to support the construction and use of models has changed out of all recognition. Our understanding of plankton science itself has also changed radically (microbial loop – Pomeroy 1974, Azam et al. 1983; viral shunt – Suttle 2007, microbial carbon pump – Jiao et al. 2010; mixoplankton paradigm – Glibert & Mitra 2022). The conceptual framework for most models, however, has changed little. The subject of simulation modelling is also not typically taught in graduate or post-graduate studies with the result that much of the developments in plankton modelling have arguably occurred in an ad hoc fashion with rather little holistic oversight from those at the forefront of empirical plankton science.

1.1 Challenging ideas

A central tenet of science, in the quest for true knowledge, is to question. Questioning can be uncomfortable for both the person presenting the challenge, and for those who perceive (rightly or wrongly) that they are at the receiving end of that challenge. The defence of the reputations of both individuals and whole research groups are often linked to the defence of their science. Caught up in this, however, is the need for all scientists to question what we do and why. It is especially important to question perceived wisdom, to ensure that it does not become dogma.

The building of simulation models of plankton starts with conceptual understanding. In the absence of clarity in the literature of plankton ecophysiology and ecology, a need to deliver perhaps to a facet of science that feels remote to empiricists, coupled with various computational challenges, modellers have made decisions on how plankton models should be built.

Traditional models have typically been built to deliver to a specific challenge. A common counter claim of a modeller, when challenged on a facet of their model, is that the model has been built to answer a specific hypothesis, and that it should not be used for other purposes. There are various problems with such a defence, including:

i) in reality the model structure is quite likely to be used for another purpose because the caveats are not explained or understood adequately (e.g., the Droop quota model – Droop 1968; Flynn 2008).

ii) for a digital twin, the model will undoubtedly be used for purposes (e.g., combinations of test scenarios) that are not limited to answering specific hypotheses; that is what a digital twin is intended for, to provide a form of decision support tool to explore 'what-if?' scenarios.

The building of digital twins offers the opportunity to revisit the construction of plankton models. The concept of the activity described herein is to robustly question the conceptual basis of plankton models. Some of those challenges will be very specific, while others are more general or holistic. For each question or challenge there may be several views; no attempt is made here to merge those views – it will be up to the reader to form an opinion, and those opinions will in any case evolve as scientific understanding itself evolves.

1.2. Some Comments About Extant Plankton Models

To place the challenge of building plankton digital twins in context, it is useful to consider aspects of the construction of extant plankton models. These are described below for different plankton types. This is not intended to be all inclusive, or to limit the direction of this work on developing sanity checks for building digital twins (and plankton simulators in general), but merely to indicate the types of descriptors used by modellers.

Biologists are not always consistent with their terminologies, and in any case the usage/meaning of words changes as science develops. This can be extremely confusing for non-experts in empirical science looking over perhaps several decades of literature; it has led to various models having plankton type names that do not accord with biologically meaningful entities. It is quite likely that agreement will not be attained on all naming conventions, but at least within this type of work consistency is required. The Glossary to Flynn (2024) provides the meanings of terms as used here.

1.2.1 Virus

Viruses are rarely described in plankton models. The most widely considered forms are lytic, while lysogenic viruses are generally not included. Even so, beyond some explorations of theoretical ecology, they are generally ignored (Mateus 2017). From a pragmatic point of view, to properly consider the role of viruses with their highly specific host interactions, typically requires a plankton model with a high level description of biodiversity in order to account for host and non-host interactions (but see Thingstad & Våge 2019). Such models are rarely deployed, and then mainly in theoretical scenarios (Thingstad 2000; Flynn et al. 2022a). To more fully explore the ramifications of virus-host interactions in an ecosystem setting also requires a consideration of the production (liberation) and then consumption of the forms of DOM released on host death, and other facets of and stemming from the virus-host interactions. While the basis for digital twins of lytic viruses exists, the computational costs to deliver it on a high temporal resolution demands that virus-host traits are prioritised to enable placement of the most important traits in the more complex ecological scenarios. The construction of lysogenic plankton virus models essentially starts with a blank page.

In passing (because they are invariably ignored in models) the challenge for describing plankton parasites (e.g., fungal infections) has parallels with that of viruses. The matter is complicated not only by the host-specific aspects, but also by ontogenic aspects of the parasite itself, including any growth phases outside of the host.

1.2.2 Bacteria

Descriptions of bacteria plankton are typically simple and with a specific focus on some facet of biogeochemistry (Butenschön et al. 2016). Often bacteria are included implicitly via degradation, nutrient regeneration and other biogeochemistry terms rather than being described in terms of the growth and activities of their own biomass and stoichiometries. Where they are described explicitly, fixed stoichiometry may be assumed, though this is known to be incorrect (Polimene et al. 2006, 2017). Pragmatically, a means needs to be found to bin the multitude of bacteria ecotypes in as few ‘types’ as possible while capturing the breadth of their ecophysiology. To satisfactorily include bacteria in digital twins, a more complete consideration of their various nutrient resources, and also of the fate of products of their activity (their own biomass, part degraded organics etc.) is required. In particular, there is a need for a description of different types of DOM (Anderson et al. 2015), their production and exploitation, not just by bacteria but also by other members of the plankton.

1.2.3 Non-diatom Phytoplankton (cyanobacteria, autotrophic flagellates etc.)

These are by far the most comprehensively modelled plankton type. There are nonetheless various challenges. Phytoplankton (sometimes generically termed ‘*microalgae*’) include both prokaryote and non-phagotrophic protist phototrophs; the latter include diatoms (see below) but have historically also included protists that we now recognise as *mixoplankton* (i.e., phototrophic protists that are also phagotrophic – see below). Non-diatom phytoplankton have often been described in models as a single or very few types spanning all allometries and physiological capabilities (Fasham et al. 1990; Yool et al. 2013). Instances where many phytoplankton have been included in models have often exploited some form of allometric or similar rule(s) (e.g., Follows et al. 2007). Traditionally, phytoplankton models have been based on a single element (often N) or assumed fixed Redfield-like stoichiometry; acceptance of the need in models for something approaching a full variable C:N:P:Si:Fe:Chl has been slow. Most detailed attention has focused on descriptions of different combinations of light, N and P nutrition, though often only pair-wise considerations have been made, and typically interactions between ammonium-nitrate-phosphate are handled in ways that do not necessarily reflect the reality of the physiological regulations. N_2-fixation is typically ignored, or assumed to be permanently expressed in a suitably labelled (‘diazotroph’) plankton functional type. Even within N and P nutritions there are various omissions, such as nitrite, urea, and DOP (and thence the need for phosphatases). Uptake of N and P resources are commonly modelled using a saturating hyperbolic function (e.g., Dugdale 1967, Titman 1976) that assumes key parameters describing nutrient uptake are static based upon information from culture experiments. However, evidence from field measurements suggests that nutrient uptake by both prokaryotic cyanobacteria and small eukaryotes acclimates to the mean nutrient environment such that uptake is a linear, not saturating, function of ambient nutrient concentration (Lomas et al. 2014; see also Flynn et al. 2018).

Photoacclimation is usually handled with reference to chlorophyll.a only (e.g., developed from Geider et al. 1998). Typically the day-average growth rate relates simply to the proportion of the day that is illuminated and the irradiance during that time; it does not follow the evidence showing the complexity of growth rate in light:dark irradiance cycles overlain with cell division cycles (Eppley & Coatsworth 1966; Paasche 1968; Durbin 1974; Iriate & Purdie 1993; Sommer 1994; Tang & Vincent 2000). Fe has also been considered in phytoplankton, though not necessarily in a way that considers interactions with light and N-nutrition (Flynn & Hipkin 1999). Although the potential for mixotrophy via osmo-phototrophy is well known in phytoplankton (Lewin & Hellebust, 1970; Burkholder et al., 2008), it has rarely been modelled. Likewise, the importance of allelopathy (Legrand et al. 2003) has rarely been considered (Mitra & Flynn 2006). Inclusion of both osmotrophy (for N, P as well as for C; e.g., Antia et al. 1981; Flynn & Butler 1986; Godrijan et al. 2022; Meyer et al. 2022) and allelopathy (including toxins), and also of the production of dissolved organics (including TEP) by phytoplankton, requires descriptions of different types of DOM in models (Anderson et al. 2015; see comment on 'bacteria', above, and in **Section 4**). Resting stages, and indeed other life cycle stages and changes in allometry and behaviour (such as diel vertical migration; Flynn & Fasham 2002) with nutritional state, are very rarely considered. There is often a tacit assumption that everything is growing everywhere in vegetative stages all the time, albeit perhaps at low growth rates and at very low abundance. Temperature effects on growth follow simple Q_{10} kinetics, with the growth rate as an emergent property of the maximum photosynthetic rate (Geider et al. 1998). DIC limitation and pH effects (Flynn et al. 2015) are most often not considered, even for coastal situations where growth can be limited by these factors.

1.2.4 Diatoms

In large measure, the same comments apply for diatoms as for non-diatom phytoplankton. Diatoms, as a type, are often described as a single type ranging across all sizes, forms (chain-forming, centric, pennate, etc.) and successional types. Links to the unique physiology of diatoms are usually simple, often being limited to a fixed Si-related stoichiometry, though complex descriptions of that facet have been developed (Flynn & Martin-Jézéquel 2000). Sedimentation (not buoyancy) of diatoms and of other phytoplankton may be described with a fixed value, unrelated to physiology. Osmotrophy and allelopathic interactions, are typically not described, nor in any detail is the release of DOM, though a generalised release is often included by all phytoplankton (supporting bacterial growth; Yool et al. 2013; Butenschön et al. 2016). Effects of temperature, salinity and pH are typically either ignored or described in a simplified fashion, rarely with a linkage to nutritional status (Cf. for pH in Flynn et al. 2015).

1.2.5 Mixoplankton

Historically these plankton, defined as protists that engage in phago-phototrophy (Flynn et al. 2019; Glibert & Mitra 2022), have been lumped in with 'phytoplankton', or perhaps (for ciliates with acquired phototrophy) with 'protistan-zooplankton' (more often termed as 'microzooplankton'). Models of mixoplankton have typically been very simple, making assumptions about physiology to the point of not reflecting reality at all. Phagotrophy in phototrophs has only recently been included in models with any degree of ecophysiological realism (Leles et al. 2021; Li et al. 2022). In addition to the issues affecting the 'phytoplankton' (**Section 1.2.3**), there are other challenges that parallel those in the protistan-zooplankton models (**Section 1.2.6**). The absence of resting stage descriptions likely represents a key omission in many instances (as it is for others, such as cyanobacteria and diatoms). The biggest challenge is simply that these organisms have very rarely been accorded any recognition for their physiological capabilities and needs (especially for acquired phototrophy – Anschütz et al. 2022); that is so even for harmful algal bloom species.

1.2.6 Protistan-zooplankton (heterotrophic flagellates, ciliates etc.)

In many models. zooplankton are either described as a single functional type (de facto acting as a closure term for 'phytoplankton'), or are divided between two fractions, nominally labelled as 'microzooplankton' and 'macrozooplankton'. In both instances the conceptual core is the same, and very simple (Mitra et al. 2014).

'Microzooplankton' technically refers to a size class and many components within it may be more appropriately labelled as 'protistan-zooplankton'. These may be modelled as separate types, for example labelled as heterotrophic nanoflagellates ('HNF'), 'heterotrophic dinoflagellates', and 'ciliates'. Protistan-zooplankton models typically use a fixed assimilation efficiency (AE) irrespective of prey stoichiometry and abundance (Cf. Sailley et al. 2015), and predation is characterised with a fixed half saturation constant and prey preference indices with an inability to modulate prey selectivity according to changes in nutritional quality (Mitra et al. 2014; Flynn & Mitra 2016). Explicit allometric or other prey-predator specific grazing interactions are not usually described; predation is assumed to follow an explicit linkage, perhaps guided by an assumed 10% size ratio between predator and prey even though this is well known to be inappropriate (e.g., Hansen et al. 1994; Aberle et al. 2007; Sherr & Sherr 2007; Sherr et al. 2013). Without care, the values of these parameters can readily give grazing rates and/or AE values that are implausible if not impossible, especially if the values are adjusted in an ad hoc fashion to obtain a predator-prey cycle that 'looks right'. The complexities that develop in predator-prey systems require careful consideration in models, with corrections of constructional errors often revealing problems elsewhere in the model (Mitra et al. 2007). More detailed descriptions of protistan-zooplankton exist, although (as for other microbial plankton) resting stages are not described. Only a cursory consideration is made of the fate of unassimilated materials (as micro-faecal pellets and DOM, and as inorganics); this issue parallels the deficiencies of models of other plankton types with regards to DOM.

1.2.7 Metazoan-zooplankton (copepods, krills, jellies etc.)

Descriptions of metazoan-zooplankton in models (often assumed, or stated, to be copepods) usually follow the conceptual core used for protistan-zooplankton. Thus, predation is described with a fixed half saturation constant for all prey (irrespective of size, motility, dietary value, or toxicity of the prey) and with application of a prey preference index (Mitra et al. 2014). To prevent excessive predation that may lead to the extinction of some prey types, models may use threshold controls or a 'kill-the-winner' predation function (Vallina et al. 2014). Except for specialist models focussed on particular species (Varpe et al. 2007; Gentleman et al. 2008), there is no consideration of egg production, of age/size/stage and allied changes in prey and diet requirements, of efficiencies in biomass production, diel vertical migration, raptorial/ambush vs filter feeding, and other facets of ecophysiology and behaviour. Only a cursory consideration is made of the fate of unassimilated materials (as faecal pellets and DOM, as well as inorganics); in models this partitioning may assume a fixed ratio. In most instances, there is little if any partitioning of metazoan-zooplankton into different functional types except perhaps nominally by allometry and then usually with an allocated allometric link to prey selection (Follows et al. 2007; Butenschön et al. 2016). Zooplankton have long been recognised as demanding significant attention in models (Mitra et al. 2014); whole groups of metazoan-zooplankton, known to impose important plankton community structuring pressures (and provide important feed for higher trophic levels) are not represented other than perhaps as a general catch-all label on a box. This includes gelatinous zooplankton (Luo et al. 2022) and groups such as chaetognaths.

1.3 Approach

Most plankton models have come together by marrying components derived from different sources, requirements, reflecting model developmental histories. Detailed modelling descriptions, where they exist, typically consider autecology, with few attempts made to bring together several plankton types with similar levels of attention to detail. Those few that have done so, and that have also been configured to replicate high resolution empirical data, demonstrate the importance of including facets that are often excluded in models (such as changing prey selectivity, allelopathy – Mitra & Flynn 2006). As most of the core equations date back 50 years or so, arguably a clean-sheet attempt is required to build comprehensive plankton models. Either way a robust consideration of the performance of plankton models set against expectations of empirical experts is required.

Interests in plankton at the base for whole ecosystem models invariably emphasise phytoplankton and zooplankton primary producers (e.g., Moloney et al. 2011). The roles of viruses and of parasites, of bacteria as competitors for resources, of mixoplankton, and of interactions between consumers and their prey in shaping the ecology of primary production has been largely side-lined. Models such as PISCES (Aumont et al. 2015) use very restricted plankton descriptions, with combinations of fixed and variable stoichiometries. MEDUSA (Yool et al. 2013) also has a restricted stoichiometric and allometric description. The Dynamic Green Ocean Model (DGOM) of Le Quére et al. (2005) used plankton groupings based upon their biogeochemical roles, including bacteria, several groups of phytoplankton (some of which we now know to be mixoplankton), and 3 size groups of zooplankton (micro', meso', macro'). What attempted applications of such models to real world scenarios reveal is not just the challenges of modelling the complexity of the plankton, but also the very real problem in validating model performance against data (e.g., Le Quére et al. 2005).

The above mentioned models pre-date interests in digital-twins, and were unapologetically simplifications intended to satisfy specific research interests limited by computational costs. That the performance of such models is critically dependant on the parameterisation of the consumer sub-models (Mitra et al. 2014; Rohr et al. 2023), shows that we are rather damned by simplicity as much as by increasing complexity. Ultimately, unless all components of the simulation model, and thence of the digital twin, 'talk' to each other and operate in ways that are deemed by empiricists as satisfactory, marine science will be unable to develop and perform in the ways expected of it.

Traditional approaches to modelling plankton have made assumptions about what matters and what does not matter sufficiently to warrant inclusion within the model. The engineering approach of objectively testing for exclusions and simplifications is not normally part of the plankton modelling process. In defence, empiricists tend to emphasise differences between organisms rather than identifying commonalities; in contrast, modelling forces scientists to work the other way around. And modellers can only work with information that is to hand, often requiring various levels of interpretation and extrapolation beyond the bounds of their capabilities and/or of robust science.

Plankton models have often either been directed at biogeochemistry or as a resource driver in fisheries models. A claim may be made that it is unnecessary to describe details of plankton biodiversity and the allied productivity dynamics, although such a claim could not been tested in the absence of suitable biodiversity-capable plankton models. Both biogeochemistry and the success of fisheries are at least in significant measure emergent properties of plankton ecology - they are directly associated with aspects of plankton biodiversity. The desire to build digital twins of plankton will help focus a reconsideration and redressing of these problems, to the benefit of all plankton research, by encouraging a dialogue between modellers and empiricists.

This task sought to test the acceptability to experts in plankton of various general and specific concepts and understandings in plankton ecophysiology and modelling.

2. Method

Contributors (listed as co-authors to this work) were asked to respond to questions and challenging statements presented by the lead author, and also to additional statements proposed by contributors. The latter were proposed for responses after the first cycle of responses had been received.

Contributors made their responses in isolation to the views and response of other contributors. The lead author did not respond to any statements.

Responses to statements were not edited, except to remove typographic errors, and responses such as 'as noted above' etc. Responses were not merged; this is because similar responses provide additional weight, or help build contrasting views, to the question or statement. Responses are provided anonymously although **Table 1** indicates the general topics to which contributors responded.

The questions and challenges are real (as rewordings of claims made by modellers or empiricists at conferences and workshops), or were developed in response to activities in previous tasks in this project (Flynn 2024). Some are presented as pseudo-rhetorical statements. Some are voiced from a modellers perspective, some from the perspective of a non-modelling biologist.

In many ways the style of the process resembled setting up an interview for radio or TV. Typically preparation for such interviews involves talking with the presenter before the recording about how to get certain points over to the audience. The interviewer will also have their own questions, questions that set the scene and some that test the paradigm. During the actual interview, the presenter then asks these questions, or makes rhetorical statements, to provoke a response. Some interview questions are combative, some are searching. The concept is similar to an interview in its delivery because contributors (de facto interviewees) were engaging with an audience (the reader of this document) who most likely comes with various levels of prior knowledge, (mis)understandings and bias.

Table 1 Contributions made by the co-authors to the results documented in **Appendix 1**. The lead author did not contribute to the results.

Name; initials	Virus	Bacteria	Phytoplankton	Mixoplankton	Zooplankton	General
Atkinson A					✓	✓
Beardall J			✓			
Boersma M		✓	✓	✓	✓	✓
Bowler C			✓			✓
Calbet A				✓	✓	✓
Dam H					✓	✓
Glibert PM	✓	✓	✓	✓		✓
Hansen PJ	✓	✓	✓	✓	✓	✓
Jin P			✓			
Lomas MW			✓			✓
Lønborg C	✓	✓	✓			✓
Menden-Deuer S	✓	✓	✓	✓	✓	✓
Mock TM	✓	✓	✓	✓		✓
Needham D	✓	✓	✓			✓
Robinson C		✓				✓
Rokitta, S		✓	✓	✓		✓
Rost B		✓	✓	✓		✓
Saiz, E					✓	✓
Schmidt K					✓	✓
Sherr E		✓	✓		✓	✓
Stoecker DK				✓	✓	✓
Thiele S		✓	✓	✓		✓
Thingstad TF	✓	✓	✓	✓	✓	✓
Våge S	✓	✓				✓

3. Results

The full responses to questions/statements are presented in **Appendix 1**, as provided by the contributors listed in **Table 1**. Here, a summary conclusion is made for each question/statement from those responses.

3.1 Plankton-Type Specific Questions/Statements

3.1.1 Virus (& their hosts)

V1. To properly explore the ecological consequences of plankton viruses requires models with a high level description of the biodiversity of their prey.

Summary response:

- Biodiversity is required, but whether the model in total requires that same level of biodiversity description is another matter; it depends on the role of the model.

V2. The host specificity of viruses is so high, set against the diversity of competing non-hosts that are described in models within the same functional type (group), that we can disregard the action of viruses in most plankton models.

Summary response:

- This depends on the level of biodiversity already in the model and whether the interest is in the role as viruses affecting the fate of biomass between, versus within, a given trophic level. Models perhaps should not be made for high biodiversity to justify inclusion of viruses; if the model describes the plankton with a high biodiversity, then consider if the addition of viruses is then appropriate or needed.

V3. We only need to consider viruses for bloom-forming primary producers. In all other instances, the ecological role of an infected host would just be replaced by another member of that same plankton functional group and the trophic dynamics would be unchanged.

Summary response:

- Generally, it depends on the level of biodiversity already required, and the criticality of the plankton forms that are most susceptible to viral attack to the biodiversity within the overall scenario. Obviously, if the target of interest is viruses then it is different.

3.1.2 Bacteria

B1. Can we get away with a single bacteria model to describe the entire suite of open water bacterial activities?

Summary response:

- The majority view is that more than one group of (heterotrophic) bacteria is required, but that two might suffice, plus nitrifiers if applicable.

B2. Do we need an explicit description of bacteria at all? – can we not just (continue to) use an implicit description of 'decay' and 'regeneration'?

Summary response:

- The majority response is yes, certainly explicit inclusion is needed. That interest is not only in the role of bacteria in consuming DOM etc., but also as prey for protist zooplankton and mixoplankton.

B3. In considering predation upon bacteria, do we need to explicitly consider their cell size, motility, and how/if they grow in clumps?

Summary response:

- Varied and contrary responses, basically depending on the level of detail required and whether appropriate data/information exists.

3.1.3 Phytoplankton (prokaryote, protist non-diatom and diatom)

P1. Most models describe changes in Chl:C only (which affects the value of the biomass-based alpha, the initial slope of the photosynthesis-irradiance curve); they take no account of changes in P_{max} with photoacclimation that would see changes in RuBisCO. Is this an acceptable simplification?

Summary response:

- The view was that certainly photoacclimation must be included, but also that changes in P_{max} should be accounted for else the description is incorrect.

P2. Describing photoacclimation to changes in photoperiod length, and to short-term changes in irradiance over the day (with clouds etc.), is essential to more correctly describe primary production. (most models cannot describe this)

Summary response:

- The majority agree that an ability to describe such changes is important.

P3. Given the typical timestep duration in models (ca. 20-40min), photodamage rather than photoinhibition is the more important feature to consider, yes?

Summary response:

- Generally the process is considered as being important to consider, and especially longer-term damage.

P4. Must we describe photodamage/inhibition as well as acclimation? If we must do so, can this be achieved simply by down-shifting the value of Chl-specific alpha at high PFD? Or should we relate PFD and nutrient status to describe a lowering of Chl:C?

Summary response:

- Photoacclimation, yes, but photodamage/inhibition only if that detail is required or if it de facto impacts emergent net photoacclimation (e.g., with nutrient stress).

P5. Temperature (Q_{10}) effects P_{max} but not alpha (the initial slope of the photosynthesis-irradiance curve).

Summary response:

- While alpha is most likely effected by T (in consequence of down-stream processes being enzymatic), Q_{10} for alpha is likely much lower than for P_{max}.

P6. We need photo-acclimation models because nutrient exhaustion drives changes in Chl:C much faster than changes in nutrient quotas (e.g., N:C) change.

Summary response:

- Absolutely, agreed.

P7. We do not need variable Chl:C models because i) light is almost always limiting in nature (so Chl:C is always maximal for a given nutrient status), ii) it can be related adequately to N (i.e. Chl:N can be considered constant).

Summary response:

- Photoacclimation requires explicit inclusion, being affected by light and nutrient status.

P8. Modelling suggests that the production of DOM, in all forms, represents an important yet poorly studied product of phototrophy – can we assume a fixed % of CO_2-fixation, or of DIN-assimilation, as being leaked? If so, what should that value be?

Summary response:

- Production of DOM cannot be assumed as a fixed % of C-fixation. It varies strongly with biodiversity and nutrient status/history.

P9. We can ignore osmotrophic mixotrophy expressed by phytoplankton as being of no consequence in nature.

Summary response:

- No we cannot ignore it, with the possible exception of spring blooms when the resource (i.e., DOM) may be absent or at extremely low concentration.

P10. Do we need to explicitly (separately) describe Prochlorococcus *and* Synechococcus in models?

Summary response:

- Contrasting views, in essence split between the ecosystem setting (coast vs oceanic), but that co-occurrence is minor. Explicit description of strains within these species may be important.

P11. How important is the reported motility of prokaryote phytoplankton – can we ignore it? (Raven & Lavoie, 2021. Prog.Bot. ***83****, 315)*

Summary response:

- Ignore unless/until shown to be of consequence in reality.

P12. Can we assume that diazotrophs (as indicated by 'omics, for example) are always fixing N_2, irrespective of the availability of DIN that may be expected to repress (inhibit) N_2-fixation?

Summary response:

- No, not acceptable.

P13. Diatoms that grow in chains should be allometrically binned in the size for the chain, not the size of individual cell. This is so both for nutrient uptake, and for considering predation.

Summary response:

- For nutrient uptake, diatoms should be binned for cell size; for predation they should be binned for chain size, though this likely depends on the predatory mechanism. In addition, chain length depends on nutrient status and other factors. Simply binning by typical cell size appears inappropriate.

P14. It is important to account for differences in photophysiology between diatoms and non-diatoms.

Summary response:

- Strong agreement; the description should reflect differences between these groups.

3.1.4 Mixoplankton

M1. Mixoplankton are too complicated to model; can't we just merge 'phytoplankton' and 'zooplankton' activities?

Summary response:

- Strongly rejected.

M2. Mixoplankton only appear to be of consequence in coastal systems, especially for HABs, can we otherwise group these organisms in with 'phytoplankton'?

Summary response:

- No, not unless they are unequivocally demonstrated to behave as phytoplankton.

M3. Because bacterivory by CMs is likely ubiquitous, and bacteria are ubiquitous, can we in essence just ignore this process and describe these organisms as 'phytoplankton' with enhanced abilities (lower half saturation constants) to acquire inorganic nutrients?

Summary response:

- No, because of the interactions between predator and prey. If the interest is only in gross photosynthesis, then perhaps, but not for explicit growth of these organisms.

M4. We can use an allometric scaling rule to relate mixoplankton size to the balance of phototrophy vs phagotrophy.

Summary response:

- No, because of the differences exhibited by different species and groups.

M5. pSNCM require so few encounters with their special prey, which supply their acquired phototrophy, that we can effectively just model these organisms as CM. (Otherwise we have to model the explicit growth and survival of those specific prey.)

Summary response:

- Perhaps for species that well preserve their acquired phototrophy; not otherwise.

M6. Elevated temperatures will promote phagotrophy more than it promotes phototrophy in mixoplankton.

Summary response:

- Generally, no.

3.1.5 Zooplankton (protistan and metazoan)

Z1. The strongly contrasting predator:prey size relationships for different types of protist zooplankton prevents a meaningful placement of all of these organisms within a single functional type.

Summary response:

- Strongly agreed.

Z2. Prey selectivity is an essential feature of grazer behaviour; placing all zooplankton in one or two boxes and all their prey in another, or in a few others, is not an acceptable simplification.

Summary response:

- Agreed, in some instances very strongly.

Z3. 'kill-the-winner' (in which the most abundant food item is most heavily grazed, irrespective of its identity) provides a pragmatic solution to describing zooplankton prey-selectivity in models.

Summary response:

- Generally, not acceptable, though there may be some exceptions.

Z4. We can usefully assume the same core physiological description, with similar parameterisations (e.g., AE, K_{pred}) for both protistan and metazoan zooplankton, or for all-inclusive protistan or metazoan zooplankton groups.

Summary response:

- Not acceptable.

Z5. Metazoan zooplankton require appropriate binning in functional type models with respect to feeding mode (e.g., raptorial vs filtration) and also with respect to allometry (sizes of prey and of consumer).

Summary response:

- Agreed; they cannot be binned together.

Z6. It is essential that models of metazoan zooplankton give appropriate descriptions of age-stage ontogenic developments.

Summary response:

- Agreed, unless the model specifically considers one stage and is of short duration.

Z7. The complexity of metazoan zooplankton ontogeny inevitably means that we have to merge the activities and biomasses of all stages into a single (or very few) biomass-based state variable(s). Which stages can be usefully merged, how few functional stages do we need?

Summary response:

- Merging to eggs, early stages (nauplii), subadults (e.g., copepodites) and adults would suffice.

3.2 General Questions/Statements

G1. Models are simplifications of reality. Inevitably, all plankton models are 'wrong'.
Summary response:

- A level of being 'wrong' is acceptable in that a model can never be complete; being wrong in that context can be informative.

G2. It is pointless having a plankton model that cannot actually provide a passable description of reality, irrespective of the arguments for saving computational effort used to justify simplicity.
Summary response:

- Accepting that simplicity is useful for conceptual/theoretical studies, and that models cannot ever be 100% accurate, agreed that it is not acceptable to sacrifice plausibility for simplicity.

G3. Which plankton types are typically ignored in models, why is that so, and why should they be included?
Summary response:

- Wide range of answers (reflecting the breadth of interests of the contributors) but in general, anything that is not simply 'phytoplankton' are ignored or trivialised. That includes de facto all consumers (bacteria, mixoplankton, protist zooplankton and metazoan zooplankton) other than a generic 'consumer' box. And viruses.

G4. Which planktonic processes are typically ignored in models, why are they ignored, and why should they be included?
Summary response:

- For abiotics – responses to temperature, water depth. For biotics – physiological/behavioural responses, food quality, mixotrophy (osmo' and phago'), exploitation of DOM and allied microbial activity.

G5. Complexity in biological models has been shown to drive instability; attempting to build large plankton models thus appears to be a futile task.
Summary response:

- The general view seems to reflect a stance that nature is complex, so if our complex models are misbehaving then their structure is wrong and we need to understand how/why that is so. Construction of large models (i.e., containing many trophic components) is not futile, but likely throws up as many questions as answers.

*G6. Problems in the stability of complex biological (plankton) models stem from a failure to adequately describe the details of the organisms (May's 'devious strategies'; May RM, 1972. Nature **238**, 413) that would in nature provide stability (Allesina, S., Tang, S., 2012. Nature **483**, 205).*
Summary response:

- G5, put in a different way, with the same basic response.

G7. Published descriptions of plankton models should always include appropriate graphics (response curves, flow charts etc.) and functional descriptions so that biologists can understand and be better able to question the conceptual basis of the model.
Summary response:

- Strong agreement.

G8. Plankton models used to describe eutrophication events must include explicit descriptions of those types of plankton associated with the events. Thus, for example, confining all phytoplankton to 'diatom' vs 'non-diatom' descriptions is inadequate.

Summary response:

- Mixed responses, in essence hinging on whether the identity of the organisms is important (e.g., HAB species) or simply if the net phototrophic production is important.

G9. Do we need to explicitly describe allometry? If so, how many groups should there be (can we just get away with 'pico', 'nano', 'micro' etc., or are these already too wide?). And must size range be a defining feature of different functional types? (e.g., can we group all 'diatoms' together, or should they always be subdivided into different size bins?)

Summary response:

- While agreed that a basic binning style (pico, nano, micro) may typically be used (perhaps especially for light and dissolved resource acquisition), this approach cannot be used to over-ride trophic interactions (especially involving predation).

G10. Is a model of plankton seasonality that ignores the role of resting stages and other life-cycle processes too far removed from reality to be useful?

Summary response:

- For coastal-zone applications, these life cycle events are important (depending on the time-frame of the simulation) and should not be excluded. They are likely not required for most oceanic scenarios.

G11. Refuges (resting stages, diapause, etc.) are important features of reality missing from plankton models that greatly damage the utility of those models.

Summary response:

- If the organisms being described (explicitly or implicitly) have such stages, those stages should be included.

G12. Climatology-links to species succession are important features of reality typically missing from plankton models.

Summary response:

- Agreed that species succession should be included as this affects trophic matching etc.

G13. In a model with only one 'Z' box, we should parameterise that group more in line with the activities of metazoan zooplankton than with protistan zooplankton because only the activity of the former contributes to the sinking of biomass.

Summary response:

- There should not be only one Z box, and protist plankton also produce materials that sink.

G14. Appropriate descriptions of prey selection and differences in dietary value are essential for any plausible description of consumer activity and thence for all ecological (trophic) models. Assuming a fixed AE, and selectivity according to a simple fixed equation is not consistent with reality.

Summary response:

- Agreed; it is not generally acceptable to assume fixed stoichiometry or fixed consequential behaviour with respect to selectivity or processing.

G15. Osmotrophy (the use of organic nutrients) is not typically worth describing given the challenges in describing different DOM fractions. The same applies to auxotrophy (use of vitamins).

Summary response:

- Disagreed. While it is problematic to study, this must spur on further research, not prevent descriptions in models.

G16. DOM must be described in plankton models because the availability of nutrients via this route (either directly via mixotrophy, or indirectly via bacteria and bactivory) can be as important for trophic dynamics as is the availability of inorganic nutrients.

Summary response:

- Agreed, accepting that it is challenging. There are also important trophic implications of DOM production/consumption beyond simply the support of bacterial production (i.e., phagotrophy of that enhanced bacterial biomass production into protists).

G17. Describing different forms of DOM occupies too much computational effort; can we get away with just having 1 or 2 'DOM' groups? If so, what would they describe?

Summary response:

- Agreed that more than one form of DOM is required, likely at least 2 (labile and semi-labile), and ideally more again because those labile and semi-labile labels are clearly inadequate to describe forms of DOM.

G18. Allelopathy is not typically worth considering as we lack sufficient data to support the modelling.

Summary response:

- A divergence of views, but clear recognition of the importance of allelopathy in reality, balanced by doubts over how to handle it.

G19. Allelopathy provides a major stabilising mechanism in nature that is missing from models. It is one of the key factors that prevent combinations of models of individual phytoplankton from describing events seen in mixed-species cultures.

Summary response:

- Strong agreement.

G20. 'Lipid' is a vital additional state variable to add to the usual C,N,P etc. state variable list for many organisms.

Summary response:

- Depends on the scenario, but for some species, certainly that is so.

G21. Relying on bulk chlorophyll concentrations (especially from remote sensing and in vivo fluorescence) does not provide a robust estimate of phytoplankton biomass useful for model calibration and validation.

Summary response:

- Agreed; exploiting such data is a pragmatic necessity always to be handled with care.

G22. The use of a fixed conversion ratio of prey biomass to predator biomass for all prey types (e.g., 10% transfer efficiency), across all quantities and different stoichiometric qualities, provides a pragmatic acceptable basis for descriptions of planktonic consumer activity.

Summary response:

- Not acceptable, as this transfer is demonstrably highly variable between consumers and with different prey types (i.e., species) and qualities (i.e., stoichiometry).

G23. Allometric-rule models, assuming a set prey:predator size ratio (e.g., 1:10), provide a good starting assumption for constructing plankton models.

Summary response:

- Not acceptable as there are too many exceptions, especially for protistan grazers. The approach may be acceptable for certain metazoan, assuming those groups are themselves explicitly described.

G24. Temperature-growth rate relationships developed from the Eppley phytoplankton-temperature growth curve (Eppley RW, 1972. Fish. Bull, ***70****; 1063) give a good starting assumption for plankton models that consider changes in temperature with climate change.*

Summary response:

- A blanket assumption is not safe. There are very many caveats to using such curves, relating to co-occurrence of other stresses, and levels of adaptation etc.

G25. It is more important to get the timing of bloom events correct than to get the magnitude correct.

Summary response:

- Mixed views, depending on applications; both are important in many/most instances because of the ripple effects on subsequent trophic dynamics.

G26. Long-term plankton data series provide a useful resource for modellers, but they need to be used with care after validation against current understanding.

Summary response:

- All agree about the general importance of such data series, but some note challenges in confirming the quality of the data for modelling, especially where survey methods have changed over time.

G27. How do we make (simulation) modelling mainstream in plankton science, with a status closer to that enjoyed by molecular biology?

Summary response:

- Accessibility and communication, gamification and other techniques are needed to support explicit teaching. Having explicit links between 'omics and modelling might help.

G28. Much plankton field work is now centred on the exploitation of molecular ('omics) approaches. How can we use such data to support the modelling of different plankton types (virus to metazoan zooplankton)?

Summary response:

- Some recognise the (very great) challenges in linking 'omics to modelling because of the semi-quantitative nature of and lack of rate determinants in 'omics data. Others draw parallels with challenges in relating classic taxonomy data to models.

*G29. Exploitation of 'omics enables us to determine the metabolic capabilities of organisms in the form of genome-scale metabolic models (GEMs). Coupling these with Flux Balance Analysis (FBA – Orth et al. 2010; Nature Biotechnology **28**, 245) enables us to determine physiological activity in nature. We can use such information to support plankton model developments tailored to individual species levels.*

Summary response:

- This only works for steady-state models (Orth et al.); some recognise these challenges.

G30. The mantra, everything-is-everywhere-(and active)-all-the-time, is not correct and/or is not useful as applied to plankton models.

Summary response:

- Agreed, it is not useful though perhaps with some exceptions (though even those will be locally adapted, and so the organisms will not actually have the same physiology).

G31. There is no strong evidence, either way, for different temperature-responses for phototrophic vs heterotrophic activities.

Summary response:

- Agreed; although more work is required, there is no evidence for a generic systematic difference in temperature responses.

G32. Do modellers need to consider the effects of ocean acidification (decreasing pH due to uptake of atmospheric carbon dioxide) on plankton community composition and food webs?

Summary response:

- Some disagreement over the significance of OA per se, but a general agreement that more information is required and that bi-directional (organism activity <-> pH) need to be represented in models.

G33. There are common principles organizing the marine planktonic food web at multiple scales. Because these allow us to capture and understand complexity by means of simple models, there is no need for what could be perceived as overly complex models.

Summary response:

- Disagree. Extant models lack sufficient complexity to be able to explain reality.

G34. Climate change (IPCC) models use plankton descriptions limited to very few 'phytoplankton' and 'zooplankton', restricted by computational costs; how can these possibly provide a plausible feedback between biogeochemistry and climate change as they cannot describe the changes in biodiversity caused by climate change which will affect the BGC-pump signal?

Summary response:

- Mainly agreed that these models are problematic; most expressed various levels of doubt as to whether such models can deliver to the needs.

4. Discussion

4.1 Plankton specific matters

The following includes insights from the general questions/statements. An overview of the status of plankton modelling, against which to consider the Results of this work, is given in Flynn et al. (2024b).

References to specific inputs of contributors to this work, supplied in **Appendix 1**, are made using the statement/question reference number given in bold (e.g., **G1**).

4.1.1 Virus (and parasites)

While the environmental and ecological importance of planktonic viruses has been widely acknowledged for several decades (Suttle 2007), inclusion in plankton models has been very limited. Due to their host-specificity, models containing viruses need a suitably high level of biodiversity description at least for that virus-host couple. Because of the consequential release of DOM, for which contributors showed a desire for a higher level of detail than just a single 'DOM' box, additional complexities in the whole model may also be essential. To the question of whether viruses need to be included (see discussion by Mateus 2017), the view was that modellers should not feel that they must include them for the sake of doing so; only if the model contained biodiversity components subjected to viral attack should they then be included. A contributor to **V1** wrote – "*It is not about high or low level* {biodiversity} *it is about what matters. Identifying keystone viruses and their hosts etc.*".

Not raised explicitly here is the role of parasites in plankton (e.g., Park et al. 204; Sime-Ngando 2012). The inclusion of such components in plankton models is arguably even more problematic than that of viruses, especially if there are multiple hosts. For both viruses and parasites, one could consider deploying a 'kill-the-winner' type of approach (Thingstad & Lignell 1997) but, within longterm simulations, such a usage (which de facto operates like a closure term) removes the quaisi-chaotic dynamics that could arise (Flynn et al. 2022b).

4.1.2 Bacteria

Bacteria are most often either ignored in plankton models, or described by a single 'box'. Neither was viewed as being acceptable by contributors. In large measure, that view appears to be linked to the desire also to expand the descriptions of components of DOM (see here and also in Flynn et al. 2024a, b). Some went further; for **B3,** one wrote, '*Bacteria are as important as euk. plankton. They need to be modelled at the same level*'.

Describing the complexity of bacterial physiology, across the 100's if not 1000's of species as typically resolved by genomics, in plankton models is challenging. It is challenging at the biological level because somehow we need to distil all that ecobiodiversity down to a few (contributors suggested 2 or 3, **B1**) functional types, and also because we need to sensibly characterise their particulate and dissolved organic/inorganic resource types. In some ways, arguably characterising the resource types is more problematic. There are approaches that can be exploited to describe the physiology deployed for multiple resource exploitation, relating to (de)repression of pathways with nutritional stress (e.g. Flynn & Mitra 2023), but packaging forms of DOM for the model when there are so few data for the composition of real DOM is problematic (Anderson et al. 2015). We know broadly what is there (different classes of biochemicals), and that these substrates are associated with different labilities, but we need measurements of them and we then need to agree how to define them in models. Each substrate to be explicitly described in the model comprises another state variable, and if it has a variable stoichiometry, that single substrate type may occupy multiple state variables; how many substrate types do we need? And if we have a model describing the consumption and interconversion of DOM by bacteria, we then also need to describe production of DOM by other plankton, characterised as leakage products from phototrophs (phytoplankton, mixoplankton) and from debris with virus and grazer activity, and also from other organism lysis events (**G16**, **G17**).

Another factor that can, depending on the needs for the model, be of importance is bacteria cell size and clumping. Views on this matter varied (**B3**); where interactions depend on cell encounter rates (virus attack, grazing by protists), this may be of importance but perhaps it is not so for a more generic removal of bacteria biomass.

4.1.3 Phytoplankton (prokaryote, protist non-diatom and diatom)

By far the most effort in plankton modelling has been expended on phytoplankton. Here, contributors considered various matters that have in the main been avoided by modellers, such as photoacclimation beyond changing Chl:C (which alone is a not an uncommon inclusion, typically developed from Geider et al. 1998), photodamage/inhibition, DOM interactions (release, consumption in osmotrophy, and allelopathy), temperature (see **Section 4.2.1**) and some specific phytoplankton subgroup issues. These matters are of importance in developing phytoplankton digital twin descriptions, in the first instance just to establish whether extant constructs may suffice as building blocks.

Responses indicate that accounting for changes in Chl:C alone is insufficient to describe photoacclimation (**P1**, **P2**, **P6**, **P7**). "*I would say unequivocally that this is not an acceptable simplification.*", wrote one contributor to **P1**. A model lacking a modulation of P_{max} is unable to describe changes in day-integrated growth rate under different light:dark regimes providing the same daily photon dose; the problem is resolved by acclimating P_{max} as well as Chl:C (Flynn unpublished, but see Flynn & Mitra 2023). Accounting for photodamage/inhibition is more problematic, requiring linkages to nutrient status, photon dose and temperature but requires attention (**P3**, **P4**). Specific differences in the photophysiology and chain-forming of diatoms were also identified as worthy of description (**P13**, **P14**). It may be possible to use similar conceptual bases for models describing *Prochlorococcus* and *Synechococcus*, though their ecological placings reflect differences in detail (**P10**).

The likely ubiquitous capacity for osmotrophy in phytoplankton, long studied in the guise of the use of organic forms of N such as dissolved free amino acids **Section 1.2.3**), means that all these organisms are potential if not actual mixotrophs (as distinct from mixoplankton, which by definition also engage in phagotrophy). Osmotrophy and the contrary release of DOM was recognised as both problematic (**G16**, **G17**) but also an important challenge for modelling (**P8**, **P9**, **G15**); "*Its omission is a greater detriment than misparameterizing it because of a lack of chemical knowledge.*" wrote one contributor to **G15**.

Simple models lack descriptions of (de)repression processes, such as those responsible for modulating exploitation of different N-sources. This topic was raised in **P12** in connection with expression of nitrogenase by diazotrophs; simple models assume that such activity always occurs, a view that was rejected as being incorrect. This discrimination between resource acclimation is an example of how 'omics may interface with modelling (see **Section 4.2.3**).

4.1.4 Mixoplankton

Mixoplankton are not new to plankton science, although the term 'mixoplankton' is, introduced to clarify ambiguity over descriptions of different types of mixotrophy. The term mixoplankton also raises the profile of photo-phagotrophy which is increasingly recognised as being displayed in many numerically abundant protist plankton, even in non-diatom protist microalgae traditionally held as exemplar 'phytoplankton', such as *Emiliania huxleyi* (Avrahami & Frada 2020). Mixoplankton have been described in various models (e.g., Leles et al. 2021, Li et al. 2022), while some form of coupled phototrophy and phagotrophy (akin to phytoplankton+zooplankton activities) has been used in others (Ward & Follows 2016). The latter approach, and other simplifications, are not considered as acceptable ways to describe the activities of mixoplankton (**M1**, **M4**; Mitra et al. 2023). Other short-cuts (**M2**, **M3**, **M5**) were considered as only potentially acceptable in certain cases, but only if it shown explicitly to be acceptable. Osmotrophy and appropriate considerations of prey selectivity and nutritional quality (**G14**, **G15**) are also considered important in mixoplankton.

In general, and consistent with comments elsewhere in this work, and in Flynn et al. (2024a,b) the view was that complexity in mixoplankton physiology and behaviour can be usefully investigated with models but that inevitably those models will be complex. Care must be taken not to gloss over complexities without understanding the ramifications of simplifications. For mixoplankton, challenges occur both for empiricists trying to understand reality and trying to disentangle what modellers have actually described in their creations, as well as for modellers often working with outdated, incorrect, concepts. Building and using plankton models to digital twin standards would hopefully work to lessen such empirical challenges.

4.1.5 Zooplankton (protistan and metazoan)

Zooplankton as a group are well recognised to provide a challenge for modelling and also to be poorly represented in the majority of plankton models (Mitra et al. 2014). Typically, zooplankton are described as a single group, or crudely partitioned into very few groups, and their physiology described in very simple and fixed terms. Even the profound differences between protistan and metazoan zooplankton (where those groups are separated) are reflected by little more than different growth rate and prey selection constants etc. Contributors to this work were not accepting of such treatment, rejecting gross simplifications in the partitioning of zooplankton (**Z1**, **Z2**, **G13**); "*The Fasham et al. NPZ model served its function 40 years ago. We know better now about the difference between meso (metazoan) and microzooplankton (protozoan) to do better in our models*.", wrote a contributor to **G13**. Of particular concern were descriptions of zooplankton grazing activity and food assimilation (**Z3**, **Z4**, **Z5**, **G14**, **G22**). "*Seems weird that as humans we are preoccupied with food: dietary value, feeding history, feeding selectivity are so talked about by us humans but we treat zooplankton like machines.*", wrote a contributor to **G14**. Likewise, descriptions of ontogeny were viewed as being important (**Z6**, **Z7**), as they are by at least some modellers (Carlotti & Nival 1992; Clerc et al. 2021) although perhaps ironically, most empirical studies of copepods have historically exploited female adults. Why zooplankton are so poorly represented in models is not overly clear; not even the basics of their physiology are described robustly, with subtle changes in equations yielding strongly divergent consequences (Flynn et al. 2021). Commentaries such as those by Ratnarajah et al. (2023) and Rohr et al. (2023), keep drawing attention to the problems, but little seems to be done. Perhaps by engaging zooplankton empiricists in the building and exploitation of plankton digital twins, progress will be made.

4.2 Generic matters

4.2.1 Temperature and pH

Temperature and pH are key factors affecting plankton growth that are, perhaps surprisingly, not frequently considered in plankton models but are considered as important by contributors to this project (this work and Flynn et al. 2024b). Two aspects of temperature relations were targeted here: differences in temperature sensitivity of phototrophy vs heterotrophy, and the form of the temperature-growth relationship in more general terms.

The metabolic theory of ecology posits that heterotrophy is more sensitive to temperature than is phototrophy. Acceptance of such a theory has serious ecological implications, and its application can result in some quite extreme plankton model projections (e.g., for the activity of mixotrophs; Wieczynski et al. 2023). However, evidence for the applicability of this concept in plankton is at best weak (Wang et al. 2019), and the view expressed here is that such a 'rule' should certainly not be universally deployed in plankton models (**M6**, **G31**). Where there appears to be some potential difference between phototrophic and heterotrophic activity is when the former is under light-limitation; the initial slope of the Chl-specific PE curve (alpha) is likely less temperature-sensitive than is the maximum rate of photosynthesis, P_{max} (**P5**).

Concerns (some strongly worded) were also voiced about the use of the Eppley (1972) temperature-growth curves in models (**G24**); "*Eppley Is a vast overestimate*", wrote one contributor. These data were not compiled for deriving such blanket relationships; problems include that the curve is too extreme, and that 'growth' could be short-term (subject to acclimations) vs longer-term (subject to adaptations). The latter was noted to sometimes result in a Q_{10}≈1 (**G24**), consistent with the evolution model projection of Flynn & Skibinski (2020).

A feature expected of plankton digital twin models is descriptions of multi-stressor environments, such as temperature, pH (**G32**) and resource-limitations. These are known to interact, notably resulting in a narrowing of the limits as other stresses increase, potentially leading to synergistic declines. Thus, nutrient stress narrows the pH range for growth, a situation worsened by the pH changes that occur during primary production that consumes those nutrients (Flynn et al. 2015). Similarly, nutrient stress impacts resistance to temperature (Siegel et al. 2023). Baker et al. (2007) and Yin et al. (2021) explore such multi-factor interactions, and how they affect plankton competitiveness. Inclusion of these interactions in plankton digital twins, especially for coastal applications, would likely be welcomed.

4.2.2 Allometry and other features

Allometry is a key trait in biology and ecology, and various attempts have been made to construct overarching trait-rules linked to organism size (e.g., Andersen et al. 2016). Tempting though it may be to use such trait rules, contributors were critical of their indiscriminate usage given the risk of over-riding differences in size-based trophic interactions, especially associated with predation (**G9**, **G23**). "*I think the ecofunction of a group is more important than the size range. What does the organism do and not* {depends on} *how large or small is it*.", wrote a contributor to **G9**. Indeed, the raison d'être for the application of broad trait rules as simplifications in plankton models appears to be questionable; complexity should be embraced and understood, rather than rejected (**G5**, **G6**, **G33**) – see also **Section 4.2.3**.

Seasonality is an important feature of plankton population dynamics. Associated with this, and especially important for shelf and coastal species, are resting stages and other refuge states. These are almost always ignored in plankton models but are considered as required features for models aspiring to best portray reality in such waters (**G10**, **G11**). Likewise, links to features of climatology were considered to be of importance (**G12**). This requires appropriate descriptions of changes in temperature, light (including cloud cover, UV and in-situ changes in light spectra with population self-shading), turbulence and pH and of those impacts on the plankton (see also **Section 4.2.1**). Asked whether bloom extent or timing has most importance, the general view appears to be that they are equally important (**G25**). To attain this goal, features that help to spatially and temporally stabilise succession need to be present. Aside from resting stages, allelopathic interactions may be important and need to be explored (**G18**, **G19**). This topic was another one, like interests in DOM in general (**G16**, **G17**), where it was recognised that the challenges in empirical science should not hold up developments in modelling. We have sufficient understanding to know what is plausible or not, to enable us to build and test models for sensitivity to such details. Assuming that the model is indeed plausible in its conceptual basis and construction, then such sensitivity tests would then be useful in designing empirical explorations.

4.2.3 Complexity and the link to omics

Complexity is often viewed as the antithesis of plankton model structures. Contrasting views on the complexity issue can be seen in response to **G5** – two examples are given here:

"*As I believe one of the main points with models is to separate the important from the less important, I am generally sceptical to complex plankton models. I would rather go for a simple model explaining how the "skeleton" works and then treat the myriad of extra features as variations on this theme when required.*"

"*Many natural systems appear to be stable due to complexity, feedback mechanisms and overlapping roles; by knowing what are the important feedbacks and "redundancies" perhaps the most important "details" can be incorporated into models and their role in stabilizing ecosystems can be explored.*"

It was not considered, by contributors, necessary to describe every species present, or indeed to name any particular species except where strictly necessary (notably for eutrophication events with HABs – **G8**, specialist non-constitutive mixoplankton – **M5**, and virus or parasitic interactions – **Section 4.1.1**). It is thus important to exploit long-term data series and broad-brush data (notably, Chl levels) with care (**G21**, **G26**), to extract and bin information appropriately. That task needs to be undertaken by experts in plankton ecology, not simply according to size or other simple metric(s).

It must be stressed that there are important roles for simple plankton models, not least in education (in the broadest possible meaning of that term) and in exploring novel concepts. Attempting the construction of aspiration digital twins requires significant maturity in empirical understanding. That the experts in empirical plankton research here expect to see the complexity of nature broadly reflected in plankton models aspiring to be digital twins (**G3**, **G4**) could simply reflect blissful ignorance of the challenges that modelling throws up. Alternatively, it could reflect a realism that sees that biodiversity in nature exists for a reason and a failure of models to account for it (**G2**, **G5**, **G6**) says as much about the history of plankton model development and resistance to change in that arena as it does about problems in deploying more complex models. The prolonged resistance by the plankton modelling fraternity to inclusion of variable stoichiometry, a feature of profound importance for biogeochemical cycling, perhaps says a lot. The need for inclusion of this feature in the minds of the contributors of this project is apparent from Flynn et al. (2024a,b). Extending stoichiometry to biochemical aspects such as lipids appears unwarranted in most instances, though likely of profound importance in others (**G20**).

The most extreme examples of variable stoichiometry would be described by biochemistry and molecular biological quantifications of organisms. The exponential increase in 'omics data (genomics, transcriptomics, proteomics, metabolomics) of plankton origin inevitably begs questions of linking such detail to plankton models. This challenge is great, with no simple way forward because 'omics do not readily generate rate data or indeed data with the high levels of quantification and in the appropriate units required for the support of modelling (Caron et al. 2017; Stzepek et al. 2022; **G28**). Data from 'omics can support steady-state flux balance approaches for individual organisms (Orth et al. 2010; **G29**), but these are unsuitable for the multi-organism dynamic scenarios of plankton ecology. For dynamic models the increase in computational load needs to be managed, as do expectations by molecular biologists. Promoting developments in this arena, and especially between experts in 'omics and in simulation modelling, is challenged by the same science-language problems as those between non-'omic plankton specialists and modellers (**G27**).

Data from 'omics can be inferred to indicate that everything is everywhere, and that an ability to enact a physiological trait means that the trait is indeed deployed; contributors to this project were not convinced by such views (**G30**, **P12**). In any case, the typical plankton model, and even the most complex plausible plankton model, could not possibly reflect more than a small fraction of the biodiversity flagged by genomic data. It is perhaps more likely that models would describe details of very few species or groups, exploiting transcriptomics, proteomics and/or metabolomics data in very specific ways. One respondent to **G27** suggested: "*Make the molecular biologist depend on your models to explain their results*." To do so, appropriate approaches are needed; examples have existed for over 25yrs (Flynn et al. 1997) but have hitherto not been expanded upon in a way that can mesh the complexity of omics and the necessary simplifications for simulation modelling of plankton communities (Flynn & Mitra 2023). A digital twin platform which enables omics-relevant data entry and extraction by the user will also be needed.

4.3 Additional implications for building plankton digital twins

An interesting and important insight from the contributors was that, as empiricists, they did not consider the (likely, inevitable) 'failure' of a model as being especially problematic (**G1**, **G2**). Rather, they considered such failures as providing useful learning and development opportunities. The caveat is that failures need to be understood, and not shrouded in issues related to inadequacies in descriptions of core facets of the model. By definition, an aspiring plankton digital twin model would have its performance validated against the knowledge of empirical plankton researchers. Specific examples of failing in extant models have already been mentioned; it is perhaps less likely that these would have persisted for so long if empiricists were fully engaged in plankton model design and application. There was an appreciation voiced for any steps that could be taken to better explain/justify the construction of models to empiricists through the use of infographics to explain exactly how plankton functionality is enacted through the model equations (**G7**). The value of training in simulation modelling for biologists was also recognised (**G27**).

Implications of the willingness to work with models that constructively fail, in the context of plankton digital twins, could be interpreted as flagging the need for a tool-kit approach in which the user can modify the description of the plankton to be used in the simulations. Simulations could thus be re-run with different configurations. These changes go beyond simply changing the values of parameters (half saturation constants, maximum growth rates, etc.) and tuning the model to data. Rather they could involve being able to modify the conceptual framework of the description of each plankton type. The ideal digital twin platform would enable the user to design and operate plankton with different configurations.

4.4 Implications for extant plankton models

The functioning of extant plankton models was not explicitly raised, except for one question concerning IPCC models (**G34**), some responses to which were blunt (e.g., *The truth is that it is quite likely most of these models are wrong*). Various matters relating to components of such models were contained in the survey. From the responses there appears to be a significant level of doubt raised concerning core facets of plankton models widely used in marine research. These include failures to adequately or correctly account for:

a) Photoacclimation
b) Prey selectivity and handling
c) Allometry
d) Biodiversity
e) Consistency with modern understanding of plankton ecophysiology and trophic dynamics

Even if one was to accept a discounting of (c), (d) and (e), on grounds of arguments for containing computational load with increased complexity, concerns over (a) and (b) are profound. An interpretation of the responses could be that the naming of ‘P’ and ‘Z’ components of extant models as ‘phytoplankton’ and ‘zooplankton’ cannot be justified, but rather they resemble only broad ‘phototroph’ and ‘consumer’ categories.

Reference to real organism groups in these models adds a level of confidence in the output that is not supportable. It is becoming increasingly apparent that changes in plankton biodiversity are linked to changes in the trophic structure up to fisheries (Atkinson et al. 2024). We need to question whether fisheries models can give plausible projections if they do not contain appropriate descriptions of plankton biodiversity from primary production levels on up. The same applies to models targeting biogeochemistry.

To draw an analogy to the representation of historical events in certain movies: the characters do not represent anything living and, while the end result may perhaps align with a real event, the path to it is inaccurate. Worse, many believe that what they see indeed reflects reality and do not question it.

A key problem, and explanation for why marine science is in this position, is that those best placed to judge whether the models are indeed describing events adequately are disenfranchised from the construction and peer reviewing process through the languages of mathematics and computer coding. The biological languages across plankton science are no less simple, often overly complex if not ambiguous, but it was notable that for the most part the contributors to this work (operating independently) were in broad agreement. The development, and deployment, of plankton digital twins would help engage empiricists with modellers. The need for addressing such needs was reflected in responses to **G7**, **G27**, **G28**.

5. Conclusions

Standout results from this work are:

- Doubts, some of which are profound, are cast upon the functionality of core parts of extant plankton models. For certain these are important considerations for building plankton digital twins; confidence in the performance of such models is critical else they cannot be considered as twins. This requires that the underpinning of aspirational plankton digital twins are reviewed with care.
- Complexity-in-depth is of greater interest than complexity-in-breadth; that is to say that digital twins describing rather few plankton types but with detail at the physiological/behavioural level appear preferable (or of more interest) rather than models in which many plankton types are described each with little detail. That preference appears all the stronger given doubts raised over the core features and assumptions made in the construct of simple models. The interests of contributors to this project (Flynn 2024) in multi-stressors (Flynn 2004a, b), also flags a need for plankton digital twins to provide descriptions with complexity-in-depth.
- Failures of models due to insufficient detail (as distinct to errors in detail) are not unwelcomed, for they flag where science goes next. In contrast, failures due to simplicity for the sake of simplicity are counterproductive, and arguably dangerous, especially if the user of such information is unaware of the problems. That some extremely highly cited plankton modelling papers contain the types of flaws identified by contributors to this work as unacceptable is indicative of the problem. This further supports the need for complexity-in-depth for digital twins but, more worryingly for plankton science, it raises questions over the value of extant plankton models, as used in basin-wide through to global science projects. While such models do not claim to be built to digital twin standards, even labelling components as ‘phytoplankton’, ‘zooplankton’, let alone as specific groups (‘diatoms’, ‘coccolithophorids’, ‘copepods’ etc.) imbues a level of confidence in the behaviour of such models which may be highly questionable.
- The failure to adequately integrate plankton simulation modelling and empirical plankton research has resulted in miss-communication and a loss of opportunity. The availability of plankton digital twins, available in some form of *in silico* laboratory, would likely help engage empiricists in modelling, while the development of those platforms would help modellers better appreciate critical nuances of plankton ecophysiology.

As a caveat to the above, this work centred on responses from a small group of contributors. Granted that they worked in isolation, were generally in agreement, and that the range of their collective skills and engagement was wide (**Table 1**), but one may question whether their views reflect those held by typical empiricist plankton researchers. The counter argument is that the onus is now on those who have contrary views to come forward with their considered opinions.

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Simulating Plankton - getting it right in the era of Digital Twins of The Ocean

Building and Challenging Perceptions

APPENDIX 1

A1. Contributors

Table A1.1 Contributions made by the co-authors to different sections of the task. The lead author did not contribute to the results.

Name; initials	Virus	Bacteria	Phytoplankton	Mixoplankton	Zooplankton	General
Atkinson A					✓	✓
Beardall			✓			
Boersma M		✓	✓	✓	✓	✓
Bowler C			✓			✓
Calbet A				✓	✓	✓
Dam H					✓	✓
Glibert PM	✓	✓	✓	✓		✓
Hansen PJ	✓	✓	✓	✓	✓	✓
Jin P			✓			
Lomas M			✓			✓
Lønborg C	✓	✓	✓			✓
Menden-Deuer S	✓	✓	✓	✓	✓	✓
Mock TM	✓	✓	✓	✓		✓
Needham D	✓	✓	✓			✓
Robinson C		✓				✓
Rokitta, S		✓	✓	✓		✓
Saiz, E					✓	✓
Schmidt K					✓	✓
Sherr E		✓	✓		✓	✓
Stoecker DK				✓	✓	✓
Thiele S		✓	✓	✓		✓
Thingstad TF	✓	✓	✓	✓	✓	✓
Våge S	✓	✓				✓

Detailed Responses have not been attributed to their originator.

All responses were made without knowledge of inputs made by others.

Not all co-authors contributed to all questions/statements. Responses are not presented in the order of the co-authors listed in **Table A1.1**.

A2. Responses

The questions/statements are presented together with the responses in the same format as seen by the contributors.

Replies are often voiced, in the words of one of the contributors, with an implicit *idea that you can switch on and off certain parts of a model depending where (global region) and what you are studying. Exploring individual processes in detail and then incorporating simpler pathways in a larger model that covers the big picture.*

Responses have only been edited to correct typographic errors, to remove introductory comments such as ‘As noted earlier’ (in which instance, as appropriate, response text may have been reproduced).

Responses such as ‘I do not know’, have not been included, though responses showing doubt have been included.

Publications cited in the responses are listed in the main document.

A2.1 Plankton-Type Specific Questions/Statements

A2.1.1 Virus (& their hosts)

V1. To properly explore the ecological consequences of plankton viruses requires models with a high level description of the biodiversity of their prey.

Response:

- If your interest is biogeochemistry, you would explicitly want to avoid the complexities and uncertainties of a resolved biodiversity model. This, however, requires a model that can tackle co-existence of viruses and predators on the same prey.
- I tend to agree (at least diversity needs to be resolved "to a sufficiently high degree – see next response"), since the presence of viruses and diversity in the prey are so tightly connected – i.e. viruses are a major source for diversity in the host and host diversity opens a niche for viruses to exist next to grazers (i.e. an important mechanisms for co-existence of both viruses and grazers competing for the same shared resource (prey/host) is the fact that viruses are more specific "top-down" controllers than grazers, and the specificity of virus top-down control is directly linked to host diversity.
- It is not about high or low level it is about what matters. Identifying keystone viruses and their hosts etc.
- Not sure
- Depends on the purpose of the model. We recently found experimentally that 3 different viruses were affecting 3 different hosts in a simple temperature manipulation. Describing, let alone modelling these interactions is proving to be very complex.
- This is not always necessary, larger "functional groups" or "groups with similar traits" could also be included in the models. However, the necessary complexity will depend on the purpose of the model, if you want to build a simple "C-Flux model" including larger groups might be sufficient, contrary if the model attempts to describe changes in planktonic diversity a higher degree of detail is clearly necessary.

V2. The host specificity of viruses is so high, set against the diversity of competing non-hosts that are described in models within the same functional type (group), that we can disregard the action of viruses in most plankton models.

Response:

- They are probably all hosts and the change between species and strains probably frequently driven by viruses. If this is important and/or of the DOM production through the viral loop is important, viruses are needed.
- I don't agree (although it depends what we want to achieve with the model). There are ways to account for high host specificity without resolving host diversity explicitly (i.e. by making host community strategies adaptive (Thingstad & Våge 2019).
- The problem is that we still do not know when and when not viruses are important and how they impact the carbon cycle. Are they only important during blooms? Are they always important? How about grazers? We don't' even know if they increase or decrease carbon export efficiency.
- The issue is that all of this is very dynamic and our knowledge is still very limited.
- I do not believe we can leave viruses out. They will increase species diversity (killing the winner)
- Depends on the purpose of the model.
- Viruses are (to my knowledge) only under certain circumstances/periods important in structuring the plankton community and impacting the flow of material CL(C,N,P etc.). So, in many models viruses do not need specifically to be included.

V3. We only need to consider viruses for bloom-forming primary producers. In all other instances, the ecological role of an infected host would just be replaced by another member of that same plankton functional group and the trophic dynamics would be unchanged.

Response:

- Maybe. But what if your interest is the population dynamics of the non-bloom formers?
- I don't agree. Viruses in general shunt part of host production away from more efficient transport to higher trophic levels down to the dissolved pool, be it in bloom events or more stable communities. Viruses do not only play a role for host diversity, but the presence of viruses also has effects on the flow of matter through the marine food web, regardless of the number and type of hosts groups that are present.
- I would think the primary role is on biodiversity rather than abundance.
- Not true, perhaps they play a role on the consumers of DOM. If two subsequent blooms occur, it may be that the bacteria that responded the first time can not respond because there viruses are still around. This hasn't been explored as far as I know.
- Would not agree.
- It could be a first approximation.
- Depends on the purpose of the model. Availability of data is another important concern. Quantifying viruses, let alone their variability is not routine.
- This will depend on the organism of interest. If the model e.g. focuses on bacterial processes the above statement is likely correct however if zooplankton are considered this is likely not the case.

A2.1.2 Bacteria

B1. Can we get away with a single bacteria model to describe the entire suite of open water bacterial activities?

Response:

- I would suggest two groups. The small “streamliners” (SAR 11 likes or “S-strategists”) and what I prefer to call “L-strategists”. The L-strategists use excess organic C to remove the tradeoff between competition and defence by becoming large and then replace the S-types. The L-type thus creates “blooms” (Vibrios, Polaribacter and others). The L and S types differs in their competition and defence characteristics and therefore alters the food web structure.
- I think there either needs to be more than one type of bacteria, or the bacterial group needs to have the possibility to change its competitive and defensive strategies over time (Thingstad & Våge 2019).
- Absolutely not. The main organism out there is SAR11, but it hardly does anything, while others, like Gammaproteobacteria, are super active under certain circumstances and do most of the carbon cycling. Others than do the other elemental cycles, and all of them are controlled differently and with different efficiencies (predation ratios), etc. So there is no chance that we can put only one box into the model for bacteria and/or archaea.
- No we cannot, as we know these are highly specific to different plankton organisms (so we cannot with other groups either)
- Of course not.
- No. bacteria includes cyanobacteria, heterotrophic bacteria (including photoheterotrophic) and chemoautotroph and also ignores archaea.
- Nope as different bacteria have significant differences in their metabolic capabilities and this needs to be taken into account.
- I do not believe so. For example, some heterotrophic bacteria can also fix- N_2.
- Depends on the purpose of the model.
- My gut feeling says that unless the model should resolve special bacterial features like nitrification, annamox, diazotrophy etc. one might go well with one.
- I would suggest at minimum that we have a generic cyanobacterium, heterotrophic bacterium and anaerobic denitrifier.
- It would be great to have several groups, but my guess is that large differences in bacterial function and activity are close to impossible to include in one single model. Also due to the large diversity, differences in physiology and activity it is very difficult to know what to include in a model and what not (“where should we draw the line”?).

B2. Do we need an explicit description of bacteria at all? – can we not just (continue to) use an implicit description of ‘decay’ and ‘regeneration’?

Response:

- To eliminate a bacterial compartment would also eliminate the process of predation on bacteria by heterotrophic and mixotrophic flagellates, which is an important route of protist growth and nutrient regeneration in food webs. Bacterial prey are significant in nutrition of mixotrophic phytoplankton, and bacterivorous flagellates are prey for larger consumers. Are bacterivorous flagellates also dispensable in a model?
- Not if your interest is prokaryotes 😊
- I think that depends on the purpose of the model. However, it is important to keep in mind that bacteria are strong competitors for mineral nutrients, i.e. they do not only have the function of remineralizers in aquatic environments, but directly compete for phosphorous, nitrogen etc with phytoplankton. If we are interested in the question of whether the system is “net-autotrophic” or ”net-heterotrophic”, disregarding the bacteria is too crude of an approximation.
- The differences in the ecofunctions of the different bacterial and archael groups make it mandatory to go a bit deeper. Sure, a complete resolution is not possible due to the super high diversity, but we

need more than just a single box or something like “degradation”. Also because the different groups are regulated differently and hence can have different dynamics.

- We do, as they play active roles in the food webs, and are more than just detritus creators
- Yes, we need explicit description.
- Bacteria are as important as euk. plankton. They need to be modelled at the same level.
- I believe we need an explicit description, at least to some degree.
- Depends on the purpose of the model.
- The mentioned (and others) specific bacterial biogeochemical processes are not resembled by decay or regeneration.
- Bacterial groups have very different physiology and activity so it would be helpful to make a more detailed description. However, in more simplistic models the role of bacteria in e.g. biogeochemical processes (e.g. DOM degradation, nitrification) could be treated “indirectly” by including their contribution in the specific process(es) term(s).

B3. In considering predation upon bacteria, do we need to explicitly consider their cell size, motility, and how/if they grow in clumps?

Response:

- Can probably be parameterized together as unspecified “defence”.
- I think things like that are important to consider. Cell size is a trait that is under strong selective pressure.
- At least partially, because otherwise the model is again to broad. It is impossible to model all predation strategies and the respective defences, but at least some major control mechanisms need to be implemented to correctly reflect the microbial loop.
- Yes we do as this affects the rates of both resource uptake and the way they are predated upon (although admittedly, predation on bacteria does not feature with many microbiologists
- Good question. I guess we still need to figure that out.
- Bacteria are as important as euk. plankton. They need to be modelled at the same level.
- Yes, I believe so.
- Depends on the purpose of the model.
- I don´t think so. But I am not a microbiologist 😊
- If the model is a highly complex/sophisticated model there is likely no need to consider this in detail. Yet, if a model is built to describe e.g. predation or the biological carbon pump such processes will be highly relevant.

A2.1.3 Phytoplankton (prokaryote and protist)

P1. Most models describe changes in Chl:C only (which affects the value of the biomass-based alpha, the initial slope of the photosynthesis-irradiance curve); they take no account of changes in P_{max} with photoacclimation that would see changes in RuBisCO. Is this an acceptable simplification?

Response:

- Probably not, but is it reasonable to model the changes of Rubisco? Do we have data of Rubisco transcriptomics or even proteomics?
- I would say unequivocally that this is not an acceptable simplification. In many instances Pmax changes as part of photoacclimation. This has important consequences for values of Ek which is often used in models of photoacclimation i.e. you can get decreased Ek, without any change in alpha. For this reason, I dislike using Ek values as indices of acclimation and prefer to see alpha and Pmax used, with both expressed on a biomass (C) basis. Mechanistically, changes in Rubisco content with photon flux also have implications for overall cellular energetics given the energy cost of protein synthesis/turnover.
- No, photoacclimation is very important and should be include in new models. Chla:C can change by a fact of 8-10
- Changes in Pmax with photoacclimation should be taken into account
- Depends on the purpose of the model.
- I think it would be better to include P_{max} {as variable} in models.
- No it is not acceptable, but its currently the best we can do.

P2. Describing photoacclimation to changes in photoperiod length, and to short-term changes in irradiance over the day (with clouds etc.), is essential to more correctly describe primary production. (most models cannot describe this)

Response:

- Describing photoacclimation is important, but the time scale is relevant. Studies show that hours timescale is needed for changes in irradiance to trigger a photoacclimation process. So knowledge is needed of the timescale of vertical mixing, changes in irradiance with ‘clouds’, etc.
- Yes, given the variability in light flux with daylength and with other factors such as cloud cover and water movement it is important to consider short term fluctuations. A complicating factor (another one!) is that respiration rate is likely to vary with light intensity as well (see e.g. Beardall et al. 1994), so measurements of primary productivity corrected for measured rates of long-term dark respiration are likely to overestimate net productivity.
- It is routinely assessed experimentally as otherwise rate measurements would be erroneous (e.g. see Morison et al. 2020).
- I would agree
- I agree with that statement
- Depends on the purpose of the model. Photoacclimation models (e.g., Geider and Kana et al) have given us insight into regulation of the photosynthetic apparatus. New types of data (for example, from PAM or FRRF measurements) give us much more data on regulation of photosynthesis and photoacclimation (NPQ etc.). Data are rapidly advancing as these instruments are being used more and more.
- I wouldn´t say so. Rehder et al. (2023) last year published a paper on *P. tricornutum* (yes, absolute lab rat), where we could show, that the cells acclimate to always achieve “sweet spot” rates in their photosynthesis. This homeostatic behaviour might be quite a generic one. If – hypothetically- all phytoplankton would tend to acclimate to one single favourite per-Chl-rate then resolving the photoacclimation would really only make sense for scenarios where one wants to specifically investigate the effect of the transitory (stress?) time when they are not acclimated.
- Yes, I agree.

P3. Given the typical timestep duration in models (ca. 20-40min), photodamage rather than photoinhibition is the more important feature to consider, yes?

Response:

- Yes.
- An issue here is the definition of photoinhibition and photodamage. I prefer to use the term 'dynamic photoinhibition' for those reactions that reversibly regulate light harvesting to avoid over excitation and consequent photodamage caused by the resulting reactive oxygen species (as e.g. damage to the D1 protein in PSII or in extreme cases chlorophyll bleaching). Dynamic photoinhibition would include processes such as non-photochemical quenching and state transitions. Non-photochemical quenching has a time frame of minutes, but D1 repair is also rapid. Some people use photoinhibition to refer to damage to D1 and the efficiency of PSII as in practice these are reversible whereas severe damage to e.g. chlorophyll bleaching is less easily reversible. I am certainly of the opinion that photoinhibition is important to consider.
- Not sure.
- I beg to differ that the typical time step is 20-40 min…depends on the model and its application. Daily time step? Sometimes longer. Photoacclimation occurs on the minutes scale; photodamage longer. Repair from photodamage also is a long process (often requiring over night).
- Since Photoinhibition is a quite rapid phenomenon and i´d interpret photodamage as a longer-term consequence of photoinhibition, i´d say yes.
- Yes

P4. Must we describe photodamage/inhibition as well as acclimation? If we must do so, can this be achieved simply by down-shifting the value of Chl-specific alpha at high PFD? Or should we relate PFD and nutrient status to describe a lowering of Chl:C?

Response:

- Yes, I feel this does need to be taken into account. In many systems algae are exposed to rapid fluctuations in light, including supra-saturating intensities, so effects involving photoinhibition/photodamage do need to be taken into account. As a first approximation, shifting values of chl-specific alpha are probably acceptable. Considering nutrient status is a further complication I guess, but is probably a separate issue, though at high PFD in a 'closed system' cultures/populations are likely to become nutrient exhausted earlier.
- Acclimation is one of the main unknowns and possibly unknowables in plankton physiology. Adequate acclimation across different processes (that have different latencies) is hard to achieve, if not impossible. I think the latter.
- I believe you need to take both PFD and nutrient status into account to get the best description.
- Yes, I believe so. I believe it should relate PFD and nutrient status
- Newer instruments (e.g., PAM) are giving us much more insight into photoacclimation and photodamage. Values of NPQ or NO can be reported and modelled. They have been shown to vary as a function of temperature, nutrient status etc. Coupling these data with data such as HPLC pigments (changes in diadinoxanthin or other xanthophylls for example; changes in accessory pigments) give us additional clues to photodamage vs acclimation—but models will depend on data availability.
- I think not for biogeo models, but for ecophysiological questions e.g. highly variable light conditions that select among the phytoplankton population, this might be relevant. I feel that solution two is more intuitive.
- I think we should aim to describe different relations between Chl:C in different conditions of light and nutrients. But to be representative of the real world we need to know how different kinds of phytoplankton modify their Chl:C in different conditions. Currently, we have little knowledge about this.

P5. Temperature (Q_{10}) effects P_{max} but not alpha (the initial slope of the photosynthesis-irradiance curve).

Response:

- Physical processes generally have lower Q_{10} than enzyme-dependent ones.
- Yes, to a first order.
- Conventionally it has always been assumed that alpha is not temperature sensitive as it is driven by photophysiology. However, some of the stages in the electron transport chain involve enzymes so in many cases rates of light-limited photosynthesis and alpha are temperature dependent (see e.g. Raven and Geider 1988, Davison 1991). Admittedly such variation of alpha with increasing temperature are not as marked as those in Pmax - and indeed may not be positive (see Davison 1991).
- I would think so.
- In general yes. However, saturating response curves depend on the physiological state of the organism so any specific curve has some arbitrariness related to the measurement protocol. The shape of the curve fundamentally changes when the environment changes. Pmax, regulated by enzyme activities, is more temperature sensitive than the light reactions.
- The Q_{10} concept is nice, as long as we´re below the thermal optimum; beyond rates typically decline rapidly. Thus, I think the Q_{10} concept helps us a lot in understanding, but it´s not helpful in modelling. I´d rather suggest to model temperature effects with some of the classic temperature response models (Blanchard, Ratkowsky, many more)
- Not really {alpha is affected}

P6. We need photo-acclimation models because nutrient exhaustion drives changes in Chl:C much faster than changes in nutrient quotas (e.g., N:C) change.

Response:

- Yes, Chla:C can change in less than a division time.
- We need photoacclimation models more because light changes more frequently than nutrient exhaustion or nutrient quota changes. Certainly, nutrient limitation/exhaustion will affect chl content and light harvesting as well as e.g. Rubisco content, so photoacclimation in the context of nutrient status is important.
- Agree
- Yes, agree!

P7. We do not need variable Chl:C models because i) light is almost always limiting in nature (so Chl:C is always maximal for a given nutrient status), ii) it can be related adequately to N (i.e. Chl:N can be considered constant).

Response:

- No, light isn't always limiting so a variable Chla:C model is needed.
- Demonstrably false.
- I disagree with this statement
- The degree to which light is limiting depends on the system and the organism physiology. Cyanos, or even some dinos, that sit right at the surface would likely not be light limited. Surface light may be inhibiting to other organisms. Chl;N is not a constant. In a recent experiment, we found that the values of chl a yield ranged from ~1µg chl a:1µM N for both nutrient enrichment conditions (+NH4 and +NO3) at high irradiance levels as well as fo r reduced irradiance with NH4 enrichment, but about twice that value, ~2µg chl a:1µM N, for samples enriched with NO3 and held under reduced irradiance.
- I´d say we need variable Chl:C models. Because it is variable in nature and it makes sense to introduce the degree of biomass pigmentation as a core variable. The problem with "limiting light" is also that

light acclimation will always adjust the apparatus so that Ik is close to the in-situ irradiance, and thus there will always be some photosynthesis potential, so by definition light will always be limiting.

- Not really (Chl:N is not constant)

P8. Modelling suggests that the production of DOM, in all forms, represents an important yet poorly studied product of phototrophy – can we assume a fixed % of CO_2-fixation, or of DIN-assimilation, as being leaked? If so, what should that value be?

Response:

- I believe this is fundamentally different in flagellates (photosynthesis proportional to nutrient uptake) and diatoms (photosynthesis proportional to biomass). *Phaeocystis* is also a special case.
- At a regional scale this could be done. Values around 20% for polar regions is supported by the literature and values around 80% are reasonable for the oligotrophic gyres. The caveat is that existing data hasn't separated passive leaking from loss associated with grazing/mortality.
- No we cannot, as this is very dependent on the availability of nutrients
- 5% as a first approach (see Bjørnsen 1988).
- Depends on the system being studied. If cells are in a state of stress or imbalance, leakage is more likely.
- I think that DOM exudation is a feature that is prominent under nutrient limitation of any kind as a means to get rid of photosynthate. When growth rates approach zero, but production rates have not yet approached zero, then, instead of becoming enriched in sugars, polygucan chains are transported to the outside of the cell, which will rip off over time.
- The production of DOM is highly variable (from 2 to 50% of carbon fixed) and it depends on several internal cell processes and environmental factors. Therefore, assuming one fixed value will likely be misleading.

P9. We can ignore osmotrophic mixotrophy expressed by phytoplankton as being of no consequence in nature.

Response:

- No, this is an important term to include.
- I would argue that it depends on the amount of mixotrophy. For bacteria it is a major part, but I am not a plankton specialist to say if this is true for plankton as well.
- No we cannot as we know more and more that complete autotrophy is not that common.
- Demonstrably false, resource competition with bacteria and subsequent consequences.
- Wrong. There are many osmotrophic plankton species and most phytoplankton are mixotrophic anyway.
- No, not at all. It may be insignificant for direct C-assimilation, but it may serve as sources of for instance vitamins (see Anderson et al 2018)
- Depends on the system under study. In an r-dominated system, such as an early spring bloom or an upwelling system where diatoms dominate, mixotrophy will be of less importance relative to DIN (NO3) but in a K-selected environment, mixotrophy generally becomes selectively advantageous. More mature environments are more likely dominated by phototrophs with variable mixotrophic capabilities.
- No. It certainly is important. If a bloom is rapidly growing and draws down nutrients, then cells will get into senescence, stop dividing, and readjust their transcriptome to enter the stationary phase mode, which includes expression of enzyme machinery to scavenge exotic external nutrients, e.g. N from chemical nitro or azo groups. If nutrient scarcity kills cells, their released constituents will be fed upon by its congeners in a mixo/osmotrophic style. So this selects for the specimens that can survive longest under nutrient starvation.

P10. Do we need to explicitly (separately) describe Prochlorococcus *and* Synechococcus in models?

Response:

- They dominate the oligotrophic regions. You may however model the prokaryote community as a collection of osmotrophs with a range of photosynthetic abilities from *Prochlorococcus* and *Synechcoccus* producing the organic material they need, via the anoxigenic phototrophs reducing their need to respire expensive DOC molecules (this includes SAR11) to the purely heterotrophic L-strategists that go for environments where DOC is in excess.
- Yes, as they maintain different seasonal and vertical patterns from each other so to capture population dynamics they must be separate.
- I don't think so, because they have the same ecofunction, the production rate needs to be flexible and can thus be used accordingly, and they are also controlled by similar predation methods (I believe).
- Only if we do the same thing for other groups and species.
- Yes. Coastal zones may require only *Synechococcus*.
- These two types of organisms have had dozens of genomes sequences, providing prime examples of why species and strains matter.
- Yes. They have very different distributions and temperature relationships and to light.
- Sure
- I do not think so.
- Depends on the purpose of the model. In global ocean models, these different picoplankton have very different niches.
- Not an expert on those, but I think not. Seemingly they´re functionally very similar.

P11. How important is the reported motility of prokaryote phytoplankton – can we ignore it? (Raven & Lavoie, 2021. Prog.Bot. ***83****, 315)*

Response:

- I guess so, because many don't move or move only to the next yummy bit to stick around there. So in larger models, this is neglectable. Growth rate is different though, this needs to be taken into account, because that changes not only the abundance in certain areas (as does motility), but also the consumption ratios.
- This should be tested in the lab and in situ.
- Yes can ignore
- Not sure.
- I would think so.

P12. Can we assume that diazotrophs (as indicated by 'omics, for example) are always fixing N_2, irrespective of the availability of DIN that may be expected to repress (inhibit) N_2-fixation?

Response:

- No.
- If we know that there is an inhibition process and we look at DIN and N2 fixation in the model, then we need to model the inhibition.
- No, it is not even clear that classically known diazotrophs can ever even fix nitrogen (Delmont 2021). Heterotrophic diazotrophs play a very unknown role. Thus it would be better to include expression in these analyses, rather than abundance of taxa.
- From what I have found with a cursory probe of relevant publications, it appears that pelagic marine nitrogen fixers can be inhibited by high concentration of ambient ammonium or nitrate, but still retain the ability to fix nitrogen (Dekaezemacker et al. 2011, Knapp 2012). Zehr & Capone (2020) have a recent review. Wrightson et al. (2022) modeled effects of ocean warming on nitrogen fixation by the filamentous marine cyanobacteria Trichodesmium and Crocosphaera, concluding that: 'Our results project a global decline in nitrogen fixation over the coming century.' It is complicated, but probably assumption of some DIN inhibition of nitrogen fixation in pelagic systems is warranted.

Increase in sea surface temperature will also be an important determinant of global marine nitrogen fixation.

- No, that we cannot assume at all! Oxygen tension in the water may also an important parameter for those species that do not have heterocysts, since N-fixation requires lack of oxygen. Remember also that now it is known that nitrogen fixation also takes place in many heterotrophic bacteria (Turk-Kubo et al 2022).
- No, this we cannot assume at all! Oxygen tension in the water may also an important parameter for those species that do not have heterocysts, since N-fixation requires lack of oxygen. Remember also that now it is known that nitrogen fixation also takes place in many heterotrophic bacteria (Turk-Kubo et al 2022)
- Fixation of N2 is variable depending on a number of factors. Assumptions related to these rates and their importance will depend on the purpose of the model, the importance of N2 fixation in the system and data availability.
- I am not sure I got the question: DIN suppresses nitrogenase activity and expression, I think the is the common notion. Also Fe is an important prerequisite and nitrogenase activity ceases under Fe limitation.
- No we certainly cannot. We need to measure rates.

P13. Diatoms that grow in chains should be allometrically binned in the size for the chain, not the size of individual cell. This is so both for nutrient uptake, and for considering predation.

Response:

- Re predation: diatom chains can be wildly different in length. Gyrodinium and Protodinium spp. Dinoflagellates, as well as some ciliates, can prey on both large sized diatom cells and fairly long diatom chains (Strom et al. 2001, Sherr & Sherr 2007, Calbet 2008, Sherr et al. 2013). Binning of diatom chains by length would probably not be helpful for microzooplankton predation.

Protoperidinium sp thecate dinoflagellate feeding on a centric diatom chain via a pseudopodial pallium, Bering Sea May 2010 [© EBS]

- For nutrient uptake cell size should be parameterized. For predation, it is less clear, but cell size is likely also the more relevant parameter.
- No, there are things that are determined by the length of the colony not the single cell. Binning should be flexible.
- For nutrient uptake they should be individual cells, for predation it depends how strong or loose cells are connected it the chain. For sinking I would consider chains.
- Mmmh, good question. Depends on if they are separatable (some diatom chains can't be broken, others can live as single cells) and if they coordinate physiological processes."
- Would make sense as far as I can tell
- No, for nutrient uptake it should be depend on actual cell size, and for grazing it should depend on chain size.

- I think this might make sense when grazers exclude certain sizes.
- To my experience, I would prefer to consider them into each individual cell.

P14. It is important to account for differences in photophysiology between diatoms and non-diatoms.

Response:

- Yes, if you want to get the right rates, you have to distinguish between different groups that have different physiologies.
- This is certainly true. Different groups would appear to have marked differences in photophysiology and responses to light (see the, admittedly old, paper by Richardson et al. 1893). Diatoms for instance would seem to be tolerant to both high and low light whereas most dinoflagellates have preferences for low(ish) light.
- Yes
- Yes, clearly, since almost all the other algal groups can be mixoplanktonic.
- Yes, I believe so, in reality separate diatoms, cyanobacteria and the rest, which are most likely mixoplankton
- Photophysiology of different plankton groups differs. New instrumentation (such as the PhytoPAM) can distinguish/deconvolute the photophysiological condition of different algal groups (brown, green, blue-green and phycoerythrin-type algae). However, distinguishing between different types of ‘browns’ (dinos and diatoms) is difficult. Again, the answer to the question depends on the system under study and extent to which appropriate data might be available.
- Owing to how different dinos, coccos and diatoms are I am tempted to say yes, but that basic mechanistics f photosynthesis works quite the same in all three. I would just constrain them with adequate rates and photoinhibition behaviours maybe.
- Strongly agree!
- Absolutely! Non diatoms must also be broken down into (at least) cyanobacteria, green algae, haptophytes, others

A2.1.4 Mixoplankton

M1. Mixoplankton are too complicated to model; can't we just merge 'phytoplankton' and 'zooplankton' activities?

Response:

- We can probably replace the two communities of autotrophic and phototrophic flagellates with one community of mixotrophic flagellates. This will however require a fitness-driven strategy variable so the gain in model complexity is moderate.
- No, because of synergisms in mixotrophy.
- Difficult yes, important even more
- Maybe but they are important
- I strongly disagree. Mixotrophy is more than just the sum of photosynthesis and prey ingestion.
- Mixoplanktonic activity fundamentally changes our understanding of planktonic food webs, enabling primary producers to acquire nutrients directly from ingestion of prey such as bacteria and algal competitors, and even from their predators. Mixoplankton thrive in conditions where simultaneous acquisition of light and nutrients become challenging. Mixotrophy in these plankton is not simply additive or substitutional with photosynthesis; rather, it is synergistic. Thus, through mixotrophy, there is provision of additional nutrients (N, P, Fe) from feeding to support primary production, together with a contribution of C to supplement photosynthesis under conditions of light limitation (including night). Moreover, the ecophysiology (nutritional quality) of the component organisms present in the ecosystem affects not only their own growth potential but also the activities of others: the cellular composition of algae, for instance, has consequences for grazers and their emergent properties, with potential for a positive feedback loop generating ungrazable primary producers. Inclusion of mixoplankton within a simple nitrogen-phytoplankton-zooplankton-bacteria-detritus (NPZBD) model results in a substantial difference in planktonic trophic dynamics.
- I think once we have math representations for processes in microalgae and bacteria it could be easier to synthesize mixotrophs from the modules.
- I do not think merging phytoplankton and zooplankton will provide any data at all about mixoplankton.

M2. Mixoplankton only appear to be of consequence in coastal systems, especially for HABs, can we otherwise group these organisms in with 'phytoplankton'?

Response:

- I am not so sure. I would rather explore a food chain model with prokaryotes – flagellates -ciliates - copepods. In this the prokaryotes would have an adaptive photosynthetic capacity (from SAR11 and Prochl-Synecho) and the flagellate community and adaptive photosynthetitic-to-mixotrophic-to phagotrophic component. As nutrients are drawn out of this system, I believe the flagellates have to increase their mixotrophic abilities and the prokaryotes their photosynthetic. If so, it would probably produce the system I believe dominates the oligotrophic eastern Mediterranean.
- Mixotrophs are as important or perhaps more important in oligotrophic oceanic ecosystems as coastal. For example, mixotrophic flagellates are very important to productivity in oligotrophic gyres . GNC mixotrophs including ciliates, some dinoflagellates and rhizaria are not "phytoplankton" and are important in open ocean ecosystems (Hartmann et al. 2012).
- Wrong, they appear everywhere and probably more than we think.
- Yes of course, if we just want to know how many fish can be produced. No of course not, if we want to understand what happens in the plankton.
- Most phytoplankton species take up DOC in one way or the other.
- No, I do not believe so (see Leles et al 2017; 2019)
- Various efforts have documented the global distribution of mixotrophs (Leles et al. 2017, Faure et al. 2019). Mixotrophs are everywhere. pSNCMs are more seasonally and spatially restricted; most CMs are found in eutrophic and coastal habitats- many CMs are also HABs.
- If mixoplankton is truly only relevant in coastal systems, then this sounds like a valid approach.

- I doubt this is correct. However, the sad reality is that we do not really know.

M3. Because bacterivory by CMs is likely ubiquitous, and bacteria are ubiquitous, can we in essence just ignore this process and describe these organisms as 'phytoplankton' with enhanced abilities (lower half saturation constants) to acquire inorganic nutrients?

Response:

- Maybe if your goal is just to get photosynthesis approximately right.
- Since the predation rates are not the same for different groups, I would argue for a more detailed model that includes different groups of predators among others mixotrophs with different predation strategies and ratios.
- No, these are completely different processes, and bacteria compete with phytoplankton for nutrients.
- No, not at all. Bacterivory is most important (also in C-units) for smaller phytoflagellates (Anderson et al 2018)
- I wouldn´t think so, since biogeochemically it´s different things to acquire nutrients by eating bacteria or by taking up inorganics. To me this seems quite discrepant, so i´d separate it.

M4. We can use an allometric scaling rule to relate mixoplankton size to the balance of phototrophy vs phagotrophy.

Response:

- No, because mixotophy occurs in picoplankton, nanoplankton. Microplankton and even mesoplankton. It is also Important to remember that mixotrophy is not just a gradient between heterotrophy and phototrophy, there are distinct types of mixotrophs, with different response curves to light, nutrients, and prey densities. Depending on the ecosystem and season, different types and sizes of mixotrophs are important. For example in subtropical gyres pico and nanomixotrophic flagellates as well as micro and meso mixtrophic rhizaria are important.
- Yes, we can do this (Wirtz et al have done so), but it might not increase our understanding as often the predators are smaller than their prey.
- I believe this is difficult for very many reasons: A) Different strategies exist among the CMs; some will always feed while others will only feed when nutrient limited (see Hansen 2011). Some species cannot utilize NO3, and thus they will feed intensively even during periods with high nitrate concentrations. B) Many CM species will depend light to be able to feed, some can feed and grow in the dark. C) Some SNCMs ingests very little, i.e. red *Mesodinium* spp, while others can ingest quite a bit *Dinophysis*. D) Ingestion rates are quite high in GNCMS, and light supplements carbon needs, i.e. Gross growth efficiency is quite high at low prey concentration and high PFD

M5. pSNCM require so few encounters with their special prey, which supply their acquired phototrophy, that we can effectively just model these organisms as CM. (Otherwise we have to model the explicit growth and survival of those specific prey.)

Response:

- There are correlations between occurrence and abundance of pSNCM and their special prey.
  pSNCM do not occur in ecosystems lacking their prey (Johnson et al. 2013; Peterson et al. 2013).
- Only true for some species (i.e. the red *Mesodinium*), not for others like *Dinophysis*

M6. Elevated temperatures will promote phagotrophy more than it promotes phototrophy in mixoplankton.

Response:

- Not sure this always is the case. Data are available for only a few mixotrophic flagellate species in culture. In nature, increases in temperature often result in changes in community composition, there is no evidence that more phototrophic mixotrophs will be replaced by more heterotrophic mixotrophs. Warm, particularly oligotrophic waters, are usually rich in several functional types types and taxa of mixotrophs.
- That depends if mixotroph physiological responses to temperature reflect a chimera of phyto and zooplankton or if they do their own thing.
- Yes (Wilken paper), but not necessarily. It differs among species. Several mixotrophic species that are primarily phototrophic have been found to have a higher photosynthetic rate and lower ingestion rates at increased temperatures. For instance, chrysophytes such as *Dinobryon sociale* and several strains of *Chromulina* showed decreases in phagotrophic ingestion with temperature elevation (González-Olalla et al., 2019; Princiotta et al., 16; Sutton 1972). Prymnesiophytes such as *Isochrysis galbana* have also been shown to depend more heavily on phototrophy than phagotrophy as temperature increases (González-Olalla et al., 2019).
- As shown by Lin et al. (2018) in mixotrophic modelling of a 10-day growth period, under a low N:P condition, the biomass (based on C) of *Karlodinium veneficum* was significantly higher in mixotrophic growth at warm temperatures compared to autotrophic growth for the same temperature, but such differences were reduced as N:P conditions changed in the model. Franze and Menden-Deuer (2020) examined temperature effects on mixotrophic (herbivorous) dinoflagellates. Growing three taxa over a wide temperature range, they observed that biomass-based growth rates were 10-fold higher than at low temperatures due to the fact that cell biovolumes increased by 50%.
- An interesting question, I do not know.
- Not according Ferreira et al. (2022) “in mixoplankton, grazing decreased in warmer temperatures, whereas photosynthesis increased”

A2.1.5 Zooplankton

Z1. The strongly contrasting predator:prey size relationships for different types of protist zooplankton prevents a meaningful placement of all of these organisms within a single functional type.

Response:

- I agree. There is long-standing (e.g. Hansen et al. 1994, Sherr & Sherr 2002) and growing, evidence that nano-flagellates (both heterotrophic and mixotrophic) mainly prey on pico-sized plankton (bacteria and pico-phytoplankton), while micro-sized phagotrophic protists prey on both nano- and micro-sized prey, including large and chain-forming diatoms. Taniguchi et al. (2023) examined prey size selection by marine herbivorous protists and concluded: 'When all consumer sizes were present, distinct dietary niches emerged, with a range of consumer-prey size ratios spanning from 25:1 to 0.4:1, encompassing the canonical 10:1 often assumed.' Two functional types are the minimum.
- Agree. For me, the size structure of the assemblage would be a valuable emergent property of a model to test against a large body of empirical data. This is particularly valuable because some models like ERSEM seem to get "preoccupied" by taxa such as diatoms and size-based simplifications are built on solid principles making no assumption on trophic mode (autotrophs v mixoplankton etc) and not excluding any functional groups.
- Yes, different protist zooplankton have both different predator:prey size relationships and sometimes requirements for particular prey.
- As well as the diversity of feeding modes, starvation capacity, reproductive modes etc. etc. It really depends on the question. For some questions they may cover a single functional type.
- I completely agree.
- It depends on the goal of the exercise and what degree of uncertainty we are willing to accept. For example, across eight orders of magnitude the conventional allometric scaling applies to feeding-related parameters, but there are significant differences among individual groups up to a factor of 10 (Hansen et al. 1997). But more recent work sees an allometric converge of ingestion and growth across 15 orders of magnitude in heterotrophic marine organisms (Kiørboe and Hirsch 2014), but not in respiration rates.
- This seems correct. Let's keep in mind protist zooplankton encompass bacterivorous and very large-prey phagotrophs.
- Yes, that is right.

Z2. Prey selectivity is an essential feature of grazer behaviour; placing all zooplankton in one or two boxes and all their prey in another, or in a few others, is not an acceptable simplification.

Response:

- It depends. No plankton model will be perfect. There should be a balance point in modelling between perfection and over-simplification that would yield meaningful results for the intended goal of a model. A 'limited box' plankton model to be mated to a climate model could be sufficient for gross depiction of a food web. A model of trophic dynamics targeted to understanding a specific system might require more compartments.
- I am mostly worried for the different feeding modes of the different mesozooplankton grazers. Copepods, Appendikularians, cladocerans and rotifers probably create very different top-down controls and thus different trophic cascades.
- Agree – My non-expert impression of models is that variability, flexibility and adaptive capacity of almost every kind is grossly underrepresented in models, which tend to turn into some kind of machine that greatly overplays the role of measurable or fashionable stressors such as OA or temperature in driving change. Variables commonly treated as constants include predator:prey size ratio, assimilation efficiency, selectivity functions, thermal niche. Also more acute responses (e.g. to temperature) often seem to be extrapolated to climate change time and space scales, purposefully ignoring a weight of literature showing the ability for acclimatation of genetic adaptation.

- Correct, selectivity should be flexible and dependent for example on the nutritional state of both predator and prey.
- True. On the other hand, some are so unselective that they even feed on sand (lithogenic sediment).
- If the question is about species diversity, then predator selectivity is important. See Landry et al. (2023) where grazers favoured heterotrophic bacteria over *Synechococcus* with implications for primary productivity.
- Yes indeed.
- Depends on the purpose of the model and the system under study.
- The major freshwater (cladocerans) and oceanic (copepod) metazoan grazers tend to be generalist/opportunistic feeders which show little selectivity (cladocerans) or perform prey switching (select for the most abundant prey). Thus, while size selectivity is indeed an important behavior, I question whether every kind of selectivity must be accounted for in a model.
- I agree. Zooplankton encompass from unicellular protozoans to large jellyfish. It would be absurd an oversimplification of such complex group.
- Yes, that is right. Size, motility, escape ability, palatability, etc, may affect prey selectivity.

Z3. ‘kill-the-winner’ (in which the most abundant food item is most heavily grazed, irrespective of its identity) provides a pragmatic solution to describing zooplankton prey-selectivity in models.

Response:

- Probably not. There is so much selectivity in predation by various classes, and species, of zooplankton, based on size and palatability of prey, and of capability of the zooplankter to handle different prey. As one example, Campbell et al. (2009) reported that in the Bering Sea: ‘Microzooplankton were preferred prey at almost all times, with the strength of the preference positively related to the proportion of microzooplankton prey availability,’ and also that the copepod Metridia longa ‘…had an extremely strong preference for microzooplankton with a 3.5-fold greater proportion in the diet relative to the prey field.’ Also, in mesocosm experiments in the North Sea, Löder et al. (2011) reported that: ‘Selective grazing by microzooplankton supported a bloom of less-favoured phytoplankton species and stabilised the shares of bloom-forming species duringthe course of the bloom.’
- My guess is that this is helping to achieve model stability but not sure it is necessarily correct. My experience of the more suspension feeding copepods is broadly and surprisingly unselective feeding in relatively rich and diverse natural seston (except non-ingestion of small cells). In other words clearance rates similar for most things except the very small which are presumably beyond their capabilities. Whereas more raptorial or ambush feeding taxa have higher clearance rates on motile cells (and very large diatom cells in the case of ambushers which presumably create hydrodynamic disturbance detectable to the ambusher). In my various krill and copepod feeding experiments I have never witnessed highest clearance rates on the most abundant or dominant cells (or peak tracking as it used to be called). Gut content analysis of in-situ freshly-caught krill (Schmidt et al 2014) basically supports the very simple idea of indiscriminate filter feeding more akin to the suspension feeding described above, albeit with a probably smaller lower size limit.
- “Kill the winner” probably does not apply in many situations. It may largely depend on a numerical response of the predator to a particular prey type. Many predators are specialists and some prey have defense mechanisms or can turn the tables on their predators.
- Not correct – selectivity should be flexible and dependent for example on the nutritional state of both predator and prey
- What I see with the polar cod is that they often have a ‘mono-diet’ (between 80-100% of prey items are from the same category (sometimes copepods, sometimes amphipods, sometimes krill, sometimes appendicularia). But for a filter feeder, it is selectivity based on filtration efficiency. If it is strictly only killing the winner, then I would say ‘no’ for zooplankton (for cod it could also be an ‘artefact’ as they might feed on specific layers of prey, like directly under the ice, where only one type of prey might be available).
- That model was formulated for viruses. For zooplankton that is a Hollings Type I response.

- I do not believe so.
- This might be the case (based on my reasoning above) for oceanic models in which copepods are the main metazoan grazers.
- Not always. We have been working on the hypothesis that protozoans may actually go for damaged phytoplankton cells, favouring by this way the healthy state of the prey population and ensuring more prey. They would do this selection based on chemical signalling (DMSP, etc).
- Not necessarily. There is lacking information about how zooplankton behaves when feeding in prey assemblages. And in some cases expectations are not confirmed.

Z4. We can usefully assume the same core physiological description, with similar parameterisations (e.g., AE, K_{pred}) for both protistan and metazoan zooplankton, or for all-inclusive protistan or metazoan zooplankton groups.

Response:

- Difficult, because grazing rates are dependent on grazing strategy and hence may differ significantly, which then has an effect on the bacterial/ protist communities and the whole food web. Filter feeder are more efficient than hunters and this should be accounted for, if possible.
- From limited evidence I have seen I would say no. Selectivity functions of the two groups do seem very different, based on data that I have seen.
- I am unaware that we know of key differences.
- This seems to be an important question for modeling ocean food webs (Eddy et al. 2020, Rohr et al. 2023). In a comparison of eleven CMIP6 marine biogeochemical models, Rohr et al. (2023) stated that: '…the largest source of inter-model uncertainty in their representation of the marine carbon cycle is phytoplankton-specific loss rates to zooplankton grazing.' Past literature reviews indicate differences in grazing kinetics, but not growth efficiencies, among proto- and meso-zooplankton. Hansen et al. (1997) concluded: '…among the protists, ciliates display maximum ingestion, growth, and clearance rates that exceed those of dinoflagellates by a factor of 2-4. Among the metazooplankton, Calanoid copepods have maximum clearance rates that exceed those of filter-feeding cladocerans and meroplankton larvae by a factor of 10.' Straile (1997) reviewed published gross growth efficiencies (GGE) of metazoan and protist zooplankton and reported: 'All taxa were found to have mean and median GGE of ~20–30%.' There is also an issue of relative grazing impact of meso- and proto-zooplankton. Fonda et al. (2005) found that: 'Microzooplankton grazing was the most important loss term of primary production in the Gulf of Trieste …', and that: 'Microzooplankton was always present in the diet of mesozooplankton…' A mesocosm study of zooplankton grazing in the North Sea (Loder et al. 2011) demonstrated '…the importance of microzooplankton grazers for structuring and controlling phytoplankton spring blooms in temperate waters and the important role of copepods as top-down regulators of microzooplankton.' Models should have at minimum both mesozooplankton and microzooplankton compartments with respective core descriptions.
- No, since some protistan grazers both with own chloroplasts as wells as those that lack their own chloroplasts also can photosynthesize. See papers by Schoener and McManus
- This may be OK to do. For example, Gross-growth efficiencies do not show strong differences between protozoan and metazoan zooplankton (Straile, 1997).
- This would be like keeping in the same group scorpions and lions. Does it make any sense? Not to me.
- I think the differences between protistan and metazoan zooplankton are very large and group specific parameters must be used.

Z5. Metazoan zooplankton require appropriate binning in functional type models with respect to feeding mode (e.g., raptorial vs filtration) and also with respect to allometry (sizes of prey and of consumer).

Response:

- Agreed.
- Yes, because grazing rates are dependent on grazing strategy and hence may differ significantly, which then has an effect on the bacterial/ protist communities and the whole food web. Filter feeder are more efficient than hunters and this should be accounted for, if possible.
- Yes, not sure about "binning" but how they feed, which dictates on what size they feed on, seems fundamental and from what I can tell seems to make a big difference on which metazoans do well under climate change (could be wrong here though!!)
- Yes, I believe so.
- How much uncertainty are we willing to accept? Prey size spectrum is narrower and shifted towards larger prey for ambush feeders than for active feeders (Kiørboe 2018).
- Yes, this seems correct. Although not doing so would be less “wrong” than merging protozoans and copepods in the term zooplankton.
- Yes. Feeding behaviours (feeding currents, ambush) and predator and prey sizes are key items to take into account.

Z6. It is essential that models of metazoan zooplankton give appropriate descriptions of age-stage ontogenic developments.

Response:

- Yes, especially when the feeding and the nutritional requirements change.
- I guess so. If there are different ecophysiologies and maybe even ecofunctions, they need to be addressed in models.
- Not sure about this and it depends on the models I guess. Obviously required for specific taxa e.g. recruitment modeling in Antractic krill and other fished species. More generally though, can it be more simplified via size-based modelling in bigger-picture simplifications??
- Yes, I agree with this statement
- If the allometry of the function radically changes with size/stage, then this may be necessary.
- Obviously, a nauplius does not feed in the same and at the same rates than an adult.
- Yes.

Z7. The complexity of metazoan zooplankton ontogeny inevitably means that we have to merge the activities and biomasses of all stages into a single (or very few) biomass-based state variable(s). Which stages can be usefully merged, how few functional stages do we need?

Response:

- Eggs, early stages, subadults, adults.
- I know too little about these stages to really make a comment, but I think looking at their ecofunction would make sense. Are they predatory, put them into predators, are they doing nothing put them into biomass without function, etc.
- I guess it depends on exact model purpose
- This depends on the function we are aggregating. For example, the allometry of respiration rate drastically changes from the nauplius to copepodid stage, but not from copepodid to adult stage (Epp and Lewis, 1980; Holmes-Hackerd et al. 2023). In case of stage/age structured populations, binning into nauplii and juvenile+ adult stages may suffice.
- Perhaps having nauplii, copepodite and adults should be enough. Note that even copepodites can be seen as smaller adults, they lack reproductive capabilities.
- Eggs, nauplii, copepodites and adults looks like a reasonable simplification.

A2.2 General Questions/Statements

G1. Models are simplifications of reality. Inevitably, all plankton models are 'wrong'.

Response:

- Models are representations of what the modeller believes are the important features of the system. If he is right, it separates the important from the less important system features (which is a kind of "truth" I suppose)
- For me, getting it wrong is actually a strength of models – in other words honestly reporting this can improve our mechanistic understanding of ecosystem functions. We can make a crude mock-up to diagnose where some process is obviously not captured right, or to suggest that better understanding of process x is needed more than process y. That is a slightly more humble approach compared to purporting to have a great model because it has been tweaked and tuned and coaxed to roughly look right even though fundamental assumptions are wrong, then wildly extrapolated to 100 years time and published in a high impact journal.
- Models are hypothesis testing tools to drive advancement of our understanding, which includes model complexity.
- Models per definition are "representations", and not "copies" or "reproductions", of something. Models are used to set focus and learn about certain aspects of reality. By this definition, I don't support the saying that models are wrong. If we however somehow were to try to make "copies" of reality (which again is not my understanding of definition of a model), these copies would almost certainly turn out to be wrong, since it basically is impossible to include all details and matters of importance in a copy (or reproduction) of reality.
- Correct, but given the complexity of the systems, especially microbial systems, this is inevitable and still models can produce valuable data.
- Yes, indeed they are, but so are our experiments and our own visualisations of reality. As a result, models are not more wrong than anything else. The just formalize what we think and as a result are more easy to criticize.
- I do not model myself, but I assume that models can reliably test certain hypotheses or effects even if being a simplified version of the natural environment.
- That seems overly simplistic. A model has a goal and a purpose. If that goal is achieved, then the model is useful. With respect to replaying reality, models should be wrong as natural processes are complex and difficulty to decipher. If a model replayed the natural event, it would likely be intractable and thus wouldn't improve understanding.
- Of course.
- Simplifications are essential to disentangle complexity for identifying key drivers underpinning evolution and adaptation.
- Of course they are simplifications, but should of course get the pools and processes right.
- Henry Bigelow (of Woods Hole Oceanographic Institution) once said, "Anybody who thinks he can predict more than 10% of plankton variability is a damn fool, but good luck" (quoted in Mille 1989, p. 273). Simplifications do not necessarily make predictions wrong. The degree of simplification depends on the applications of the model and the questions it is designed to address. Moreover, a lot can be learned when a model does not predict accurately… what was missing? What made it wrong?
- That is certainly true, but looking at what´s wrong tells you what you´ve not yet understood. They´re essential to test our understanding of things. So I´d say it with George Box: " most models may be wrong, but some may be useful"
- I agree with this statement. However, it depends on your definition of what is 'wrong' and how 'wrong' wrong is. There are many caveats and biases in the measurements that we make – especially the rate measurements that I make – so I would also say that most measurements we make of rates in the artificial environments we create in laboratories are 'wrong' to some degree – we decompress samples from great depths, confine them in small bottles for long periods of time in the dark or

artificial light, warm them up / cool them down etc. etc. – so most rate measurements are also 'wrong' to some degree.

- I would not say wrong, but at present most of them do not mimic reality accurately or can be used for actual predictions. However, they are very useful to disentangle an understand certain processes.
- Indeed, models are simplified but if "built and calibrated" correctly they are not necessarily wrong. In my view models are very useful for testing new hypothesis (e.g. would happens if we do "x") and testing/predicting how "changes in the environment" could impact plankton communities. Such knowledge is useful for both researcher and managers.
- I don't' agree. I think models are useful tools to approach questions that cannot be solved experimentally, and also to get into deeper levels of knowledge on underpinning processes and on forecasting responses.

G2. It is pointless having a plankton model that cannot actually provide a passable description of reality, irrespective of the arguments for saving computational effort used to justify simplicity.

Response:

- No plankton model will be perfect. There should be a balance point in modelling between perfection and over-simplification that would yield meaningful results. How to test model outcomes for such results could be tricky.
- Maybe there are situations where only the outputs from the system are important (e.g., sinking flux). A function that produces the correct flux without a sensible description of the plankton system may then be OK (if such a function exists). Even it works today, I would however be worried whether it could be used to predict a changing world.
- Agree that ease of computation in itself is absolutely not a justification for an inaccurate model.
- Models need to start somewhere, we need to learn what processes are most/least important in various systems. I think a problem is when we don't keep pushing empiricists to fill the mechanistic data gaps that modellers need to improve (ie., make more realistic) the models.
- I don't agree, models help us to learn about reality without being actual copies of reality. Understanding complex systems depends on an understanding of more simple processes that either cumulatively or in an emergent manner lead to complexity, and it is not wasted to work on understanding sub-sets of processes or details.
- This depends on the complexity of the model. Models with very low complexity might not reflect reality enough and are therefore pointless. Hence, a certain level of complexity and accuracy is needed for the model to be meaningful.
- The issue is the definition of a passable description of reality: even if our formalized models have outcomes that are clearly not in congruence with what we observe, this tells us that we have not understood what is happening. Hence, in a way the models that do not show what we expect are more enlightening than those that do.
- No, it depends on the scenario that is modelled.
- Models that have nothing to do with reality can be very useful, e.g. sensitivity analyses, scaling arguments.
- Not exactly, gives us something to work toward.
- No because reality is never comprehensible as our ability to describe it is limited.
- Agree completely with this statement.
- Models are important in hypothesis testing. Even simple conceptual models are the basis for formulating or testing hypotheses.
- If the description of reality delivered by the model is truly "not passable" to answer the posed question, this statement might be true; having an insufficient model and applying it knowingly might really be pointless. However, scientists can control the complexity of the model (i.e. making the output passable by adding more processes), but also the complexity of the questions; and simpler questions can be answered with simpler models: With a known growth rate as well as POC and PON quotas, it is possible to make pretty good predictions about the final cell concentration in a cell culture. It is natural, that with increasing complexity and detail, model uncertainties grow. With

respect to digital twins, and possibly resulting simulations, I would say that different questions (ecological succession, vertical export, trophic cascades) certainly require different levels of detail in the model.

- It depends on what we define as a 'passable description of reality'. Ocean physical models don't capture temperature or oxygen in the deep sea correctly, yet are very useful in other depths / regions / questions. It's a question of knowing when the model is close to reality and when it is not and using it within those constraints.
- If the aim of the model is merely to describe reality and it does it very wrong, there is no much use for it. However, many models are intended to understand pieces of reality, interactions and processes. In this cases models may be very useful.
- Models that do not provide a good description of the underlaying data are in my view not very useful. However, it should be kept in mind that a model cannot be expected to describe all parts (diversity, carbon flow etc.) of a plankton community 100% correctly.
- It depends. If it is for exploring possible paths and responses, I found it reasonable. No need to really provide a 100% description of reality. It can stimulate further investigation.

G3. Which plankton types are typically ignored in models, why is that so, and why should they be included?

Response:

- Larger sized phagotrophic protists: NPZ models have historically focused on copepods and other mesozooplankters as the major grazers of phytoplankton production. The 'microbial loop' reviews of Azam et al. (1983) and Ducklow (1983) fostered the concept of phagotrophic protists as consumers of bacterioplankton and small sized phytoplankton, and as nutrient regenerators. However, there is abundant evidence that phagotrophic protists, especially those in the 20-200 micron size class, rival mesozooplankton as herbivores, including as consumers of large and chain-forming diatoms (Sherr & Sherr 2007, Calbet 2008, Löder et al. 2011, Liu et al. 2021). Microzooplankton are also a significant food resource for mesozooplankton. (Calbet 2008, Campbell et al. 2009, Löder et al. 2011).
- Just talking in terms of metazoans here, as far as I can tell they seem to be represented by a generic copepod- type of beast, most likely even a *Calanus*-type copepod (and an adult female one at that) so anything departing from this is under-represented. Examples are micrometazoa, meroplankton, fine filter feeders including appendicularians, salps, some meroplankton, cladocerans, some krill. Obviously carnivores and gelatinous forms as well. A simple reason for their inclusion is the fact that they span multiple trophic levels, as well as having fundamentally different biology.
- RHIZARIA: (including Forams, Acantharea, and Radiolaria are typically ignored, probably because they have complex life cycles and many are mixotrophic during at least part of their life cycle. They should be included in models of open ocean ecosystems because they are important grazers/predators on other protists and on metazooplankton, are relatively large in size, can sink and contribute to organic C flux out of the mixed layer and some have carbonate, silicate, or strontium sulphate test and thus have unique roles in biogeochemical cycles and formation of oozes that cover the deep sea floor (Michaels et al. 1995; Dennett et al. 2002; Caron 2016). CILIATES AND HETEROTROPHIC DINOFLAGELLATES: These microzooplankton are usually lumped but in some environments they have distinc.t roles. For example, large non-thecate dinoflagellates can be important grazers on microplanktonic diatoms and often "mop up" blooms. They can produce fecal material that sink. In contrast, in general ciliates consume pico- and nanoplankton. (Buck & Newton 1995). LARVAL STAGES OF ZOOPLANKTON often contribute as much or more biomass and feeding activity than their adult stages, at least in certain seasons. For example, copepod nauplii can often dominate crustacean zooplankton biomass. Nauplii may be particularly important as prey for first feeding fish larvae Merrell & Stoecker 1998; Turner 2004). GELATINOUS ZOOPLANKTON include a variety of taxa, some, like the salps, and larvaceans. Are important in removing and using pico and small nano-size prey. They produce fecal pellets and larvaceans also discard their old houses, which contribute to marine snow and particle flux. Others, like thecosome pteropods, are important food for fish as well as important to vertical C flux in some regions (Bruland & Silver 1981; Beauchamp et al 2007; Martin et al 2017).

- I most often see bacteria, as a plankton type, excluded in models. Their function is sometimes included but it isn't based upon their biology, rather some math function used to 'close some budget' (e.g., nutrient recycling). I guess they are excluded as data on their physiological function may be limited, but I think they should be in the model, especially as we learn and appreciate more the dissolved organic matter pools.
- Heterotrophic Bacteria and Archaea are often ignored, because they are not phototrophic and hence don't contribute to the main primary production. However, they are the main secondary producer and play important roles in virtually all nutrient cycles.
- Essentially all the types, as currently the amalgamation of groups, especially in the larger ocean/ecosystem models is still far too much of the NPZ type
- Models focus on a subset of organisms, trophic levels or interactions and ignore the rest. Models that focus on phages often ignore carnivores that can generate substantive DOM. There is not one type that is consistently ignored, although the proponents of that type generally claim it is. The focus on subsets of the community is necessitates by the artifice of including many, poorly constrained interactions.
- Viruses, but unfortunately nobody even knows if they increase or decrease efficiency of the biological pump, it probably varies overtime; for instance during blooms vs oligotrophic conditions.
- Intraspecific diversity which often is more important than interspecific diversity. Also, understanding the rise and maintenance of this diversity is important because it underpins speciation and adaptation.
- Mixoplankton in general. Bacterial heterotrophic N-fixers. Because they are quantitative important and changes the way be usually describe plankton functional groups.
- Many models include only one or two plankton types. Bacteria and viruses are typically ignored and we know that they play critical roles in cycling of energy and materials. Virus and bacterial interactions can strongly influence both the formation and termination of blooms.
- Probably those organisms that are the numerical minorities and those entities that are more difficult to observe and classify e.g. viruses. Whether they should be included depends. Low-abundance phytoplankton taxa are low for reasons, i´d suppose, and consequently also contribute less to net Primary production, i.e. less interest for biogeochemistry-focused people. Outstanding ecological properties would certainly justify inclusion (N2 fixation, toxin production, calcification, etc.). For viruses modelling, I have a too little understanding: I imagine that one could implement virus burst-sizes, dilution of virus particles, a threshold-controlled infection of other cells, an incubation time until the cell burst etc. but doing this without further context and knowledge of the virus-host ecology, it might very likely introduce either weird artifacts, or (on the other side of the spectrum) simply increase the mortality rate.
- We don't tend to have sufficient information on different types of zooplankton and have to clump them together into broad functional groups. This means the model misses some of the processes that subsets of plankton types do but not the whole 'model determined type'.
- It largely depends on the model. From viruses to microzooplankton, and obviously mixoplankton are the usual suspects generally ignored in models. Another aspect ALWAYS ignored in models is intraspecific variability.
- In the case of copepods, the early stages.

G4. Which planktonic <u>processes</u> are typically ignored in models, why are they ignored, and why should they be included?

Response:

- Role of temperature in controlling metabolic processes, behavior and distribution of planktonic organisms of all size classes and taxa (e.g. Benedetti et al. 2021). The occurrence of marine heat waves in the world ocean as global warming proceeds will affect both individual species and food webs. Unfortunately, there is sparse information on how temperature affects various classes of plankton in situ. Lab studies have investigated temperature effects on certain species. For example Calbet et al (2022) found that the phagotrophic dinoflagellate Gyrodinium dominans showed similar growth rates at 12 and 18°C, but a marked decrease in growth rates at 25°C. However Lopez-Abbate (2021) concluded from limited data that traits of microzooplankton confer their communities with '…a buffering capacity that helps maintain community connectivity and stabilize marine food webs…' as the ocean warms. Investigations of in situ plankton response to marine heat waves such as those of Suryan et al. (2021) and Arteaga & Rouseseau (2023) have already shown dramatic impacts of high temperatures on community composition and food web response.

- My non-expert impression of models is that variability, flexibility and adaptive capacity of almost every kind is grossly underrepresented in models, which tend to turn into some kind of machine that greatly overplays the role of measurable or fashionable stressors such as OA or temperature in driving change. Variables commonly treated as constants include predator:prey size ratio, assimilation efficiency, selectivity functions, thermal niche. Also more acute responses (e.g. to temperature) often seem to be extrapolated to climate change time and space scales, purposefully ignoring a weight of literature showing the ability for acclimatation of genetic adaptation.
- Death by anything except by predation/grazing is often ignored. Disease and parasitism are important in demise of both protistan and metazoan plankton, probably particularly when populations reach high densities (Park et al 2004; Skovgaard et al. 2012). Succession of phytoplankton/mixoplanktonic flagellates is often ignored. This is probably because they are usually not identified, even to family, in many field studies. However with molecular techniques, it is becoming easier to identify and roughly quantify their populations Flagellates vary in their food quality as well as their light and nutrient requirements. Some, for example cryptophytes are linked to growth of both Mesodinium, and indirectly Dinophysis spp. Phaeocystis appears to play a distinct role in some ecosystems. (Hansen et al. 2013; Fiorendino et al. 2020)
- Heterotrophic Bacteria and Archaea are often ignored, because they are not phototrophic and hence don't contribute to the main primary production. However, they are the main secondary producer and play important roles in virtually all nutrient cycles. Predation processes are mostly ignored. This is potentially the case because they are extremely complex, mostly unknown, and not considered important for the ecosystem, although they are the regulating factors in many ecosystem and therefore an important part of the dynamics. This includes viral lysis.
- Consequences of stoichiometric imbalances of food. They are ignored because partly the definition of the groups of plankton (see above) is far too course, and also because this would create needs for multiple currencies that potentially increase computational demands. Also, (especially in the larger models), the structures are so in place that the models simply will not allow many of these things.
- I think the depth is often ignore, e.g. where in the water column are food or nutrients taken up and where are pellets released, where are the predators, how do organisms migrate/sink/get uplifted through the water column. The vertical dimension separates species and processes and enhances to options for resource acquisition.
- There are no processes that are never considered, maybe expect very rare or infrequent events (e.g. inactive bacteria persisting for years on recalcitrant DOM). But never are all processes considered simultaneously (too complicated).
- Parasitism and grazing, because they effect efficiency of the carbon pump (Guidi et al. 2016).
- Adaptive evolution, effective population size
- **A:** Mixotrohy: feeding in Constitutive mixoplankton, and photosynthesis in Non-constitutive mixoplankton. They are typically ignored because 1) until recently they were not considered quantitative important, 2) most field data on distribution of plankton protists are typically not grouped in this way. **B:** Heterotrophic N-fixation: generally overlooked, but it has been shown to be quantitatively important. **C:** Allelopathy/release of lytic compounds. Overlooked but can be super important when studying HAB high biomass blooms and their dynamics. **D:** Acidification. It is important because it will impact the "scope for growth" of algal blooms.
- Depends on the model of course, but mixotrophy is generally ignored. In many models, "N' is characterized as total N rather than different species of N (NH4, NO3, urea, DON etc). Many models are single currency models. We know that mixotrophy changes the dynamics in multiple ways; it has consequences for grazers and their emergent properties. Changes in stoichiometry has consequences for growth, respiration and food webs. Many models are 1D and do not account for

processes such as vertical migration. Benthic biogeochemical processes are often ignored. If a specific HAB is being modelled, inclusion of toxin production may be warranted.

- Respiration seems to be often ignored, since most models look at biogeo effects. Looking at cell physiology, it would be good to have respiration resolved I think.
- I think the cycling of DOM and linkage to lability, the microbial carbon pump and microbial loop. Also mesopelagic respiration – typically ignored since we have insufficient information to parameterise it explicitly in models. If respiration and the MCP more generally play a tipping point role in ocean carbon storage then we need to know how to model it.
- From my perspective, grazing is usually poorly addressed in models. Generalization usually precludes the inclusion of selection in models, diel rhythms, role of mixotrophy, etc. All this being said, we should keep in mind that we will poorly model something that we do not understand nor have accurate measures of. For instance, if we are unable to obtain good estimates of abundance and biomass of many groups, such as algae and protozoans, how are we even thinking we fully understand the processes they are involved in?
- Acclimation and multigenerational adaptive processes are typically ignored in models.

G5. Complexity in biological models has been shown to drive instability; attempting to build large plankton models thus appears to be a futile task.

Response:

- As I believe one of the main points with models is to separate the important from the less important, I am generally sceptical to complex plankton models. I would rather go for a simple model explaining how the “skeleton” works and then treat the myriad of extra features as variations on this theme when required.
- My non-expert impression of models is that variability, flexibility and adaptive capacity of almost every kind is grossly underrepresented in models, which tend to turn into some kind of machine that greatly overplays the role of measurable or fashionable stressors such as OA or temperature in driving change. Variables commonly treated as constants include predator:prey size ratio, assimilation efficiency, selectivity functions, thermal niche. Also more acute responses (e.g. to temperature) often seem to be extrapolated to climate change time and space scales, purposefully ignoring a weight of literature showing the ability for acclimatation of genetic adaptation.
- Many natural systems appear to be stable due to complexity, feedback mechanisms and overlapping roles; by knowing what are the important feedbacks and “redundancies” perhaps the most important “details” can be incorporated into models and their role in stabilizing ecosystems can be explored. Do not give up!
- If complexity in models drives instability, this should not prevent us from working with complex models. Rather, it should motivate us to investigate whether the model instabilities teach us something about real-world instabilities.
- It is going to be a challenge, no doubt about that.
- No, this would be a very interesting outcome of the models. It means that, since nature is not typically very instable, we have not understood the system as yet.
- I do not see a problem with adding complexity to certain aspects while keeping others simple. It depends on the questions we are studying. So, you can have a large model build off various sub-models and then switch on or off these sub-models depending on the aim of the study.
- I do agree that complexity invites unverifiable responses but a good model can be complex as long as it is focused and has well constrained questions that contrast specific modelling scenarios.
- Not a futile task, but we need better molecular (wet-lab) tools to actually derive plankton interaction networks. Bioinformatic/statistical approaches are extremely limited in this regard.
- We need smart not large plankton models.
- It can be a risk, but that is something we need to work much more on in the future.
- Such a comment is reminiscent of the responses many early plankton ecologists received when they tried modelling. The quantitative approach taken by Victor Hensen (in the late 1880s) was considered “totally repugnant to many German biologists during the late nineteenth century” (Mills 1989, p. 37).

A century later, Gordon Riley found that his papers that had extensive statistical analysis were met with a “dull thud” (Mills 1989, p. 287). Even John Strickland of Scripps Institute of Oceanography complained that “models restate the obvious” and that they are data-poor and premature, to which Riley responded that “models clarify thought, but they should be combined with the detailed study of biological processes to yield the best understanding of the complexity of biological relationships (Mills 1989, p. 305).

- Don´t tend to agree. I think some instability might be realistic?
- If this is true, maybe we should stop doing science, right?
- This is a very difficult balance. A model has to contain sufficient amount of complexity to be realistic, but it also should not be overly complex. The degree of model complexity should therefore be balanced by the type of research questions asked (e.g. models set out to address global climate impacts vs. those describing phytoplankton culture studies).
- Maybe large plankton models are not always necessary to answer your questions.

G6. Problems in the stability of complex biological (plankton) models stem from a failure to adequately describe the details of the organisms (May’s ‘devious strategies’; May RM, 1972. Nature ***238****, 413) that would in nature provide stability (Allesina, S., Tang, S., 2012. Nature* ***483****, 205).*

Response:

- There are many ways to stabilize and destabilize the neutral Lotka-Volterra equations. Efficient recycling is one stabilizing factor. I also think evolution via selection of species and strains with higher fitness has a stabilizing function. This is perhaps in agreement with May’s “details of the organisms?)
- I can see how this can be true – only small differences in interaction parameters of food web models can determine whether dynamics are stable, cyclic, chaotic.
- Without reading the papers, I would agree. Especially for predation processes, but also for nutrient cycling, although there ecofunctions are more important than organisms/ species.
- Maybe, but it sort of contradicts the previous statement that more detail creates instability
- I would agree with this. We have shown that intra-specific variability in physiology, morphology and behavior can impart considerable stability to organism co-existence and biodiversity (e.g. Menden-Deuer et al. 2021).
- We do not need to understand all details, we need to identify the driving mechanisms and build on them.
- Agree very much with this statement
- I would call it models unstable when not every model run yields more or less the same result, but instead results scatter massively, or when sometimes runaway-effects take over and the simulations slides off into nonsense. However, if this happens in e.g. 10 of 100 runs, and in the 90 good runs, meaningful results are obtained, maybe the 10 unstable runs can be tolerated?

G7. Published descriptions of plankton models should always include appropriate graphics (response curves, flow charts etc.) and functional descriptions so that biologists can understand and be better able to question the conceptual basis of the model.

Response:

- Good idea, but these can be included as supplements to the paper, not necessarily in the text.
- I guess so, but I suppose that even relatively simple models would need a lot of functional response curves. Often details of a model are hard to extract from the paper that actually presents the model itself (it may be a tweak of a model published elsewhere, or worse still: an ensemble of models presented in 15 other places).
- Yes, this would help non modellers to understand models and provide constructive comments.
- I agree, seeing flow charts and response surfaces will help point out where the gaps are in our understanding and thus advance our knowledge.
- I agree that graphical illustrations or potentially pseudo-code highlighting the processes that the model represents are very useful and should be strived for.

- YES!
- This would be very useful, the models should definitely be based on biological interactions, which is, however not easy, as there are not many experimentalists measuring stuff that is easily put in a differential equation, which means that in many cases there is a strong disjunction between the equations in the models and the stuff that gets measured.
- Yes.
- There is a misconception that biologists are non-quantitative. I have no idea why that is so persistent. That said, publications that can effectively visualize their results are more impactful.
- Agreed
- Agree very much with this statement
- This depends on the purpose of the model. Data repositories are available for such information.
- I agree very much. Visualizations help a lot.
- That's a great idea – would definitely help move the topic forward and enable more experts to co design the models.
- Indeed, this would be helpful.
- Such information would generally be quite helpful, without such information it is very difficult for a "non specialist" to understand how well the model works and performs.
- Yes, I think it is very important that the non modellers are able to assess what has been done, in which way (important if you want to believe on the outcome) and to appraise the outcomes.

G8. Plankton models used to describe eutrophication events must include explicit descriptions of those types of plankton associated with the events. Thus, for example, confining all phytoplankton to 'diatom' vs 'non-diatom' descriptions is inadequate.

Response:

- I suppose it depends on the focus of the modelling effort. For example, models of nutrient enhanced blooms could bin phytoplankton into diatom and non-diatom, but HAB models would certainly require knowledge of the specific harmful alga that is blooming.
- Not necessarily. If you primarily need the chlorophyll levels you need the edibility and the predator food chains to get the top-down controls right. You get a lot of this with diatoms and non-diatoms.
- It depends on the purpose of the model, but if there is interest in harmful algal blooms, explicit descriptions of different types of phytoplankton/mixoplankton are necessary because they respond differently to nutrient ratios as well as over all nutrient loading and different spp. Have different affects on other plankton and fish. Some primarily affect ecosystem function due to their biomass whereas others due to specific toxins or irritants.
- This depends upon what plankton respond. If one is talking about the spring bloom (light and nutrients) where diverse assemblages of diatoms respond, then it is likely OK, if you are talking about a HAB bloom where the diversity of plankton is narrowed down to a very few species (or just one) then we clearly need the unique biology and trophic interactions with that species.
- It would be good to increase complexity, but this should be independent of eutrophication events.
- Probably, since not all diatoms are equal, and especially in the interactions with other organisms it does not make much sense to group Cosinodiscus and Thallasiosira for example
- Yes, I agree. I would certainly add cyanobacteria as a separate category and include size (e.g. small diatoms, large diatoms)
- Depends on the question. As long as the contrasts between the organisms are large enough the groupings can be coarse. Some models might not need any types at all but contrast r or K specialists, different metabolic pathways or physiological capacities or tolerances.
- Agreed
- Completely agree with this statement
- Depends on the purpose of the model. If it is regionally specific, and the event is cyanobacterial or perhaps a raphidophyte, then diatom vs non diatom may not be adequate. If a specific HAB event is

to be modelled, one approach is to represent the individual HAB species with a detailed model, but to represent other groups by aggregate (e.g., diatom or non-HAB). One approach that has been applied is to examine habitat suitability, rather than predicting biomass or growth rates of specific taxa. Habitat models take the output of other models (and rate processes0 to define a suite of environmental conditions that intersect the growth niche of a particular species…a "window of opportunity". Windows of opportunity for different taxa can be developed.

- Reactions to environmental parameters are often mechanistic, so that more nutrient allows higher phototroph biomass. If that is the question, the model would be adequate. If the question is, who will outnumber the others in a lake, the model certainly needs to depict the most important phytoplankton player, and one needs to know the physiological differences between those when it comes to the state variables modelled.
- More than inadequate is a wrong oversimplification of the problem.

G9. Do we need to explicitly describe allometry? If so, how many groups should there be (can we just get away with 'pico', 'nano', 'micro' etc., or are these already too wide?). And must size range be a defining feature of different functional types? (e.g., can we group all 'diatoms' together, or should they always be subdivided into different size bins?)

Response:

- To minimize confusion and model complexity, the standard pico-, nano-, and micro-plankton categories are sufficiently useful in most cases. Past reports have traditionally binned plankton in these groups, so data about plankton size – e.g. for phytoplankton, or protist zooplankton – available to be used for models will be in these size ranges. There are nano-sized diatoms, but when diatoms dominate the phytoplankton it is generally in blooms of larger sized and chain-forming species. Prey size does make a difference in type of predator, but the pico-, nano-, and micro- size classes should be sufficient for modelling food web interactions.
- Most models have a decreasing nutrient competitivity with size and a shift in dominant predators from flagellates to ciliates to mesozooplankton. This creates the balance between alternative food chains from limiting nutrients to mesozooplankton. Allometry is thus a fundamental structuring property of the food web. But there are small diatoms eaten by ciliates and a complete model would need a mechanism telling when you get small and large diatoms (I don't think the ammonium = small nitrate=large hypothesis works satisfactorily).
- For me, the size structure of the assemblage would be a valuable emergent property of a model to test against a large body of empirical data. This is particularly valuable because some models like ERSEM seem to get "preoccupied" by taxa such as diatoms and size-based simplifications are built on solid principles making no assumption on trophic mode (autotrophs v mixoplankton etc) and not excluding any functional groups. For this reason size is a major consideration.
- The basic size bins are generally good as far as size alone goes, but, depending on the ecosystem and the purpose of the model, the physiological and behavioural properties of organisms are also important.
- Size is a convenient metric when there isn't another specific function that can be used to define plankton (e.g., N2-fixation, calcification, silicification, etc.). Size can play a role in trophic and biogeochemical interactions and thus should be included. How many size groups depends upon the objectives of the model, and how the processes impacted each group are modelled. E.g., it doesn't make sense to me to have 3 size groups that all have nutrient uptake modelled the same way without some modifier based on surface area/volume.
- I think the ecofunction of a group is more important than the size range. What does the organism do and not how large or small is it.
- I think we need as many traits as there are that affect interactions within the food chain, and with the abiotic world.
- Definitively have pico, nano and micro size classes. Size is key to nutrient and light uptake, predator-prey relationships, sinking rates, degradation processes etc.

- These size groupings are attainable rapidly through automated measurements and even remote sensing. Thus they are useful. Yet the considerable within species and even strain variability for single plankton types makes it clear that size is insufficient to distinguish e.g. see the work on *Procholococcus*. Or our work on *Heterosigma* (e.g. Harvey et al. 2015).
- The question is how important is size, morphology etc. and how is it evolving?
- Yes, allometry should be included. No, we cannot get away with these rather large groupings when we deal with allometry (see Maranon et al 2013) . Also diatoms should be split into different size groups.
- Size influences growth, photosynthesis, nutrient uptake and sinking rates, as well as grazing, excretion and reproduction. These processes have profound implications for biogeochemical cycling, biodiversity, food web structure etc. Both cell volume and surface are have long been considered major factors in nutrient uptake rates, transformations and allocation of energy and materials. Small cells have higher S/V but being too small places constraints on other aspects of metabolism. Cell size is related to diversity and biogeography. As Penny Chisholm once wrote, “Phytoplankton ecologists fall out in two groups: Those who delight in finding patterns in nature that can be explained by size, and those who delight in finding exceptions to the established size-dependent rules…The simplicity of the general relationships serves as a stable backdrop against which the exceptions can shine. By understanding the forces that have driven these exceptions, we can begin to understand the ecology that has shaped past and present ecosystems.” (Chisholm 1992).
- It depends on the goal of the exercise and what degree of uncertainty we are willing to accept. For example, across eight orders of magnitude the conventional allometric scaling applies to feeding-related parameters, but there are significant differences among individual groups up to a factor of 10 (Hansen et al. 1997). But more recent work sees an allometric converge of ingestion and growth across 15 orders of magnitude in heterotrophic marine organisms (Kiørboe and Hirsch 2014), but not in respiration rates.
- This would depend on the question to be answered. Our {most recent work} shows that environmental parameters, e.g. temperature, differentially affect the processes of biomass production and cell division, so that with e.g. stable net POC production, but increased division rates, cell size and quotas decrease. Since cell size is an important property when it comes to grazing and associated selection pressures, this might be very important when ecological questions are to be answered.
- I think that allometry has to be included. And not only size, but carbon or nitrogen content. Organism with the same size can have quite different elemental content.

G10. Is a model of plankton seasonality that ignores the role of resting stages and other life-cycle processes too far removed from reality to be useful?

Response:

- Yes, especially as it is essential for the population dynamics of some plankton.
- It depends on the question of the model. I think resting stages can be ignored for the most part until they become the seed bank for e.g. a new bloom. Then they need to be in the model.
- No of course not, if the starting conditions of the model are ok, it does not matter much where the organisms come from.
- Depends on the location. In shelf regions or sea ice habitats, resting stages of algae should be included, but in mid-ocean other things might be more important.
- Depends on if the cysts etc are important factors in the population cycle. E.g. some dinoflagellate cysts have reintroduced species to areas in Puget Sound they had not been seen in 3 decades. If the spores/cysts. Are just removed and sedentary then the model should be fine. No model can do everything.
- Yes, of course. Most plankton do not have resting stages or life-cycles. Cyanobacteria, small phytoplankton. How often in the ocean are phytoplankton, bacteria, types completely absent? Maybe there are regions which need to consider it for example shallow waters or polar regions.

- Life cycle stages need to be taken into account as they underpin the biology and physiology of plankton.
- Especially in shallow coastal waters, I believe resting stages and other life-cycle groupings should be taken into account.
- Depends on the purpose of the model.
- Ì´d say no. True, these resting stages carry over the new starting populations for the next year, but if looking at the seasonal succession in only one year, I feel it should be possible. Even if multiple years are looked at, then it should be mathematically feasible to implement a diversity carryover between years.
- Many times, I have seen presentations on seasonal plankton models completely far from actual data and surprisingly this fact seemed not to concern the modeller. Obviously, for organisms largely relying on resting stages these should be modelled as well.
- It depends on your question.

G11. Refuges (resting stages, diapause, etc.) are important features of reality missing from plankton models that greatly damage the utility of those models.

Response:

- I believe the copepod diapause is the clue to understanding how the Arctic microbial ecosystem is top-down controlled. Can be simple modelled with copepod stock as a driving function with a 1-year periodicity. The role of bottom vegetation as a physical refuge for dladocerans is a well-documented key element in shallow lake ecology.
- I don't know if their omission 'greatly' damages the models, but it does create 'reset' problems when modelling seasonality in multi-year runs.
- It depends on the question of the model. I think resting stages can be ignored for the most part until they become the seed bank for e.g. a new bloom. Then they need to be in the model.
- No, I do not think that this can be stated like this. There might be species where this is very important, for many it will not.
- It depends, if it is about carbon flux or life cycle models then diapause is important, likewise if in polar regions. However, if it is a model on the autumn bloom then possibly less important.
- Too harsh an assessment that they damage the model. If the resting stages are not part of the question (e.g. nutrient utilization) then the model is fine.
- In the open ocean is this important at all? This seems like a really coastal issue?
- Agreed
- I agree with this statement
- Depends on the purpose of the model.
- That might be. But i´d formulate this positively and say that scientists know that the model have weaknesses depicting behaviour and its ecological and biogeochemical consequences. On the other side, these things have been investigated for decades, it should be possible the implement the expert opinion on how diapause works into such models?
- This seems correct for a bunch of organisms. For instance, you cannot properly model HABs without knowledge on their resting stages.
- Not necessarily. It depends on the kind of question you address.

G12. Climatology-links to species succession are important features of reality typically missing from plankton models.

Response:

- Given climate change, climatological links are particularly important to include in models, because different populations respond differently to combinations of daylength, daily PAR, water temperature etc. Changes in timing of population growth, reproduction or migration can either couple or uncouple interacting populations. Cushing's match vs. mismatch hypothesis is important to more than fisheries.

- Agree.
- Again, no model can do it all. Decadal trends are probably best assessed with longterm time series and for plankton that means focusing on a few crustacean species or Chl a or dominant diatoms, dinoflagellates.
- Agreed
- Agree
- Depends on the purpose of the model. Many models are now including climate forcings. From changes in temperature to CO2 and pH, as well as changes in physical structure (stratification) and frequency of extreme evens (hurricanes, droughts etc), there is considerable effort to now understand these factors and effects on planktonic systems.
- I do not know whether this is the case but i´d assume that climate as a driver would be very much desired in models

G13. In a model with only one 'Z' box, we should parameterise that group more in line with the activities of metazoan zooplankton than with protistan zooplankton because only the activity of the former contributes to the sinking of biomass.

Response:

- Three considerations here: 1) Mesozooplankton fecal pellets contribute a variable but often low proportion of total organic carbon sinking flux (e.g. Gonzalez et al. 2000, Wang et al. 2023). 2) Phagotrophic dinoflagellates consuming diatoms produce mini fecal pellets enriched in Si from egested diatom frustules (e.g. Buck et al. 2005, Saito et al 2006), which could slowly sink or be incorporated into sinking particles. 3) Larger sized phagotrophic protists are both major consumers of phytoplankton and are important food resources for mesozooplankton (Calbet & Saiz 2005, Calbet 2008, Löder et al. 2011), which would require at least two Z compartments.
- Most of the grazing of phytoplankton/mixoplankton biomass is due to protistan grazers, not metazoa. Protists are responsible for most to nutrient regeneration that keeps the systems going. Rhizaria, particularly radiolaria and formaninifera, contribute to sinking of biomass. Large dinoflagellates can produce sinking fecal pellets. There are many reasons that protist mixo- and zoo-plankton should not be ignored. Probably the oceans would function well biogeochemically without metazoa, the same cannot be said for lack of procaryotes and protists.
- That depends what one wants to do with the model: if the aim is to investigate the biological pump, maybe, if the aim is to understand what is happening in the plankton absolutely not.
- Disagree. Protistan zooplankton can modify sinking rates. One 'z' box is not acceptable.
- Protists contribute to export production in many ways, from fecal pellet production (Buck & Newton L&O 1995), to feeding on marine snow (Kiørboe 2001, and others), to alerting to community composition, size distribution and abundance of the surface plankton community. Knowledge of protist feeding can also constrain export pathways (McNair et al. 2021).
- One Z-box is not enough! Feeding and growth is very different in the two groups! Protistan grazers also contribute significantly to the pool of sinking material.
- No, even if this model is strictly focused on questions narrowly relevant to the biological pump. The Fasham et al. NPZ model served its function 40 years ago. We know better now about the difference between meso (metazoan) and microzooplankton (protozoan) to do better in our models.
- My gut feeling says zooplankton. The sinking fecal pellet argument is a good one. Maybe also because the activities of protists are functionally very similar to those of bacteria in models (POM⍰DIC, and associated processes).
- Not sure – would be interesting to know how wrong the remineralisation term would then be without the contribution of protistan zooplankton.
- I disagree. µZ is crucial to understand the carbon cycle, including sinking.

G14. Appropriate descriptions of prey selection and differences in dietary value are essential for any plausible description of consumer activity and thence for all ecological (trophic) models. Assuming a fixed AE, and selectivity according to a simple fixed equation is not consistent with reality.

Response:

- Depends on the purpose of the model. You can get a lot of reasonable population dynamics out of fixed stoichiometry models, but you can not represent phenomena such as the rapid response in copepod egg production following phosphate addition to Mediterranean waters. For this you need the rapid change in prey stoichiometry.
- Agree, I had understood that AE is a variable just like most other, varying with feeding rate, according to the concept of superfluous feeding. Seems weird that as humans we are preoccupied with food: dietary value, feeding history, feeding selectivity are so talked about by us humans but we treat zooplankton like machines.
- Yes, here some complexity is needed to include all different processes.
- Correct, but again depending on what one wants to do with the model. However, for a proper description of flows of energy and nutrients through the food web, this is essential.
- I agree that for trophic models group-specific differences in dietary value, selectivity and AE need to be included if we are looking at growth rates or egg production etc.
- OK, I guess I have answered a variation of this type of question: there is one size approach that if it is not used the outcome is garbage and to me, those arguments can be easily refuted by carefully formulating the question.
- I guess so
- Agree completely with this statement
- The major freshwater (cladocerans) and oceanic (copepod) metazoan grazers tend to be generalist/opportunistic feeders which show little selectivity (cladocerans) or perform prey switching (select for the most abundant prey). Thus, while size selectivity is indeed an important behavior, I question whether every kind of selectivity must be accounted for in a model. Gross-growth efficiencies do not show strong differences between protozoan and metazoan zooplankton (Straile, 1997).
- It is true that the extreme case described in the question is likely inconsistent with reality. But there are valuable models that visualize and help to understand and predict predator-prey interactions. I know that especially the Dutch have a rigid monitoring and management system of their watersheds and they rely on models made by scientists, and the models do a comparably good job. Management is better than without.
- The truth is that I do not think we have enough data to answer this question. However, I am inclined to think selectivity is far more complex than we think.
- True. It is very important. But it is difficult to obtain reliable estimates of AE for most organisms.

G15. Osmotrophy (the use of organic nutrients) is not typically worth describing given the challenges in describing different DOM fractions. The same applies to auxotrophy (use of vitamins).

Response:

- Marine bacteria grow by uptake of organic nutrients such as simple carbohydrates, amino acids, fatty acids, etc., either by direct assimilation from dissolved labile DOM or by enzymatic breakdown of complex organic compounds. This is an important pathway of organic C, N, and trace minerals in food webs. Direct assimilation of organic compounds by phytoplankton, e.g. mixotrophic flagellates, is not nearly as significant as secondary acquisition of organic nutrients via ingestion of bacteria.
- Its omission is a greater detriment than misparameterizing it because of a lack of chemical knowledge.
- It might be too much to describe this in detail, but at least on the bacterial level, some complexity should be added by using different bacterial phyla/ groups and their DOM preferences.
- Leave it out if it is too difficult? We did not get to the moon with that attitude. Of course it is challenging, but since we simplify organisms we may also simplify DOC sources.

- Osmotrophy should be included in plankton models. If it is difficult to describe then lab experiments with specific settings might help to gain a better understanding.
- I'd think we have better methods of characterizing and tracing DOM type and flux.
- Wrong. There are many osmotrophic plankton species and most phytoplankton are mixotrophic anyway.
- I disagree. It is right the DOC as such not to large extent contribute to the carbon metabolism. BUT, the DOM pool may contribute vitamins and micronutrients to the primary producers.
- Depends on the purpose of the model- and on availability of data. Sources of organic nutrients are changing on many systems, from inputs of organic fertilizers to releases from increasing aquaculture systems, to inundation from sea level rise and losses of coastal wetlands and mangroves. Humic acids have been shown to be bioavailable and to also impact cycling of NH4. Brownification of freshwaters acts synergistically with temperatures and have been shown to enhance cyanobacterial blooms and their toxins. The challenge, of course, is having adequate data for the region of interest, and far fewer data are available for different DOM fractions and for vitamins.
- I disagree. It is likely an important mechanism to assure survical under nutrient starvation. Mechanistically this might be simple to implement, since it likely an ability of most phytoplankton cells, and i´d suppose cells engage it when external concentrations run under certain threholds. In high recycling-systems this might be an important aspect to investigate.
- I disagree, given the importance of the microbial carbon pump.
- That something is challenging does not mean it is not worth considering.
- Generally, I disagree but this will depend on the purpose of the model. Organic nutrients are important in sustaining planktonic activity, however if the model deals with topics such as zooplankton growth including a detailed description of osmotrophy is likely not important.

G16. DOM must be described in plankton models because the availability of nutrients via this route (either directly via mixotrophy, or indirectly via bacteria and bactivory) can be as important for trophic dynamics as is the availability of inorganic nutrients.

Response:

- This is a bit confusing. The major categories of marine DOM are small molecular weight molecules such as amino acids and urea, and high molecular weight compounds such as exopolymers or fragments of cell debris. Small molecular weight N-containing DOM (DON) is typically recycled quickly in the microbial loop to ammonium, so available as DIN. High molecular weight DON is decomposed to ammonium more slowly. Organic P is recycled in the food web as phosphate, so there is no major P-containing DOM component. The bacteria-bacterivory route is a well-described microbial loop regeneration pathway. Of course the regenerative pathway for N and P nutrients is the most important for availability of inorganic nutrients in food webs under oligotrophic conditions. Or does the 'availability of inorganic nutrients' in the question only refer to outside inputs via upwelling, deep water mixing, or other physical processes? Also, is 'mixotrophy' here meant only as osmotrophy – the direct uptake of labile DIN? Mixotrophy also includes bacterivory by phytoflagellates (Stoecker et al. 2017).
- The microbial-loop food chain and the species change in the prokaryote community from SAR11 to Vibrios (and other usually rare taxa) are totally dependent upon the supply of DOM. This will influence the phytoplankton-bacteria competition for limiting nutrients and change the defensive properties of the prokaryote community. If these features are of interest, some kind of DOM production and consumption must be included.
- I agree with the statement, and its important to understand turnover of the DOM pool so that nutrients (ie., C) doesn't 'accumulate' there leading to incorrect assumptions about carbon storage in the ocean.
- Yes!
- Yes, it is an important pathway,
- Agreed

- Agree, need to know when it is highly available vs not. Perhaps two boxes for DOM, labile and refractory.
- Yes
- Yes, DOM most be included in plankton models for reasons listed above and because the labile and semi-labile DOM can be utilized by bacteria and channelled up the food web. Also, heterotrophic N-fixers are dependent on the DOM pool (labile and semilabile pools).
- Depends on the purpose of the model.
- I´d say yes. DOM can be a product and a substrate of/for phytoplankton and bacteria and thus likely plays interesting roles, e.g. as a cryptic nutrient buffer.
- Perhaps not at the same level than inorganic nutrients, but very important indeed.
- I agree that this is important to include. Especially in many oligotrophic systems organic nutrients play a larger role in fuelling plankton productivity than inorganic nutrients.

G17. Describing different forms of DOM occupies too much computational effort; can we get away with just having 1 or 2 'DOM' groups? If so, what would they describe?

Response:

- The traditional DOM categories of small molecular weight, fast turnover DOM and high molecular weight, slower turnover DOM should be sufficient for modelling.
- As always: depends on the purpose of the model. If it is sufficient to divide the prokaryote community into SAR11 and "others" it may be sufficient with one DOM pool. If your interest is when the "other" is Polaribacter you will need to specify a glucan pool. If you are interested in different strains of Polaribacter you will need to know which glucans.
- I think that you could get away with 2 pools, perhaps a refractory and non-refractory description. It would be a useful first step.
- Maybe not 1 or 2, but rather some 2-3 more. I would use complex carbohydrates, long chain carbohydrates, short chain carbohydrates, fatty acids, and "other" DOM.
- Of course we can, just like we have 1 or 2 Z groups, so of course we cannot, just that 1-2 Z- groups is not enough
- DON and DOP
- Perhaps OK!
- The different pools of DOM has to be dealt with. A large fraction of DOM is refractory and as such not important for plankton models!
- Depends on the purpose of the model. In an agriculturally impacted region, urea may be important to include. In a coastal wetland, humic acids may be more important.
- One idea would be do depict DOC, and use C:N:P stoichiometry of DOM to calculate DOP and DON. This would however only work for unprocessed fresh DOC. If cells scavenge N and P this will change cause deviation ind DOC:DON:DOP which are difficult to predict. If I had to drop one, i´d drop DOP, since my gut feeling says that exudation of DOP is likely less common and less intense that of DON: Many exudates are polyglucans, that are quite often aminated but much more seldomly phosphorylated. P is too precious i´d think.
- With the present knowledge on DOM dynamics, I think having 2 DOM groups is possibly enough.
- This will strongly depend on the time scales considered. If the model is setup to describe processes over shorter time scales (days to weeks) 1 or 2 DOM pools should be sufficient, however if longer timescales (months to years) are considered additional DOM pools need to be included.

G18. Allelopathy is not typically worth considering as we lack sufficient data to support the modelling.

Response:

- It is worth considering, but we probably cannot, as we do not have enough information to quantify any relationship.
- I don't know much about the effects in planktonic realms. I could see this being important for predator-prey interactions in the sense of repellents or toxins produced as grazing defence. But I

honestly don't see how this could be modelled, because it is extremely complex and barely anything is known.

- I think the focus of this question concerns competition among phytoplankton species. As LeGrand et al. (2003) stated in their review: 'Allelopathy, as defined here, applies only to the inhibitory effects of secondary metabolites produced by one species on the growth or physiological function of another phytoplankton species.' Apparently some research does support the contention that allelopathy reduces competition and allows for greater diversity of phytoplankton species (e.g. Graneli & Hanson 2006, Felpeto et al. 2018). However, these interactions are complicated. Prince et al. (2008) found that the common diatom: '… S. costatum reduced the growth-inhibiting effects of bloom exudates, suggesting that S. costatum has a mechanism for undermining K. brevis allelopathy.' Poulson-Ellestad et al. (2014) reported that: '… co-occurring species may have evolved partial resistance to allelopathy via robust metabolic pathways. In contrast, a "naïve" competitor, T. pseudonana, which does not co-occur with K. brevis blooms, suffered greater metabolic disruption and growth suppression when exposed to K. brevis allelopathy,' Apostolopoulou et al. (2022) concluded that '…species show a range of responses with the most common being biomass suppression, and less frequent biomass enhancement and intracellular P storage. Filtrate from the green microalgae Tetraselmis caused the most pronounced negative effects suggesting that non-HAB species can also cause negative chemical interference.' It does seem that too little is known about allelopathy among phytoplankton to be able to successfully incorporate these interactions into models.
- Wrong
- Disagree very much with this statement. There are increasing amount of useable data on this. And more will come in the future!
- Depends on the purpose of the model. Our knowledge of allelopathy is increasing at a rapid pace.
- Our new paper reiterates that the ratio of POC production to cell division decides about POC quota and thus, we might have a handle to model size in response to environment.
- Again, not having data about a process does not mean we should ignore it, but the opposite.
- Agree

G19. Allelopathy provides a major stabilising mechanism in nature that is missing from models. It is one of the key factors that prevent combinations of models of individual phytoplankton from describing events seen in mixed-species cultures.

Response:

- Allelopathy is important in planktonic ecosystems, but many allelopathic interactions are poorly described and often appear to be species, strain, and growth state specific for both producer and target organisms. Thus allelopathy is difficult to currently include in models of natural ecosystems. Modelling could be useful in understanding and quantifying allelopathy in mixed spp. Cultures and mesocosms, hopefully this would at some point be included in models of natural systems.
- I don't know much about the cross talk between larger plankton species. There will be some, I am sure. But is it possible to model it? I doubt it. It might make sense to look into the main bloom forming organisms and their chemical cues, but if it comes to bacteria, who communicate nearly exclusively chemically, this would very quickly get out of hands.
- With respect to the idea of allelopathy as a stabilizing mechanism in pelagic food webs, a broader interpretation of how allopathic interactions might affect phytoplankton species diversity in situ is grazer deterrence. Chemicals produced by certain phytoplankton species may inhibit grazing, thus giving those species a competitive advantage. One example is the osmolyte DMSP released by the coccolithophore Emiliania huxleyi when it is grazed. In laboratory experiments DMSP has been shown to be a deterrent to protist predators, though such effects have been equivocal in field studies (Fredrickson & Strom 2009). Toxic metabolites produced by harmful algal bloom (HAB) species can affect predation in marine food webs (Mitra & Flynn 2006, Graham & Strom 2010). In the latter study, phagotrophic ciliates and dinoflagellates preferred non-toxic prey to the HAB species Heterosigma

akashiwo in the laboratory, but in the field: 'Bloom-concentrations of H. akashiwo were harmful to the smallest grazers and beneficial to larger Gyrodinium/Gymnodinium dinoflagellates that were able to ingest and grow on the alga.' Jeong et al. (2005) reported significant grazing by a thecate dinoflaellate on H. akashiwo. Davis et al (2011) found that: '…natural mesozooplankton were better grazers of both toxic and non-toxic strains of Microcystis than their cultured counterparts.' There might be enough information for harmful algal bloom models to account for predation deterrence by toxic metabolites, with caveats that predatory protists are able to graze HAB algae, and laboratory results may not accurately depict in situ grazer behavior.

- Agreed
- I agree very much with this statement.
- Agree

G20. 'Lipid' is a vital additional state variable to add to the usual C,N,P etc. state variable list for many organisms.

Response:

- In P-limited systems, the ability to exchange phospholipids with sulpholipids is interesting and important for the fitness. May be important to understand population shifts in stoichiometry in systems with border in time and/or space between N and P limitation.
- I would agree for certain regional models. In the Arctic where 'lipids' are the currency shuttled between phytoplankton and copepods it makes sense, the oligotrophic ocean, much less so.
- Maybe not 1 or 2, but rather some 2-3 more. I would use complex carbohydrates, long chain carbohydrates, short chain carbohydrates, fatty acids, and "other" DOM. Not only lipid, but splitting carbon sources a bit more than just "C" is valuable.
- I am not sure, C will probably do a pretty ok job as a proxy for lipid, most likely there are other markers that are more important (single FAs, sterols etc)
- I agree for polar regions, not sure about L4.
- Not sure.
- Agree. Especially in Arctic food webs, where large lipid rich Calanus are on the decline.
- Not sure this is vital. Put another way, if someone asked if protein should be a vital component, I would answer that the protein/N ratio is fairly constant. I imagine it is the same for lipids?
- I think it might be, especially in cases where the lipid content of cells directly influences SVs in grazers.
- Lipids are clearly important, but as cells contain many other important compounds (proteins, carbohydrates etc.) these other compounds also should be included with sufficient detail.
- Yes.

G21. Relying on bulk chlorophyll concentrations (especially from remote sensing and in vivo fluorescence) does not provide a robust estimate of phytoplankton biomass useful for model calibration and validation.

Response:

- A longstanding issue is the relative value of high-resolution remote sensing data versus low-resolution field collected data. High-resolution data supply a valuable overview of large-scale spatial and temporal variability, while low-resolution field collected data is higher quality. The optimum is to use field data to validate high-resolution data, and then high-resolution data may more confidently be used in modelling. For example remote sensing of chlorophyll shows high-resolution patterns of phytoplankton biomass, and can be complemented by field studies in the same regions of the ocean that collect data using pigment extraction and fluorometry of size fractions of phytoplankton and visualization of phytoplankton taxa.
- If you need a correct Chl:C:nutrient coupling for the deep chl maximum you need the light dependence of the Chl:C ratio.

- Of course it is not robust but in a recent meta-analysis I am doing surface Chl a ranges 600-fold so in this context sateliette derivable values are probably reasonable to a first approximation. So this question depends on the purpose of the exercise.
- It is an estimate with large caveats associated with photoacclimation, nutrient stress, etc. It is important to have those qualifiers in the model. Relying on bulk chla without them is dubious.
- No it does not, but it is the best we have, so unless we increase our observational power enormously, this is what we have to use
- I think chlorophyll is fine when looking at (large,) ocean scale differences
- It is of limited utility but having global coverage with high uncertainty is extremely useful. Some as many questions above" don't throw out the baby with the bathwater.
- At least we need to know which phytoplankton classes are present. Better if taxonomy can be described as even within diatoms some of course are exported efficiency and others not, and they can dominate different times of year.
- Depends
- Agree!
- Depends on the model. No metric is perfect. Bulk Chl certainly informs us when a bloom occurs. Cell numbers are often not available, or not available for the entire community (i.e., one species may be counted). It is a useful starting point and if the model does not fit the data, then ask why.
- Maybe we should be careful with the exact numbers, and also should obtain more information about nutrient status,- since Chl:POC changes with this status, but patterns seen with satellites should be obtainable with models as well.
- True. Because its simplicity we rely a lot in Chl, although we all know it is not an accurate proxy for phytoplankton biomass.
- For "field studies" I generally agree, as there are very large variations over time and space. Using only one data source is also problematic and studies should consider using multiple data sources (e.g. combine bottle data + remote sensing data).
- Yes. Chlorophyll content can be very variable and it is a rough estimator of biomass. Moreover, surface chl values from remote sensing may not represent the actual phytoplankton environment experience by zooplankton as does not take into account the vertical structure.

G22. The use of a fixed conversion ratio of prey biomass to predator biomass for all prey types (e.g., 10% transfer efficiency), across all quantities and different stoichiometric qualities, provides a pragmatic acceptable basis for descriptions of planktonic consumer activity.

Response:

- Is transfer efficiency the same as Gross Growth Efficiency (GGE)? GGE is typically higher than 10% for protist predators. Straile (1997) reviewed published GGE of metazoan and protist zooplankton and reported: 'All taxa (i.e. nano/microflagellates, dinoflagellates, ciliates, rotifers, cladocerans, and copepods) were found to have mean and median GGE of ∼20–30%.' Rose et al. (2009) reported that a heterotrophic nanoflagellate cultured from Antarctic waters had a GGE of about 40%. 10% GGE for all predators is not justified.
- Patently false assumption. For a start 10% is likely too high for many plausible predator: prey mass ratios (PPMRs – see Atkinson et al L and O (2021) and also importantly PPMR tends to increase with organism size in the pelagic, from picoplankton up to fish, and this is widely reported from a whole range of studies. Based on linear normalised biomass size spectra (also reported from a wide range of studies) this can only mean that TTE is not a constant.
- 10% TE does not really apply planktonic ecosystems, at least not to protists. Many protistan zooplankton have growth efficiencies ~30%. NCMs often have much higher growth efficiencies than 30% for ingested C, particularly under food limitation (Ohman & Snyder 1991; Maselli et al. 2020).
- I think the body of knowledge is getting to the point where we don't have to assume a fixed number any longer, or at least can put better bounds on its variability between regions, seasons and over time.

- I would try to add complexity, as different predation systems, strategies, state of the predators etc. will change the outcome of predation and the stoichiometry.
- I would keep that variable and see what happens. Apparently, in the SO, the predator biomass (zooplankton) often exceeds their prey biomass (algae) – possibly due to diapause and long starvation periods.
- It's demonstrably wrong but might be good to show what if scenarios.
- Gross growth efficiency is more in the range of 30%, but it can actually vary depending on nutrient status of the system. So, it will be a very rough conversion.
- Depends on the model. It is a useful starting point and if the model does not fit the data, then ask why.
- I think it makes sense to assume an average that has been measured in many grazers. But if better data for the different grazers is available, it should be implemented.
- This is a oversimplification of nature, aggravated by the fact that we usually ignore who are the actual predators and how many trophic levels are in between two groups.

G23. Allometric-rule models, assuming a set prey:predator size ratio (e.g., 1:10), provide a good starting assumption for constructing plankton models.

Response:

- Probably not. Many reports have shown a large and variable prey:predator size ratio for various predators. For example, Taniguchi et al. (2023) examined prey size selection by marine herbivorous protists and concluded: 'When all consumer sizes were present, distinct dietary niches emerged, with a range of consumer-prey size ratios spanning from 25:1 to 0.4:1, encompassing the canonical 10:1 often assumed.' In terms of predators of bloom-forming diatoms, *Gyrodinium* and *Protodinium* spp. Dinoflagellates, as well as some ciliates, can prey on both large sized diatom cells and fairly long diatom chains (Strom et al. 2001, Sherr & Sherr 2007, Calbet 2008, Sherr et al. 2013), with a prey:predator ratio of > 1:1.

Two views of the same heterotrophic dinoflagellate, Gyrodinium sp., greatly distorted with an ingested diatom chain, collected in Bering Sea in April 2008. The normal size of the dinoflagellate is about 60 um long. [© EBS]

- Patently false assumption. For a start 10% is likely too high for many plausible predator: prey mass ratios (PPMRs – see Atkinson et al L and O (2021) and also importantly PPMR tends to increase with organism size in the pelagic, from picoplankton up to fish, and this is widely reported from a whole range of studies. Based on linear normalised biomass size spectra (also reported from a wide range of studies) this can only mean that TTE is not a constant.
- Prey:predator ratios vary widely in the plankton (Hansen et al. 1994). For example, gelatinous zooplankton can be important in demise of plankton blooms, size ratio can be near 1:100+. Heterotrophic Dinoflagellates are important grazers on diatoms etc and can have 1:1 ratio.

- Probably not very good when you get to the smaller protozoa. (fundamentally wrong of course if you include viruses among predators).
- It could work for the bacterial and archaeal world.
- Yes, they do, especially as it will show us that it is wrong
- In krill the ratio can be 1:30000, which makes the trophic transfer very efficient. I don't like fixed ratios.
- It's demonstrably wrong (e.g. Hansen et al. 1994) but worthwhile to examine how important the exceptions are.
- I disagree strongly! Different types of grazers have very different prey:predator size ratio?, 1:1 het dinoflagellates, 1:8 ciliates; 1:30 Copepods, 1:80 for Cladocerans, meroplankton larvae and rotifers
- Size influences growth, photosynthesis, nutrient uptake and sinking rates, as well as grazing, excretion and reproduction. These processes have profound implications for biogeochemical cycling, biodiversity, food web structure etc. Both cell volume and surface are have long been considered major factors in nutrient uptake rates, transformations and allocation of energy and materials. Small cells have higher S/V but being too small places constraints on other aspects of metabolism. Cell size is related to diversity and biogeography. As Penny Chisholm once wrote, "Phytoplankton ecologists fall out in two groups: Those who delight in finding patterns in nature that can be explained by size, and those who delight in finding exceptions to the established size-dependent rules…The simplicity of the general relationships serves as a stable backdrop against which the exceptions can shine. By understanding the forces that have driven these exceptions, we can begin to understand the ecology that has shaped past and present ecosystems." (Chisholm 1992).
- Not a terrible assumption (Bergreen et al. 1988): "Optimum, relative particle sizes corresponded to 2 to 5% of prosome length independent of developmental stage. Since the biomass of particulate matter is approximately constant in equal logarithmic size classes in the sea, food availability may be similar for all developmental stages in the average marine environment."
- Perhaps for copepods (and I have serious doubts), but they not work for protozoans.

*G24. Temperature-growth rate relationships developed from the Eppley phytoplankton-temperature growth curve (Eppley RW, 1972. Fish. Bull, **70**; 1063) give a good starting assumption for plankton models that consider changes in temperature with climate change.*

Response:

- The Eppley curve (if I remember correctly) concerns maximum growth rates. In nutrient limited systems the important parameter is the affinity which is defined by diffusion transport. This should theoretically have a temperature dependence as the viscosity of water (Q10 around 1.3).
- Only if there are practical thresholds on the temperature response. With temperature increases phytoplankton groups are replaced by others and it isn't appropriate to assume the physiology of the warmer species is the same as that of the colder species.
- Effects of temperature on growth and other plankton processes need to be updated. There has been much subsequent data reported for various types of plankton that show variability in temperature – growth relations. In addition, growth of plankton in situ can show different response to temperature compared to growth in lab experiments. A case in point is results from dilution experiments in the Bering Sea at temperatures of < 4oC, where growth rates of herbivorous microzooplankton were greater than growth rates of bloom-forming diatoms (Sherr et al 2013), refuting the theory, based on data from lab studies, of Rose and Caron (2007) that cold sea water temperatures at high latitudes let diatom blooms escape grazing by microzooplankton. This is supported by the results of Franze & Menden-Deuer (2020), who concluded: '…the predicted decline in growth at lower temperatures, suggested as one of the mechanisms that allows phytoplankton blooms at high latitudes, is not reflected either in the laboratory observations contributed here, nor in prior in situ observations of herbivorous protists growing at their maximum rates at temperatures below 5°C…'

- I wish there was more movement in this regard. Eppley is the upper envelope of the rates (as he himself identified) and has led to over estimates. For phytoplankton (see Anderson et al. 2022) and heterotrophic protists (Franze & Menden-Deuer 2020). Eppley Is a vast overestimate.
- I guess so.
- To some extent. However, the Q_{10} only works for a certain range of temperature (at low and high temperatures this is different. It will differ in organisms isolated from Arctic, temperate, and tropical waters. Thus, Arctic phytoplankton species do better at low temperatures, while tropical species can tolerate much higher temperatures before growth levels off or even decline. So, some differentiation is required.
- Even Eppley noted that temperature-response curves can be altered by ambient conditions, such as salinity, and more recent studies have examined interactive effects of temperature and light availability and nutrient status. The interactive effects are not simple. Yes, Eppley's relationships provide a good starting point. It is a useful starting point and if the model does not fit the data, then ask why. Siegel et al. (2023) found that N limitation reduces the magnitude of thermal variability over which stable species coexistence occurs and impacts the ability of the less competitive species to recover; thus, community composition may change in unpredictable ways as different abiotic variables fluctuate in conjunction with changes in temperature.
- Using this relationship provides an estimate (rather than a good estimate) of the plastic response of maximum phytoplankton growth rate vs temperature. Using this or any other such relationship ignoring the potential for temperature adaptation is a major limitation (Barton et al. 2019). Also, there have been advances in modelling phytoplankton thermal performance curves since then (Barton et al. 2019).
- I think there are many nicer equations out there, that often fit the data better; have a more convenient math (crossing the X axis vs. not crossing), and have parameters that have a meaning in real life. etc. But yeah, for a start, one can start with this.
- We noticed in our past and present projects that the effects of temperature cannot be addressed as we have been doing it. Plankton adapts to the changes in temperature, within reasonable ranges and as long as enough time is provided. Then, we end up having Q10 values of 1 for many physiological rates after proper acclimation (or adaptation).
- Generally, yes. However, these relationships are not "fixed features" as they depend on e.g. resource availability and the organism levels (e.g. bacteria, phytoplankton) considered.

G25. It is more important to get the timing of bloom events correct than to get the magnitude correct.

Response:

- Depends on the purpose of the model
- Both are important.
- That totally depends on the purpose of the model. In my opinion, neither exact timing or exact magnitude might be necessary if the model is build to learn about the system in a qualitative way. In that case, getting the sub-set of important mechanisms ("the inside of the model") that influence the timing and magnitude right is more important. However, if the model is used to improve forecasts, the inside of the model is less important, as long as the output proves to be well-enough aligned with the observed reality. Like, Newtonian mechanics overlooks a lot of stuff going on "on the inside of reality", but it's output is good enough to plan for and conduct moon landings.
- For the bacterial and archaeal realm the timing is irrelevant, the amount and type of "food " produced is relevant.
- Depends what the idea of the model is. If the interest is to get an idea on transfer of mass and nutrients, I do not think it is.
- Disagree. Both are important, e.g. harmful algae blooms.
- Depends on your question. Both are important, why focus on one over the other?
- No, it may be related to one another, but timing, besides the temporal scope, has no relevance. A quickly terminating bloom vs dragged out longer.

- Both are important
- Disagree
- Depends on the purpose of the model.
- The battle between ecologists and biogeochemists 😊 I´d say both are equally important, a priority might be given based on the higher interest of the modelling exercise.
- For many seasonal species this is true.

G26. Long-term plankton data series provide a useful resource for modellers, but they need to be used with care after validation against current understanding.

Response:

- Yes, such data sets should be useful for plankton models. A problem would be inconsistent parameter collection (methodology, type of measurement) within a single data series and among diverse data series. One long-term data series is that carried out in the upwelling system off the Oregon coast: Data from seasonal transects off the Oregon coast from 1997-2004 are available on-line and could be used to check DT model assumptions. Many intense diatom blooms were sampled. Data sets and papers can be viewed and downloaded at: https://ir.library.oregonstate.edu. See also Wetz et al. (2005, 2006), Huyer et al. (2007).
- I would agree that long term plankton data are really valuable (with care) for models. If I knew that copepods have already declined over the last 50 years of warming in the NE Atlantic, I would be more inclined to believe a model that said that this would continue under continued warming even if the extent is uncertain.
- Yes.
- If this statement refers to classification and data management procedures that change over time then I totally agree. We have to be careful to work with the correct (consistent) currencies.
- Definitely for bacteria as the methods have changed massively and the accuracy has improved a lot.
- They are the observational tool for modellers, it is the only way to ground-truth models.
- I agree with the first part of the sentence.
- Not sure what care means here. There is a lot of uncertainty in the long term data sets but they worth their weight in gold.
- I don't understand the question, and I am heavily involved time-series approaches my entire career. Long term data should be the gold-standard.
- Agreed
- Completely agree
- Depends on the quality of the long term data. If methods changes occurred during the time series this needs to be considered. The rapid pace of advancement in tools and methods is improving our detection capability, but creates challenges for consistency in data reporting. The example of primary production data comes to mind. 14C used to be the standard, but variable fluorescence measurements are being used more commonly now. They do not measure the same thing but such differences (while obvious to phytoplankton ecologists) may not be readily apparent to modelers.
- I agree.
- Completely agree.
- Yes, these can be valuable data resources, however if the long-term data is not validated/of high quality it is not a very useful for models. Therefore, both the underlaying data and the used models need to be of a high quality.

G27. How do we make (simulation) modelling mainstream in plankton science, with a status closer to that enjoyed by molecular biology?

Response:

- Make the molecular biologist depend on your models to explain their results (may at least help).
- I thought it already was? For me it would be even more mainstream if it also had more humble ambitions. At the moment most modelling studies I can most easily recall (and which involve

plankton) are looking forward 80 years with a global projection in a high impact journal. Perhaps this is the fault of the journals accepting this kind of thing. Models are the only way we can do this but in so doing they are setting themselves up as non-mainstream. I am pushed to try to think of any really significant new insight about zooplankton ecology that was based on a model, so perhaps more focus on model-based understanding of present day ecosystem operation (integrally alongside empirical data) would help modelling become a more of “another tool in the toolbox” rather than something that has its own research group and its own session in conferences.

- I suppose it would have to start and become a more integrated part of undergraduate education.
- The first thing, spoken as a biologist, is to make it understandable and accessible. Bioinformatics are upcoming, but that is mostly the use of modules in ready made programs, such as R. Writing the source code for models is a different level and require more mathematical understanding. Therefore, most biologist don’t do it. If there are programs available that work e.g. in R, this would increase the use of models a lot. Less math – more biology.
- By increasing the communications between experimentalists and modelers, making sure that we talk about the same things when we think we do.
- Provide packages (like mini computer games) where people can just change a few variables and some control path that scores how realistic the settings are.
- Document that the insights gained are fruitful. Molecular ecology has led to discovery of novel processes, true discovery. Nobody suspected diatoms to have a urea cycle. Molecular ecology also can probe processes without preassigning the outcome. Models need to be formulated so they are limited by what the research knows/focuses on.
- Omics is capable of analysing systems with millions of dimensions (dimensions being genes, transcripts etc.) under diverse environmental conditions and evolutionary scenarios. AI is pushing our analytical skills to the next level now. I suppose, similar tools can be applied to plankton science once we have defined the dimensions we want to include in our mainstream modelling.
- Good question, which I cannot provide the answers to.
- Models are now integral to understanding and predicting how aquatic systems function and how they are changing. Every student now is–or should be¬– familiar with basic modelling. Students do not have to be modelers to think in these terms.
- Visualizations, animations, play-around interfaces for user experiences. Hide the scary math, especially the horrific nabla symbol 😊 You lose and scare away people instantly.
- We need to teach it explicitly at undergraduate and postgraduate level for all plankton scientists. Perhaps provide online training materials and example projects for undergraduate and masters dissertations. Online courses for PhD students and postgraduates would also be useful.

G28. Much plankton field work is now centred on the exploitation of molecular (‘omics) approaches. How can we use such data to support the modelling of different plankton types (virus to metazoan zooplankton)?

Response:

- The resolution below community (prokaryotes, flagellates, diatoms) now largely depends on omics data. To explain the population dynamics observed at species and strain levels the experimentalists need models combining competition with defence against both predators and viruses. The molecular biologist arguably depends on your models to explain their results.
- I think linking phytoplankton diversity to co-measured variables would be a good start to inclusion of phytoplankton diversity in models and in particular its change in response global warming and covarying ocean responses.
- Same way that old school phytoplankton counts and diversity studies were used (Metabarcoding), same way as rate measurements for biochemical cycling were used (MetaGs and Ts), the rest is still to far away from mainstream to be considered.
- Currently, not at all, as there is hardly any basis for quantification. It will allow the creation of networks etc, not the creation or parameterization of any useful quantitative model.

- We can see which organisms are mutual connected (benefit from the same conditions or are in symbiosis or derive from the same source).
- See Biogeoscapes. Those efforts are underway.
- Really, the -omic based tools are not enough. We need molecular tools that maintain information about who was associated with whom, instead of doing it always in bulk.
- Omics is capable of analysing systems with millions of dimensions (dimensions being genes, transcripts etc.) under diverse environmental conditions and evolutionary scenarios. AI is pushing our analytical skills to the next level now. I suppose, similar tools can be applied to plankton science once we have defined the dimensions we want to include in our mainsteam modelling.
- It can help describing the species diversity in the different plankton groups.
- This difficulty is two-fold. First, new instrumentation and methodologies (especially omics) are inundating researchers and modelers with a ‘data deluge’. Second, relating genomic and proteomic data to more standard biomass and rate measurements is more than complicated. It will take time for methods and approaches to be main stream for incorporation of these new types of data.
- Certainly time-courses of taxonomic composition help understand the spatial and temporal distribution of plankton. Transcriptomics explain what happens underneath the cell surface and sheds light on very basic demands that need to be fulfilled, thus they often point to unifying principles.
- It would be interesting if the omics approach can be really paired to the magnitude of rate processes. At the end we need to quantify rates somehow. In the case of copepods, I would like to know how much they eat, what they eat and how much they grow/reproduce.

*G29. Exploitation of ‘omics enables us to determine the metabolic capabilities of organisms in the form of genome-scale metabolic models (GEMs). Coupling these with Flux Balance Analysis (FBA – Orth et al. 2010; Nature Biotechnology **28**, 245) enables us to determine physiological activity in nature. We can use such information to support plankton model developments tailored to individual species levels.*

Response:

- If you have a food web model you can use this to generate the biotic environment of an organisms and use it as a driver for your GEM.
- Yes, and things have progressed a lot. The culture independent methods are particularly exciting.
- I disagree.
- Good idea

G30. The mantra, everything-is-everywhere-(and active)-all-the-time, is not correct and/or is not useful as applied to plankton models.

Response:

- I don’t think it is 100% correct but may be useful in models resolved to species level. (Traditional food and sanitary microbiology practices always assumed that this is wrong: You only get antidotes against tetanus and rabies for certain kind of injuries)
- It depends on scale of model (time and space), for the ocean as whole over long time spans, maybe.
- It is not correct for phyto and zooplankton, but it is at least partly correct for bacteria. “The environment selects” is the key part of the quote though. Nothing is active all the time, they are all active the moment that the environmental variables provide their favorite niche. And this is what we want to model.
- It’s demonstrably false. 90% of bacteria are inactive.
- Correct, not useful.
- Local adaptation is important and shapes diversity and evolution. However, some things are everywhere.
- I do not believe it is correct. It is based on the morpho-species concept.
- Depends on the purpose of the model.

- Season and previous history are important and must be taken into account. Of course, it always depends on the question you try to solve.

G31. There is no strong evidence, either way, for different temperature-responses for phototrophic vs heterotrophic activities.

Response:

- The review of Chen and Laws (2017) provided evidence that there is not for phytoplankton and protozooplankton: '…the median E_a values estimated from individual experiments did not differ between phytoplankton and heterotrophic protists.' They concluded that: 'In particular, our analysis questions the widespread belief that the temperature sensitivity of phytoplankton is lower than that of heterotrophs.'
- Not in the microbial part of the food web. I believe the dominant temperature effects on the microbial food web to come indirectly via the external drivers: Water column stability (affecting photic zone nutrient content) and metazoan predators (egg production, life cycle, diapause) affecting top-down trophic cascades.
- When there are no other limitations, it is clear that temperature responses are different. Realized responses are much more similar.
- Not for bacteria as far as I know.
- See the work of Bingzhang Chen; e.g. Chen et al. 2023. The data for heterotrophs esp. is not sufficient to distinguish trends. Considerable acclimation potential in phytoplankton (e.g. Strock & Menden-Deuer 2021) and herbivorous protists (Franzè & Menden-Deuer 2020) show that rates are maximized at localized temperature and acclimation can eliminate temperature constraints that would affect rates (within temperature limits).
- Would not agree.
- I disagree. Unfortunately, the literature is still limited and show different responses.
- There is evidence that phagotrophy is favored over photoautotrophy at warmer temperatures, However, such effects also depend on the nutrient status of the cells. Respiration generally increases faster than photosynthesis at warmer temperatures, and, as Eppley predicted, warmer waters should become more heterotrophic. Temperature affects more than growth rates. It affects motility, germination, pigment content, enzyme reactions and other processes.
- Probably both types of processes exhibit hump shaped or similar temperature performance curves. But their shapes and optima may be different, so that net biomass buildup is changing with temperature.
- I think there is strong experimental evidence that heterotrophic activities are more temperature sensitive than phototrophic activities.
- There is some evidence for this, but some studies do not find any proof. The metabolic theory of ecology suggests that autotrophic and heterotrophic processes react differently to temperature. But this can in natural systems be "obscured" by e.g. lack of nutrients, availability of organic matter, and/or food web community composition and structure. In addition, do planktonic communities (e.g. bacteria) in open ocean and coastal waters also seem to have different temperature dependence.

G32. Do modellers need to consider the effects of ocean acidification (decreasing pH due to uptake of atmospheric carbon dioxide) on plankton community composition and food webs?

Response:

- I would say it depends on the model and question. If the model goes far into the future or deals specifically with the effects of climate change, then yes. If it is a short term model or deals e.g. only with bacteria and not calcified phytoplankton, then not, because the small changes in pH have limited (and mostly unknown) effects on them.
- In my humble opinion and from what I have read, plankton seem to have quite strong abilities to cope (via acclimation) with OA (and temperature change as well) . There are a few important

exceptions among certain calcifiers but these tend to be in situations where they were not major taxa to start with, e.g. polar pteropods which are in the mid-second division of importance overall there, despite suggestions to the contrary). So from what I have read I would suggest OA is lower down the list of stressors, compared for example to big ones like nutrient supply and its interplay with light availability.

- Reviews and laboratory experiments of potential effects of ocean acidification on marine plankton predict negative impacts on some marine taxa, especially coccolithophores, foraminifera, and pteropods, that produce calcareous skeletal structures (Fabry et al. 2008, Kroeker et al. 2010, Olson et al. 2016). Studies of impact of ocean acidification on marine plankton communities have demonstrated significant effects, especially on certain species of phytoplankton (Dutkiewicz, et al. 2015, Sommer et al. 2015, Schlüter et al. 2016, Spisla et al. 2021). More work on this issue is needed as atmospheric carbon dioxide continues to increase and surface ocean pH continues to decrease.
- Yes, they do. Many plankton organisms are quite resistant to acidification, but it is important to include pH in the models, because it affect "the scope for primary production" leading to denser algal blooms in the future with much effect on the flora and fauna due to "lytic toxins".
- Depends on the purpose of the model. The complexity of projecting the effects of the many stressors under which our current and future ocean is experiencing, and will experience, is extremely challenging. The physiology of acquiring and concentrating CO2 for C fixation will change with OA. Numerous studies suggest that diatoms and calcifying taxa may be disfavored in the competition with cells that rely to a lesser extent on CCMs. Yet, OA is changing against a backdrop of multiple stressor changes. The effects of OA on rates of N2 fixation, for example, depend on the extent of other stressors, such as Fe and PO4 limitation. Toxicity of HABs may change with OA.
- As ocean acidification can impact the model function it needs to be considered. However, as the potential impact of acidification varies both temporally, spatially, with species composition and prevailing environmental conditions (e.g. nutrient levels) it is generally challenging for models to handle.
- Yes
- Yes.

G33. There are common principles organizing the marine planktonic food web at multiple scales. Because these allow us to capture and understand complexity by means of simple models, there is no need for what could be perceived as overly complex models.

Response:

- I disagree to the extent that we have not reached a level of sufficiently complex models to explain interactions correctly and satisfyingly. If we reach that point, sure, we could discuss if we really need factor X and Y on top and what they would add to the model. But in my opinion, we are not there yet. We only put in the very basics and maybe global principles, but there are a lot of small things with large impacts that are missing. Although, this argument can be used into infinity...
- No, I don't agree with that at all, but there should still be a place for simple focused models on specific processes which help us avoid getting bogged down in complexity. I think a bigger structural (underlying principles) diversity of models is more important than their degree of simplicity. Things like body size do indeed offer a degree of simplicity for understanding pelagic systems, but even this (e.g. PPMR strongly dependent on body mass) seem to be deceptively complex and still poorly understood mechanistically.
- I disagree very much with this statement. Many current models do not include essential functional groups in the models, and I would say that many models are overly simplistic!
- Overall I disagree because biology is inherently complex and therefore difficult to constrain in models, but at the stage of current knowledge I agree.
- I have always thought that small scale is relevant. Perhaps we cannot go into the very detail of all things, but in my opinion oversimplification is not the solution either. Just a simple allometric scaling

model, log-log, helpfully simplifies a lot the variance around the fitted line and is useful. In occasions, however, the variance around predicted values can be relevant. Not much used, but quartile regression can be very useful in ecology to determine patterns between variables and get rid of the variance on unknown factors.

G34. Climate change (IPCC) models use plankton descriptions limited to very few 'phytoplankton' and 'zooplankton', restricted by computational costs; how can these possibly provide a plausible feedback between biogeochemistry and climate change as they cannot describe the changes in biodiversity caused by climate change which will affect the BGC-pump signal?

Response:

- Big question that is being discussed by the IPCC authors as well. I would agree that it cannot and needs to be more detailed, especially when it comes to the biological carbon pump. Most models disregard or simplify the effect of bacterial degradation on marine snow and hence get wrong results for the sequestration rates. And this is also true for copepods, which eat the snow etc. Usually these models assume a fixed rate, but changes in diversity will change the rates etc.
- Same question as above, phrased differently. But here the excuse for simplicity is based on a totally different and wrong (bogus) reason of computational efficiency.
- The 'phytoplankton' and 'zooplankton' boxes in plankton models are more representative of functional types than of communities of individual species (biodiversity). Models assume that the behavior of broad functional types, e.g. diatom vs. non-diatom phytoplankton, will not be appreciably affected by change in species composition within those types. A case in point is the functional type of heterotrophic bacterioplankton, which is comprised of high and variable species diversity; but for model purposes what matters is their combined activity in organic matter decomposition and nutrient recycling. Ongoing ocean heating is likely to have more profound effects on the functional dynamics of ocean food webs than is change in species composition within functional types due to climate change (Kirby et al. 2009, Ullah et al. 2018, Du Pontavice et al. 2020, 2023).
- I completely agree with this statement!
- Models, however imperfect, can be useful for understanding, or testing the strength of particular factors or variables on outcomes. Running in silico experiments in which different forces are turned on and off or tuned to different levels give clear clues as to the importance of such factors for present and future conditions.
- The truth is that it is quite likely most of these models are wrong.
- Highly complex models are not always the answer to a problem. Sometimes "simplistic" models are better at describing complex feedback as they will "even out dumps on the road". So yes, simpler climate change models can provide useful information.
- To go beyond current concepts I believe it would be helpful to develop BEF (biodiversity-ecosystem function) approaches for the ocean. BEF is well advanced for terrestrial systems, but hardly at all for the ocean at the moment.