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More realistic plankton simulation models will improve projections of ocean ecosystem responses to global change

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Plankton models form the core of marine ecosystem simulators, with uses from regional resource and ecosystem management to climate change projections. In this Perspective, we suggest that stronger alignment of models with empirical knowledge about plankton physiology, diversity and trophic roles will improve model utility and the reliability of their outputs regarding biodiversity, ecophysiology, trophic dynamics and biogeochemistry. We recommend key steps to resolve the disconnect between empirical research and simulation models accounting for well-established plankton processes with an aim to increase the utility of such models for applied uses. A central challenge is characterizing the complexity of plankton diversity and activity in ways that are amenable to model incorporation. We argue that experts in empirical science are best placed to advise the development of next-generation models to address these challenges, and we propose a series of actions to achieve that engagement, including involvement of these experts in the design and exploitation of plankton digital twins.

Plankton have pivotal roles in biogeochemical cycling, carbon sequestration, climate regulation and functioning of marine food webs[1]. These roles critically depend on the composition of the plankton communities, including their diversities in form, function, interactivity and consequential growth and loss dynamics[2–6]. Simulation models provide important research tools for predicting the future and what-if testing of marine ecosystems. This capacity is required for resource and ecosystem management, for considering the safety and efficacy of geoengineering strategies such as iron fertilization[7] and ocean alkalinization, and for making climate change projections[8] of processes affecting and affected by planktonic organisms and the biogeochemical cycles they mediate[9–12]. Confidence in simulation outputs underpinning such activities requires confidence in the conceptual base of the models.

The past few years have seen the emergence of a new type of simulation model known as digital twins. There is no single definition of 'digital twins', but they typically provide an interactive platform for exploring a virtual representation of reality, with a comprehensive graphic user interface enabling their ready exploitation by stakeholders rather than

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just by modellers and data analysts per se. Used as decision-support tools, digital twins thus enable users without expertise in modelling to interactively use simulations to explore different scenarios. However, it is vitally important that digital twins are built on solid empirical and modelling foundations that are continuously updated and integrated to provide a plausible 'twin' experience to users of such platforms. Applications in marine science are exemplified by the United Nations' Digital Twins of the Ocean initiative (https://ditto-oceandecade.org), with an example being the Bridge Black Sea demonstrator (https://bridgeblacksea.org).

While plankton may be expected to be common components of marine ecosystem digital twins, the building and use of digital twins has been proposed[13] to also offer a route to bring together disparate plankton research strands into a holistic dynamic description of the ecology of organisms that dominate the largest continuous ecosystem on Earth, the ocean. To this end, a project entitled 'Simulating plankton—getting it right in the era of Digital Twins of the Ocean'[14] commenced in 2023, exploring the needs for constructing a plankton digital twin (PDT) platform. This enterprise involved experts in various aspects of plankton empirical and modelling science, most of whom are authors of this Perspective. Contributors were asked to bring their broad understanding of plankton to the project, focusing on holistic phenomenological data rather than just numeric data. This engagement provides "expert witness validation"[13], an analogue of a Turing test, to provide confidence that models of individual plankton types and of their ecologies behave in convincing ways. As part of the project, we considered the need for core ecophysiological and ecological (that is, trophic) functionalities expected in PDTs. In doing so, we identified disparities between descriptions provided by extant plankton models and the state-of-the-art knowledge about plankton ecology, physiology and biogeochemistry[15].

Building from our project[15], in this Perspective, we work through the challenges that lie ahead in resolving the disparities between extant plankton models and advances in empirical plankton science, not only for the development of PDTs but also, arguably more importantly, for enhancing the structure and functioning of all ecosystem models that include representations of plankton.

The need for a new generation of plankton models

In addition to deployments in digital twins, it is essential that the conceptual and simulation models that underpin marine research (including the development of the next generation of artificial intelligence and big-data analyses) are consistent with recent empirical findings. Furthermore, the development and implementation of next-generation environmental monitoring technologies are inevitably influenced by the needs for specific types of data at appropriate spatial and temporal resolution, details that may be guided by the needs of modellers. It is therefore necessary to periodically examine whether extant plankton-containing models remain fit for purpose. The inclusion of the role of microbiology in Earth systems models has recently been subjected to such questioning and found wanting[16], while a general marine-facing opinion piece on the interface between models and observations has also been presented[17]. Although there is evidenced skill across plankton model systems (that is, simulation output aligns with empirical data[18]), the modelling community is also acutely aware that there are substantial uncertainties and inter-model variability[6,19].

Data on natural plankton populations and activities are fragmentary in their coverage of diverse organisms, as well as their temporal and spatial variability. As such, these data are insufficient for providing high levels of confidence in model output. There are also potential risks of extrapolating from models that produce the right answer for the wrong reason—for example, misdirecting loss process between grazing and non-grazing mortality rates[20]. Judging realism in simulation outputs must thus also consider the broad conceptual framework on which models are built. This is especially important for deployments used to explore what-if behaviours beyond the bounds of any empirical data used in model testing (calibration and validation).

Our consideration of the status of the building blocks of extant plankton models[15] draws us to identify important areas in which current plankton models need to be improved to avoid being overly simplistic in their description of physiology and/or in trophic connectivity. These areas include descriptions of the plankton community (that is, the number of plankton functional types used and their trophic linkages), their type-specific physiological features and the emergent biogeochemical activities. Specific concerns include aspects of fundamental processes such as primary production, resource acquisition, prey selectivity, efficiencies and stoichiometries of trophic transfers, and temperature effects[15].

It is especially timely to raise these concerns because accumulating evidence shows that plankton diversity, size structure, nutritional value for higher trophic levels and biogeochemical functioning are all changing from local to global scales through time and space[21–25]. There are a range of plankton descriptions in the most commonly used marine system models, from 'phytoplankton' and 'zooplankton' in simplistic terms, that are at times split into additional labelled sub-groups[26]. More complex models include several plankton functional groups (for example, up to 11 in PlankTOM11 (ref. 27)), but none can truly claim to represent real ocean biodiversity, let alone biological variation at genotypic or phenotypic resolution (for example, populations or ecotypes). Core features of plankton models, such as physiological interactions and trophic connectivities, can also be problematic[15]. There is thus an urgent need to consider enhancing these models and perhaps even developing a new generation of plankton models.

Development of plankton models versus advances in empirical science

The foundation of most existing plankton models dates back more than 50 years[28–31], with the classic nutrient–phytoplankton–zooplankton model[32] that forms the core of major plankton ecosystem models now surpassing 30 years of use. Over this period, the science of marine ecology and related aspects of research have undergone profound transformations, much allied with applications of molecular biology[33]. Conceptual shifts, such as the recognition of the microbial loop[34,35], the viral shunt[36], the microbial carbon pump[37], predator and viral derived population dynamics[38], and mixotrophy and the mixoplankton paradigm[39,40], alongside more general developments such as ecological stoichiometry[41] and recognition of the broad scope of resource acquisition processes[1] and species interactions, have collectively resulted in radical advances in our understanding of plankton ecology. Such advances have prompted calls for fundamental revisions of plankton modelling approaches[42,43], but these have only partially materialized.

Specific advances (for example, in simulating multi-stressor impacts[44], phytoplankton biodiversity[45] and stoichiometric modulation of predation[46]) have, by and large, not been included in mainstream ecosystem models. This is presumably because these innovations were not thought to make a sufficient improvement to justify the effort and computational cost of their implementation and/or because of a scarcity of numeric data for their configuration and validation. Indeed, the relative simplicity of extant models is not due solely to aspirations for simplicity and reduction (that is, the application of Occam's razor); a key problem invariably highlighted by plankton modellers is the lack of robust numeric data needed to aid in the construction and testing of alternative model formulations[47]. Empirical science does, however, offer extensive phenomenological understanding of plankton, and these forms of data are at variance with the core conceptual underpinnings of plankton models with respect to both physiological details (autecology) and trophic connectivities (ecology).

The vast majority of exploratory developments in plankton models have focused on phytoplankton, a group that we now realize is confounded by historic inclusion of the photo-phagotrophic mixoplankton[40]. This means that the 'phytoplankton', as well as a fair proportion of the 'protist- (or micro-) zooplankton', actually include organisms that act simultaneously as primary producers and consumers. The dual functionality of plankton that simultaneously produce and consume organic matter poses a profound challenge to traditional plankton models. Equally fundamental, perhaps, given the long-standing interest in the biological carbon pump in plankton models[48–51], are the well-recognized issues surrounding the descriptions of zooplankton ecophysiology[52], which still remain unresolved over a decade later[53]. To these we can add the role of viruses[54], the microbial carbon pump[37] and the roles of prokaryotic functional guilds[55,56], none of which are usually incorporated in these models. At the level of physiology, challenges include such fundamental aspects as the arrangement of the consumer model equations[57], making unrealistic assumptions over predator-to-prey size ratios[58] and the handling of multiple prey types[59,60].

Developments in ecosystem-focused plankton modelling, and indeed textbooks on plankton, take a long time to catch up with empirical discoveries in plankton physiology and ecology. We are concerned that the evident gap between empirical plankton research and modelling is widening still further. This poses the distinct risk that the decision support tools required to assist in the management and safeguarding of regional to planetary-scale ecology and biogeochemistry (for example, climate change responses) may not be fit for delivery to those tasks.

Integrating modelling with empirical science

Traditionally, empirical scientists have had little if any active input into plankton model design or exploitation, although the few publications that discuss such collaborations[27,61] flag the value of such engagements. As a consequence, the discussion as to what to include and exclude in plankton-facing models[42,47] appears to lack a comprehensive perspective from empirical science. Why is this so?

Challenges arising from the current situation are presented, with possible solutions, in Table 1. From this it is clear that many if not most of the issues are actually 'owned' primarily by empirical science (Table 1; Challenges 1 and 3–11). However, we suggest that the underlying problem is a lack of dialogue between research communities[42]. The lack of good data to support plankton modelling (Table 1; Challenges 6–11) is thus in large part because the needs for such data have not been communicated sufficiently to those conducting empirical studies; the benefits to those empiricists have likewise not been made clear enough to engage them. The funding mechanisms needed to support required developments for both empirical and modelling components may also present major obstacles at the national and international levels. That is more likely if stakeholders are under the (we would argue, mistaken) impression that plankton modelling science is de facto in the application phase, with most core development complete. Working together will help to overcome such challenges.

Explanations for the lack of progress based on the complexity and computational costs of better describing plankton can seem difficult to accept for those conducting empirical studies, especially considering the advancements in other areas of data science over recent decades, such as in genomics. Indeed, the vast bulk of that extra computing power applied to modelling has been expended on increasing the resolution of the physics description from about 1° to about 1/36°, with additional resolution in depth (Table 1; Challenges 13–15), leaving the biological description in most models substantially unaltered for decades. The higher-resolution physics description will benefit, and arguably warrants, improved descriptions of plankton physiology and trophic interactions.

Although the increase in computational cost related to the improvements of plankton descriptions in models needs to be properly considered, empiricists and modellers need to work together to achieve an acceptable compromise between simplification (which is part of any modelling exercise) and the conceptual robustness of the process descriptions, consistent with current empirical knowledge. That robustness is crucial if we want to apply models beyond the bounds of the data used to configure them, especially now that climate change is pushing the natural system beyond those historic bounds[62–66]. Relying on simplistic plankton models, irrespective of how well they align with empirical data/knowledge from the past few decades, appears to be inappropriate for the challenges we face.

To the question of which is better placed to judge the structure of plankton models, empirical or modelling science, the answer is that obviously both are required. When modelling science flags the absence of certain lines of information or data that are deemed to be of importance, we need a means to transmit that necessity back to empirical science (and to their funders) to resolve such problems. Likewise, if empirical science identifies problems with model descriptions and outputs, collectively we must not ignore those concerns.

Confronting the challenges

We suggest that the root of the challenges in enhancing the descriptions of plankton in models would be overcome by integrating simulation modelling as a tool into the core of empirical marine plankton science on a broad scale (Table 1; Challenges 5, 15 and 16). We can perhaps learn from the integration of molecular biology and multi-omics approaches into plankton research. Both the development of molecular tools and the emergence of readily accessible computing occurred during the 1980s. While the former rapidly found favour among plankton scientists and is now a common research tool (for example, the Tara Oceans project[67–69]), simulation modelling did not become a common tool to aid empirical science. More often than not, plankton empirical and modelling sciences operate separately, as witnessed by session configurations at conferences and workshops. Is this just because the languages used by different groups of scientists are not understood or recognized by each other, or are the reasons more profound?

One reason for the difference in the uptake by plankton scientists of molecular biology versus simulation modelling may be that the language of the former was not novel, even though the techniques were. The core topics of omics have been taught to all undergraduate biologists (especially biochemists, geneticists and microbiologists) for decades; molecular biology is clearly owned by biologists. Simulation modelling of planktonic organisms, however, was/is more the preserve of process bioengineers (for microorganisms), physicists and mathematically inclined oceanographers. Critically, modelling has also typically required a sound knowledge of computer coding. While molecular techniques have become increasingly streamlined, now bypassing the original logistic hurdles of undertaking analyses of the 1990s, plankton modelling perhaps remains too daunting, with few introductory texts aimed at the absolute novice[70] and no quick entry point. Even texts aspiring to provide a primer[71] may strike at too technical a level. It is also possible that while advances from the introduction of omics into empirical plankton research may be clear, insights to be gained from modelling may appear less compelling or too theoretical. Modelling itself may thus appear less appealing as a research tool in which to invest time and effort. It is thus interesting to note that modelling studies are cited when they support the interests of empirical science; that is so despite the lack of involvement of empiricists in most model developments and therefore the likely ignorance over what exactly has been done to secure a given set of simulations. Embedding simulation modelling in the teaching of plankton science can represent a key action.

The implicit common enthusiasm of many field and laboratory researchers for finding ever more diversity of life forms and novelty in ecology diametrically contrasts with the pragmatic reality for modelling in having to drastically restrict the number of organisms, or ecotypes, that can be represented. However, locating unifying themes has historically been central to many avenues in empirical science. Attempts have been made to determine general rules and apply

Table 1 | Challenges and potential solutions to factors affecting the improvement of plankton models

Challenge		Comment/explanation	Owner(s)	Potential solutions and links to other challenges
1	Confusing ambiguous terminologies	Ambiguous empirical terminology is problematic for modellers; 'tech-speak' is common in all sectors	Empirical; part modelling	Agreed usage requires rigorous application; historic literature usage will remain problematic
2	Simplicity versus complexity	Empirical complexity needs merging with data availability rationalized for simplicity in modelling	Empirical and modelling	Allied to Challenges 3 and 4; requires acceptance that simple models may be especially inappropriate for multi-stressor scenarios (Challenge 8)
3	PFT groupings and allied trophic framework	Models require useable/robust PFTs, supported with numeric data; trophic linkages between PFTs and nutrients and biogeochemistry need clarity	Empirical; part modelling	Undertake studies at various levels of complexity consistent with modelling needs and computing capabilities
4	Exploitation of omics data	Increasing amounts of omics data but no clear route for exploitation in models	Empirical	Needs transformation of omics data into biomass (Challenge 6) and rate (Challenge 7) data; allied to Challenge 2
5	Integration of empirical and modelling approaches	Empiricists need to routinely engage with simulation modelling	Empirical; part modelling	Establish simulation modelling as a core tool in marine biology teaching, akin to statistics
6	Biomass determinations	Chlorophyll or organism counts are empirical defaults; models need biomass	Empirical	Developers of autonomous methods need to be alert to this challenge; allied to Challenges 9 and 10
7	Process rate determinations	Rates rarely measured, often with complex interpretation; often poor units and controls for modelling	Empirical	Embed modelling in empirical science at planning and execution phases; allied to Challenge 9
8	Multi-stressor interactions	Multi-stressor (including temperature, pH, O_2 and salinity) studies are rare and applied to few organisms	Empirical and modelling	Multi-stressor interactions require more holistic empirical and modelling studies; allied to Challenges 2 and 11
9	Data resolution	Data over time/space with poor detail across PFTs and nutrients (especially dissolved organic matter)	Empirical	More inclusive discussions on the design and operation of autonomous and allied monitoring systems; allied to Challenges 6 and 7
10	Unit transformation	Empirical science rarely provides data in units required for models	Empirical	Agreed best practice for transform routines; caveats (errors/uncertainties) need to be identified
11	Generalizations from empirical science	Studied organisms and ontogenic stages are not exemplars of reality; trophic studies are too narrow for holistic overview; hype in literature obscures generalities	Empirical; part modelling	Clear identification of caveats and non-generalization of empirical studies; expert witness validation has a role here
12	Generalizations from simulation output	Hype and ambiguity in literature obscure real-world generalities	Modelling; part empirical	Clear identification of caveats and non-generalizing of simulations; engage empiricists in peer review of modelling papers
13	Allocation of computing effort to describing ecology	Enhanced computational power allocated to enhancing physics resolution	Modelling	Re-match efforts on biological descriptions in models; alert funders and users of the need to enhance those components
14	Development of modelled core functionality	Questionable core functionalities date from the 1960s to 1980s	Empirical and modelling	Revisit biological descriptions to enhance performance with little to moderate increases in computational cost, exploiting expert witness validation
15	Stifling of development	Apparent lack of enthusiasm by modellers to exploit new/alternative empirical concepts	Modelling; part empirical	Associated with Challenges 13 and 14 and a failure/inability of empiricists to become involved (Challenge 12); complicated by Challenge 11 and probably countered by Challenge 5
16	Plankton models fit for purpose	Plankton models are exploited in simulations beyond development scenarios; especially problematic for digital twin and far-future simulations	Empirical and modelling	Involve/embed empiricists in model design and testing; enabled by Challenge 5

The resolution to each challenge is indicated as belonging to empirical or modelling science; in some instances ownership involves partial (secondary) involvement by the other science rather than being shared more equally. PFT, plankton functional type.

these in plankton research[72]; for example, body size is often a primary trait to simplify both modelling and empirical approaches[73–76]. At the same time, attempted applications of these trait rules highlight where organisms bend the rules (for example, via tissue dilution[77] or exploiting extreme predator/prey size ratios[58,78]); concepts underpinning some of the trait-based rules that modellers may expect to provide a route to simplification are not necessarily robust[15,79]. Interfacing molecular biology (omics) data with simulation modelling provides different challenges[13,80]. Although there have been various calls to integrate omics with plankton models[81,82], and genetic differences

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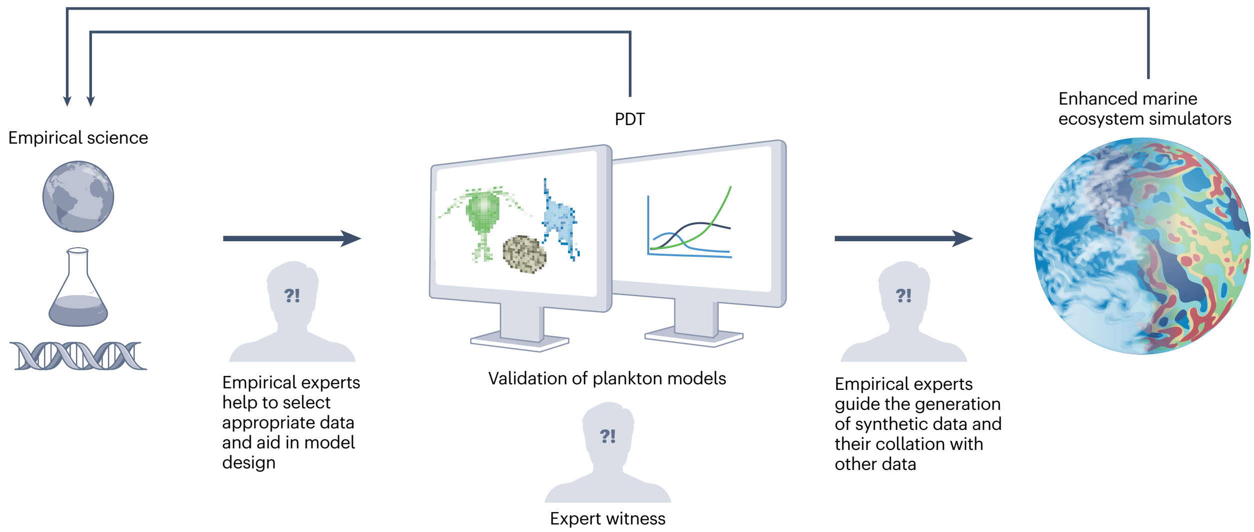

Fig. 1 | Proposed route to enhancing the representation of plankton in marine ecosystem simulators. Empirical science from roles such as molecular biologists, laboratory workers and oceanographers helps to inform the selection of data and conceptual bases for configuring next-generation plankton descriptions. This includes the exploitation of PDTs to enable expert witness validation of plankton model behaviour. Synthetic data generated from such PDTs, plus expert-validated simplified plankton models (as/if required), would support the development and validation of enhanced ecosystem simulators. Both the PDT and ecosystem simulator outputs would inform subsequent empirical science.

appear with the adaptation of plankton to new conditions[83,84], the possession of genes for traits can be inappropriately exploited in models with an assumption that the trait is expressed all the time. We have not found that approach to be acceptable[15]. Indeed, modulations of both biogeochemical and behavioural aspects of physiology are key facets of trait expression that are lacking in most models[85–87]. Similarly, the phenotypic heterogeneity (that is, intraspecific variability) that emerges in virtually all empirical studies and has adaptive function that sustains plankton diversity[88] is invariably lacking. If such characteristics and modulations are absent from models, then the explanations and consequential caveats need to be made clear. Indeed, this should apply for all simplifications, even for the use of rectangular hyperbolic descriptions of nutrient uptake, which are almost invariably deployed in plankton models and claimed as mechanistically realistic even though there can be variable interpretations of empirical data on nutrient uptake[77].

Problems with integrating simulation modelling with empirical science (Table 1) cannot be attributed solely to any specific science grouping. While modellers are typically aware of the limitations of their models (as aware as those undertaking empirical studies are of the limitations of their observations), they are probably less aware of the problems inherent in empirical data. It is easy for the non-expert to misinterpret the nuances of empirical data and concepts extracted from the literature, a situation that perhaps may be worsened by the development of artificial-intelligence-assisted data-mining tools[89]. Applying numeric data from different methodologies, as in the measurement of primary production, for which there are many techniques that measure different component processes[90], is a prime example. Explaining differences between strands of information (complicated by changes in methodologies, interpretations and terminologies over the years) can challenge the most expert individual, let alone someone whose primary skill sets are very different. Misinterpretations of classic temperature–growth work[91,92] and of applications of the metabolic theory of ecology[93] in models[15] might have been avoided if those models had been built in collaboration with people who had appropriate understanding of the subjects.

Kreft et al.[94] examined three approaches to modelling microbial systems, comparing metabolic flux, gene-centric and individual-based models to capture single-cell activities to population-level processes. Of these, only the individual-based models were found to work effectively with cell-to-cell heterogeneity, although these were also the most limited by the availability of rate formulations and parameters for resource acquisitions and processes leading to growth. Given that numeric abundance is probably the most common metric in plankton science, having model outputs given directly with units of organisms rather than just biomass is most probably highly desirable for many researchers. The flip side, of course, is that it would greatly help if empirical studies reported elemental biomass (Table 1; Challenges 6 and 10) with sufficient data to determine the mass balance of major nutrients in experimental systems.

A route for bringing modellers and biologists/ecologists together in data-rich studies scaling from organisms to ecosystems is via systems biology, exploring the dynamics of intracellular and extracellular biochemical networks—for example, targeting from signalling pathways and biological interactions to biogeochemical consequences and feedbacks[95]. Although such computer-intensive approaches may remain inappropriate for current large-scale ecosystem models due to their complexity, we can probably learn much from using and then attempting to exploit the knowledge to produce improved simple plankton models. Models explicitly exploring plankton processes are likely to be more insightful than statistical models, as they provide scope for mechanistic understanding and causality[96]; we need to find a middle way to incorporate sufficient complexity. That middle way may even require considering starting from a clean sheet, a route that may be necessary to prevent problems encountered when attempting incremental changes[20,47].

Several steps could be considered to enhance the engagement of experts in empirical science with plankton models, such as basing model descriptions in publications around infographics, rather than relying solely on mathematical equations that can be difficult and time consuming to follow. A similar argument can be made for the use of infographics and terminologies in the reporting of empirical science. For example, the indiscriminate use of the terms ‘phytoplankton’ and ‘zooplankton’ does little to enforce the need to recognize the ecological importance of biodiversity and functional types. It is difficult to believe that an analogous usage of ‘plant’ and ‘animal’ in reporting terrestrial ecology would be considered acceptable; it is notable in this context that terrestrial-focused contributions to even IPCC (Intergovernmental Panel on Climate Change)-level models describe multiple vegetation types[97].

Although the lack of involvement of empirical-science experts sufficiently well versed in modelling in reviewing plankton model manuscripts is an important issue of concern, so too is the lack of involvement of modellers in the review of all those empirical-facing grant applications and papers that claim justification through the newly generated data being useful for modelling. The fact is that the bulk of empirical studies of plankton, even those conducted in laboratories, do not provide the types of numeric data useful for the construction and testing of simulation models[13,42,47]. That extends most basically to not expressing results in the currencies often used by modellers, such as carbon or nitrogen, but includes also measurements of the fate of non-limiting nutrients (for example, of phosphorus in nitrogen-limited systems).

Engagement of the research community to identify the abovementioned challenges and constructively interact represents an urgent and foundational challenge to plankton science. The need for scientists to 'sell' (hype) the generality of their results to funders, often failing to clearly identify limitations in their studies, is also a concern (Table 1; Challenges 11 and 12). Too many results from modelling papers are cited as fact in support of empirical science, and too many species-specific empirical results are cited as generalized fact in support of both empirical and modelling science. Some of the blame probably rests on the academic peer-review system, where scale (using generalization and ambitious projections) often leads to prestige (enhanced through publishing in high-impact journals).

We do not expect failures in models to be uncommon, but we do expect to be able to usefully learn from such failures; and we do not anticipate failures to arise solely from gross simplifications[15]. We also view simplicity in models favourably, recognizing the need to combine organisms into groups, as is often also undertaken in empirical research. The caveat is that descriptions of such simplifications and groupings have to make biological sense, with a balance struck over the inclusion or merging of different producers, consumers, decomposers and so on as true functional types as per the biological meaning of that term[98].

One approach to making progress through all of this is for the structure and performance of simulation models containing plankton to be critically assessed by scientists who are undoubtedly well placed to undertake that role[61,86,87], through the aforementioned process of "expert witness validation"[13]. This approach also provides a route to overcome the absence of robust comprehensive numeric data series required to support computational model tuning and validation methods. Expert witness validation, however, requires that experts in empirical plankton science have tools that enable them to readily configure and test the simulation model. Platforms are required with user-friendly interfaces, which empirical science can exploit without the need to learn programming languages. Access to such platforms would enable experts to configure descriptions for individual plankton types to digital twin standards, and then, by operating those models collectively in ecosystem scenarios, they could generate synthetic data to be exploited in the development of simple models with levels of confidence exceeding that with which model comparisons are normally undertaken[99].

We see the development and deployment of digital twin platforms as a core mechanism for drawing modelling into the toolkit of empirical science. We propose that they must also be integral to the development of next-generation plankton ecosystem models as a means to bring empirical and modelling science together (Fig. 1). Drawing on interests and phenomenological data of empirical science (including omics data), this could guide the development of computationally simpler models and enable the development of research platforms to engage all plankton researchers. The development of PDTs, initially in the form of digital laboratory flasks, microcosms and mesocosms, would also provide tools enabling the conducting of in silico experiments to test the responses of individual plankton type (ecotype) descriptions through to exploring biotic interactions as part of ecosystem dynamics under multi-stressor conditions, and resolving how best to describe biodiversity for a given application. Large-scale simulation models containing expert-witness-validated components could then provide more confidence than is currently the case with extant models. Importantly for future marine science, by normalizing a role of simulation modelling as a tool in support of empirical plankton science, those researchers will also be more likely to collect data types of direct use in modelling as well as being able to provide the arguably more important conceptual understanding[13].

We have better understanding and ways of working together to improve plankton models than we did decades ago when much of the basis for extant plankton ecosystem models was developed. Holistic developments such as building PDTs[13] would provide a stimulus to help to enhance the vital role of modelling in marine science in support of twenty-first-century challenges. Even if, after all these efforts, the end results for climate change and fisheries projections are similar to those we obtain using extant simple models, we will have increased confidence in their messages. An additional benefit will be that, in the meantime, empirical plankton science will also be better engaged with collecting data types required in support of the robust modelling that we all need for the ocean we want[100].

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