

7<sup>th</sup> October 2020

We sincerely thank the reviewer for their insightful comments, which have greatly helped to improve and clarify our manuscript. We respond in detail to each comment in the attached document, and clarified the points raised by the reviewer. In response to these comments we have implemented the following general changes:

- All parameter values for the jellyfish PFT have been added, with the expansion of tables in the main manuscript and the addition of tables in the appendices, along with further descriptions of the model structure and additional equations.
- Carbon and primary production have been added to the results section and discussion, along with diagrams of the carbon flow within the model.
- The discussion has been expanded throughout to about twice its original length.

We provide full details in the attached, with our replies to reviewers' comments [in blue](#), and the new text provided in the manuscript highlighted [in red](#).

Rebecca Wright, on behalf of the author team.

## Response to the comments

### Reviewer #2

#### General Comments

The manuscript fits perfectly in the scope of Biogeosciences in that it considers the role of plankton within marine biogeochemistry. It uses a currently developed model PlankTOM10 and adds a jellyfish plankton functional traits (PFT) to further resolve the global ocean plankton system. Gelatinous zooplankton within the Cnidaria and Ctenophora have been neglected in virtually all models, yet we know that they have the potential to play a significant role in structuring plankton food webs directly and indirectly via predation, and facilitate the flux of organic carbon to the seafloor via the production of mucous, messy feeding, carcasses (also known as jelly falls) and to a much lesser extent faecal pellets. The pelagic tunicates (salps, doliolids) can form substantive bloom events and have the capacity to graze particles down to only a few microns, but these have also not been included. Although the authors appear to have used appropriate methods and scientific assumptions, it is difficult to make firm judgements about this as there not a detailed justification of the parameter values used. I would expect in a paper such as this for a detailed summary of all sources of parameter inputs listed in the Appendix for readers to check themselves and also reproduce the models. Without this a reader has to go on a fact finding mission themselves. The interpretation of the results are sound but not particularly substantive. The inclusion of jellyfish in the PlankTOM model is a significant step forward but the authors have not really explored this as much as I would have hoped. When I first read the title of the paper I expected a model of carbon flows from one PFT to another presented rather than just biomass outputs, and this left me feeling somewhat disappointed. If these concerns were addressed it would make the work far more powerful and novel.

[Thank you for your comments. All new and altered parameter values have been added, either within the main manuscript or in the appendix. Carbon flow results, analysis and discussion have also been](#)

included, with the discussion section expanded to almost double its previous length. Please see below for specific details.

### Specific Comments

**L33** - I am not sure jellyfish play a unique role. They do play a role, as do all the other functional groups. What are you suggesting by the term unique?

'Unique' had been removed from the title and abstract. Although all PFTs are unique, indeed there is maybe not a case here to argue why jellyfish are more unique than others.

**L34** - There have been a (very few) instances where jellyfish have been considered in plankton ecosystems, e.g., Ruzicka et al 2012 for the California Current System.

Previous examples of jellyfish modelling have been added to the discussion, the sentence here has been adapted to highlight that there has been no previous inclusion of jellyfish in a **global** plankton ecosystem model.

In the abstract;

"Overall the results suggest that jellyfish play an important role in regulating **global** marine plankton ecosystems, which has been **generally** neglected so far."

In the discussion;

"Jellyfish have been included in a range of regional models, the majority are fisheries-based ecosystem models, namely ECOPATH and ECOPATH with ECOSIM (Pauly et al., 2009). These include regional models of the Northern Humboldt Current system (Chiaverano et al., 2018), the Benguela Upwelling System (Roux et al., 2013; Roux and Shannon, 2004; Shannon et al., 2009) and an end-to-end model of the Northern California Current system, based on ECOPATH (Ruzicka et al., 2012). Jellyfish have also been included in regional Nutrient Phytoplankton Zooplankton Detritus (NPZD) models, representing small-scale coastal temperate ecosystems with simple communities, for example, Schnedler-Meyer et al. (2018) and Ramirez-Romero et al. (2018). These models have provided valuable insight into jellyfish in the regions studied, but the focus on coastal ecosystems and either a top-down approach (ECOPATH) or a highly simplified ecosystem (NPZD) limits their scope. PlankTOM11 offers the first insight into jellyfish on a global scale, from a modelling perspective."

**L86** - You do not mention, or make clear, what the composition of the macrozooplankton group is. Does it include pelagic tunicates, which are going to graze down to a smaller food size than crustacean macrozooplankton such as euphausiids. This would make a difference to how your model runs.

In the following sentence macrozooplankton are described as 'crustaceans' and the reader is directed to Table 1 which contains definitions of the PFTs, where macrozooplankton is further described as 'euphausiids, amphipods and others'. We have added '**crustacean**' to Table 1 and '**euphausiids**' to the text descriptions to enhance clarification.

**p114** - What are the size definitions of the two particulate detrital pools? The terms small and large are vague. You do not specify the contribution of each of the PFTs to each pool. For example, jellyfish produce virtually nothing in the way of particulate / solid faecal pellets.

A new section has been added to the Methods 'Organic Carbon Cycling Through the Plankton' which describes the contribution of PFTs to each pool, along with a schematic (Figure 1b) of the processes in the organic carbon cycle in PlankTOM.

#### "2.1.5. Organic Carbon Cycling Through the Plankton"

In PlankTOM11, the growth of phytoplankton modifies dissolved inorganic carbon into DOC, which then aggregates into POC<sub>S</sub> and POC<sub>L</sub> (Fig. 1b). POC<sub>S</sub> is also generated from protozooplankton egestion and excretion and is consumed through grazing by all zooplankton. POC<sub>L</sub> is also generated

by aggregation from POC<sub>s</sub>, egestion and excretion by all zooplankton, and from the mortality of mesozooplankton, macrozooplankton and jellyfish, and is consumed through grazing by all zooplankton. The portion of POC<sub>s</sub> and POC<sub>L</sub> which is not grazed, sinks through the water column and is counted as export production at 100m (Fig. 1b). The sinking speed of POC<sub>s</sub> is 3 m/d<sup>-1</sup> and the sinking speed of POC<sub>L</sub> varies, depending on particle and water density. Proto-, meso- and macrozooplankton excretion is largely in the form of particulate and solid faecal pellets, while this makes up very little of jellyfish excretion. Jellyfish instead produce and slough off mucus as part of their feeding mechanism (Pitt et al., 2009), which is represented in the model in the same way as the faecal pellet excretion, as a fraction of unassimilated grazing contributing to POC<sub>L</sub>.”

**p135** - What is MGE?

Modelled Growth Efficiency

“and *MGE* is the modelled growth efficiency.”

**p147** - You mention that jellyfish growth rates were compiled as a function of temperature from the literature, but you do not provide any indication of which papers were used, how many were used, which taxa the growth rates were compiled from etc. It is this level of detail that is absent from the methodology which makes traceability of the data impossible to verify.

A table of references for the growth values used has been added to the appendix (Table A1) and referenced in the text. The table also includes information on the species, life stage and number of data for each reference.

**p165-166** - Continuing with the issues of transparency, the values for GGE are obtained from the literature (Moriarty, 2009), but this is difficult to verify as that is a PhD thesis. You should make it clear that the data from the literature have been collated by Moriarty, 2009. How many values were collated? What are the range of values? Stating these will make readers far more confident about the inputs into the model.

“GGE is the portion of grazing that is converted to biomass. This was previously collated by Moriarty (2009) from the literature for crustacean and gelatinous macrozooplankton for the development of PlankTOM10. We extracted the data for jellyfish from this collation (all scyphomedusae) which gave an average GGE of  $0.29 \pm 0.27$ ,  $n=126$ .”

**p178** - Do you have evidence that ephyrae do have a higher clearance rate for autotrophs. There are not many papers that have analysed diet of ephyrae and there are mixed messages about diet. For example, how can you take into account selective vs non-selective feeders and time of year (relative to the spring phytoplankton blooms)?

The time of year (and spring phytoplankton blooms etc) occur as emergent properties within the model as the PFTs react to temperature and light changes, rather than being directly accounted for in the preferences or parameterization. Selective vs non-selective feeders are not accounted for, grazing depends on the biomass of each PFT in that location and the temperature. The sentences on ephyrae feeding has been edited for clarity as follows;

“There is little evidence in the literature for jellyfish actively consuming autotrophs. One of the few pieces of evidence is a gut content analysis where ‘unidentified protists... some chlorophyll bearing’ were found in a small medusa species (Colin et al., 2005). Another is a study by Boero et al. (2007) which showed that very small medusae such as *Obelia* will consume bacteria and may consume phytoplankton. Studies on the diet of the ephyrae life cycle stage are limited in comparison to those on medusa, but the literature does show evidence for ephyrae consuming protists and phytoplankton (Båmstedt et al., 2001; Morais et al., 2015). We assume that ephyrae are likely to have a higher clearance rate of autotrophs, due to their smaller size as with the small medusa, but this will have a minimal effect on the overall preferences and the biomass consumed, so preferences for autotrophs are kept low.”

**L299** - It would be useful to include a map showing the global distribution of jellyfish for the reader to gain a better understanding of the spatial distribution and coverage.

A global map of JeDI observations (replicated from Lucas et al., 2014) has been added to Figure 6. The maps of jellyfish biomass from PlankTOM11 have been adapted to replicate the units and colour scale (log) in the Lucas panel. The following text has been added to section 3.1 to accompany the adapted figure 6;

“However, PlankTOM11 underestimates the range of observations in the top 200m (Fig. 6). PlankTOM11 overestimates the minimum values and underestimates the maximum values. However, part of this discrepancy may be due to under-sampling in the observations. For instance, the highest values in the observations (>100, orange and darker) are from cells with the lower number of observations (Fig 6; Lucas et al., 2014).”

Are the Cnidaria data used from the upper 200m only, as you indicate that in the original dataset jellyfish were available for a much wider depth range. Again, this is for transparency purposes. The Cnidaria data for the whole depth range are used, this has been clarified in the text by adding the following sentence;

“Data from all depths are included in the analysis.”

**L319 and 327** - Why do you express the values for jellyfish biomass as 0.46 - 3.11 pg C on line 319 in the methods and just 0.46 pg C on line 327 at the start of the results (where other published values are expressed as a range)?

This has been rectified so that the PlankTOM11 jellyfish biomass is always expressed as a range.

**L342-344** - It is obvious that the majority of jellyfish biomass is distributed around the coasts because a) that is where the majority of sampling has taken place and so there will be sampling bias, and b) it is likely that the majority of jellyfish collected are scyphomedusae with a metagenic life cycle requiring a hard substrate for the benthic polyp population.

The following sentences have been added to the end of this paragraph;

“A key caveat in jellyfish data is that the data is not uniformly distributed spatially or temporally and not proportionally distributed between various biomes of the ocean, with collection efforts skewed to coastal regions and the Northern Hemisphere (MAREDAT; Lilley et al., 2011; Lucas et al., 2014). This sampling bias and sampling methods also tend to favour larger, less delicate species, which are often scyphomedusae with a meroplanktonic life cycle.”

**L417-418** - You state there is a high preference for jellyfish on protozooplankton. The vast majority of diet and feeding studies on jellyfish suggest that mesozooplankton are the preferred prey for the majority of jellyfish. Smaller taxa and juvenile forms (ephyrae) would consume protozooplankton, but this is not the case for most of the scyphomedusae. In the jellyfish dataset used for the PlankTOM11 model, are the classes or genera listed? If so, it would be helpful to briefly indicate the make up of the jellyfish community used in this study.

Further clarification of prey preferences has been added to the methods (see comment **p178**). A table has also been added to the Appendix (Table A3) with the references for jellyfish grazing, along with information on the jellyfish species and the prey preference for each reference.

The high prey preference of jellyfish for protozooplankton is in comparison to the PFT's other than mesozooplankton, which has the highest prey preference of any of the PFT's. The section has been edited as follows to clarify this and to also discuss the impact on mesozooplankton;

“The addition of jellyfish changes the zooplankton with the highest biomass from macrozooplankton to protozooplankton and reduces the biomass of mesozooplankton, in both the north and south (Fig. 11). However, the impact on the biomass of mesozooplankton and protozooplankton is small, despite mesozooplankton being the preferential prey of jellyfish, followed by protozooplankton. The small impact of jellyfish on mesozooplankton and protozooplankton biomass may be due to trophic

cascade effects where jellyfish reduce the biomass of macrozooplankton, which reduces the predation pressure of macrozooplankton on meso- and protozooplankton, whilst jellyfish simultaneously provide an additional predation pressure on meso- and protozooplankton. The decrease in predation by macrozooplankton may be compensated for by the increase in predation by jellyfish, resulting in only a small change to the overall biomass of mesozooplankton and protozooplankton.”

**L453** - The grid resolution is stated as ~20 x 10, but the original dataset were gridded in 1 x 1 degree. Why was the resolution changed?

We used the same grid as provided for the other PFTs in the MAREDAT data so all PFTs were treated the same way. The published data were gridded to 1x1 (Buitenhuis et al., 2013), which is the grid used by the World Ocean Atlas.

**L472** - Brotz et al. 2012 is not the most appropriate reference to support the description of jellyfish reproduction alternating between a sexually-reproducing pelagic medusa and asexually-reproducing benthic polyp, as the Brotz paper is about global distributions of gelatinous zooplankton and not reproduction.

The reference has been changed to Lucas and Dawson (2014).

**L472-479** - Be careful about saying that increasing temperatures increase growth of jellyfish, which they do, but it is an oversimplification of the whole life cycle as ephyrae are typically produced following colder than average winter temperatures (certainly for temperate populations of the common jellyfish *Aurelia*, which likely dominates datasets).

This whole paragraph on life cycles has been expanded and rewritten as follows;

“A key limitation of the representation jellyfish in the model is the exclusion of the full life cycle. Most jellyfish display metagenesis, alternating between a polyp phase that reproduces asexually and a medusa phase that reproduces sexually (Lucas and Dawson, 2014). PlankTOM11 currently only characterises the pelagic phase of the jellyfish life cycle, with parameters based on data from the medusae and ephyrae. The biomass of jellyfish is maximal during the pelagic medusa stage, as medusae are generally several orders of magnitude larger than polyps and one polyp can release multiple ephyrae into the water column (Lucas and Dawson, 2014). Although most hydromedusae persist in the plankton for short periods of time, larger scyphomedusae can live for 4-8 months and individuals in some populations can survive for more than a year by overwintering; something that may be facilitated by global climate change (Boero et al., 2016). Polyps develop from planula larvae within 5 weeks of settlement, and can persist far longer than medusae owing to their asexual mode of reproduction and the fact that they can encyst, which allows them to remain dormant until environmental conditions are favourable for budding (Lucas and Dawson, 2014). Unusually, mature medusae of *Turritopsis dohrnii* can revert back to the polyp stage and repeat the life cycle, which effectively confers immortality (Martell et al., 2016). Our understanding of polyp ecology is almost entirely based on laboratory reared specimens of common, eurytolerant species, with the patterns observed being locale- and species-dependent. We know that temperature changes can trigger the budding of ephyrae by scyphopolyps, which may lead to an increase in the medusa population (Han and Uye, 2010; Lucas and Dawson, 2014), but the number of species whose polyps have been located and studied in situ is minuscule and so estimates of polyp abundance or biomass are impossible even to estimate.”

Overall the discussion is rather brief and does not fully explore the differences between the different model outputs and the mechanisms driving those differences. The discussion feels rather superficial and far more explanation is needed to make it robust.

A substantial section on carbon fluxes in the model has been added to the discussion, and the original discussion has been expanded on throughout as per reviewer comments.

Technical Corrections

**L55** - benthic polyp (delete s) [corrected](#)

**L177** - Obelia in italics [corrected](#)

**L195** - Aurelia in italics [corrected](#)

**L197** - data were (not was) [corrected](#)

**L394** - picophytoplankton (lower case p) [corrected](#)

**Table 1** - italicise genus names [corrected](#)