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UNIQUE ROLE OF JELLYFISH IN THE PLANKTON ECOSYSTEM REVEALED USING A GLOBAL OCEAN BIOGEOCHEMICAL MODEL

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ABSTRACT

Jellyfish are increasingly recognised as important components of the marine ecosystem, yet their specific role is poorly defined compared to that of other zooplankton groups. This paper presents the first global ocean biogeochemical model that includes an explicit representation of jellyfish, and uses the model to gain insight into the influence of jellyfish on the plankton community. The PlankTOM11 model groups organisms into Plankton Functional Types (PFT). The jellyfish PFT is parameterised here based on our synthesis of observations on jellyfish growth, grazing, respiration and mortality rates as functions of temperature and on jellyfish biomass. The distribution of jellyfish is unique compared to that of other PFTs in the model. The jellyfish global biomass of 0.13 PgC is within the observational range, and comparable to the biomass of other zooplankton and phytoplankton PFTs. The introduction of jellyfish in the model has a large direct influence on the crustacean macrozooplankton PFT, and influences indirectly the rest of the plankton ecosystem through trophic cascades. The zooplankton community in PlankTOM11 is highly sensitive to the jellyfish mortality rate, with jellyfish increasingly dominating the zooplankton community as its mortality diminishes. Overall the results suggest that jellyfish play an important and unique role in regulating marine plankton ecosystems, which has been neglected so far.

1. INTRODUCTION

Gelatinous zooplankton are increasingly recognised as influential organisms in the marine environment, not just for the disruptions they can cause to coastal economies (fisheries, aquaculture, beach closures and power plants etc.; Purcell et al., 2007), but also as important consumers of plankton (Lucas and Dawson, 2014), a food source for many marine species (Lamb et al., 2017) and as key components in marine biogeochemical cycles (Crum et al., 2014; Lebrato et al., 2012). The term gelatinous zooplankton can encompass a wide range of organisms across three phyla: Tunicata (salps), Ctenophora (comb-jellies), and Cnidaria (true jellyfish). This study focuses on Cnidaria (including Hydrozoa, Cubozoa and Scyphozoa), which contribute 92% of the total global biomass of gelatinous zooplankton (Lucas et al., 2014). The other gelatinous zooplankton groups, Tunicata and Ctenophora, are excluded from this study because there are far fewer data available on their biomass and vital rates than for Cnidaria, and they only contribute a combined global biomass of 8% of total gelatinous zooplankton (Lucas et al., 2014). Cnidaria are both independent enough from other gelatinous zooplankton, and cohesive enough to be represented as a single Plankton Functional Type (PFT) for global modelling (Le Quéré et al., 2005). For the rest of this paper pelagic Cnidaria are referred to as jellyfish.

Jellyfish exhibit a radially symmetrical body plan and are characterised by a bell-shaped body (medusae). Swimming is achieved by muscular, "pulsing" contractions and animals have one opening for both feeding and excretion. Most scyphozoans and cubozoans, and many hydrozoans, follow a meroplanktonic life cycle. A sessile (generally) benthic polyps buds off planktonic ephyrae asexually. These, in turn, grow into medusae that reproduce sexually to generate planula larvae, which then settle and transform into polyps. Within this general life cycle, there is large reproductive and life cycle variety, including some holoplanktonic species that skip the benthic polyp stage as well as holobenthic species that skip the pelagic phase, and much plasticity (Boero et al., 2008; Lucas and Dawson, 2014).

Jellyfish are significant consumers of plankton, feeding mostly on zooplankton using tentacles and/or oral arms containing stinging cells called nematocysts (Lucas and Dawson, 2014). The large body size to carbon content ratio of jellyfish creates a low maintenance, large feeding structure, which, because they do not use sight to capture prey, allow them to efficiently clear plankton throughout 24 hours (Acuña et al., 2011; Lucas and Dawson, 2014). Jellyfish are connected to lower trophic levels, with the ability to influence the plankton ecosystem structure and thus the larger marine ecosystem through trophic cascades (Pitt et al., 2007, 2009; West et al., 2009). Jellyfish have the ability to rapidly form large high-density aggregations known as blooms that can temporarily dominate local ecosystems (Graham et al., 2001; Hamner and Dawson, 2009). Jellyfish contribute to the biogeochemical cycle through two main routes; from life through feeding processes, including the excretion of faecal pellets, mucus and messy-eating, and from death, through the sinking of carcasses (Chelsky et al., 2015; Lebrato et al., 2012, 2013a; Pitt et al., 2009). The high biomass achieved during jellyfish blooms, and the rapid sinking of excretions from feeding and carcasses from such blooms, make them a potentially significant vector for carbon export (Lebrato et al., 2013a, 2013b).

Anthropogenic impacts from climate change, such as increasing temperature and acidity (Rhein et al., 2013), and fishing, through the removal of predators and competitors (Doney et al., 2012), impact the plankton including jellyfish (Boero et al., 2016; but see Richardson and Gibbons, 2008). Multiple co-occurring impacts make it difficult to understand the role of jellyfish in the marine ecosystem, and how the role may be changed by the co-occurring impacts. The paucity of historical jellyfish biomass data, especially outside of the Northern Hemisphere, has made it difficult to establish jellyfish global spatial distribution, biomass and trends from observations (Brotz et al., 2012; Condon et al., 2012; Gibbons and Richardson, 2013; Lucas et al., 2014; Pitt et al., 2018).

Models are useful tools to help understand the interactions of multiple complex drivers in the environment. This paper describes the addition of jellyfish to the PlankTOM10 global ocean biogeochemical model, which we call PlankTOM11. PlankTOM10 represents explicitly 10 PFTs; six phytoplankton, one bacteria and three zooplankton (Le Quéré et al., 2016). The three zooplankton groups are protozooplankton (mainly heterotrophic flagellates and ciliates), mesozooplankton (mainly copepods) and macrozooplankton (as crustaceans; see Table 1 for definitions). Jellyfish is therefore the fourth zooplankton group and 11th PFT in the PlankTOM model series. It introduces an additional trophic level to the ecosystem. To our knowledge, this is the first and only representation of jellyfish in a global ocean biogeochemical model at the time of writing. PlankTOM11 is used to help quantify global jellyfish biomass and the role of jellyfish for the global plankton ecosystem.

2. METHODS

2.1. PLANKTOM11 MODEL DESCRIPTION

PlankTOM11 was developed starting from 10 PFT version of the PlankTOM model series (Le Quéré et al., 2016), by introducing jellyfish as an additional trophic level at the top of the plankton food web (Fig. 1). A full description of PlankTOM10 is published in Le Quéré et al. (2016), including all equations and parameters. Here we provide an overview of the model development, focussing on the parameterisation of the growth and loss rates of jellyfish and how these compare to the other macrozooplankton group. We also describe the update of relationship used to describe the growth rate as a function of temperature and subsequent tuning. Growth rate is the only parameterisation that changed since the previous version of the model (Le Quéré et al., 2016).

PlankTOM11 is a global ocean biogeochemistry model that simulates plankton ecosystem processes and their interactions with the environment through the representation of 11 PFTs (Fig. 1). The 11 PFTs consist of six phytoplankton (picophytoplankton, nitrogen-fixing cyanobacteria, coccolithophores, mixed phytoplankton, diatoms and *Phaeocystis*), bacteria, and four zooplankton (Table 1). Physiological parameters are fixed within each PFT, and therefore, within-PFT diversity is not included. Spatial variability within PFTs is represented through parameter-dependence on environmental conditions including temperature, nutrients, light and food availability.

The model contains 39 biogeochemical tracers, with full marine cycles of key elements carbon, oxygen, phosphorus and silicon, and simplified cycles of nitrogen and iron. There are three detrital pools: dissolved organic carbon (OC), small particulate OC, and large particulate OC. The elements enter through riverine fluxes and are cycled and generated through the PFTs via feeding, fecal matter, messy-eating and carcasses (Buitenhuis et al., 2006, 2010, 2013a; Le Quéré et al., 2016). Model parameters are based on observations where available. A global database of PFT carbon biomass that was designed for model studies (Buitenhuis et al., 2013b) and global surface chlorophyll from satellite observations (SeaWiFS) are used to guide the model developments.

The PlankTOM11 marine biogeochemistry component is coupled online to the global ocean general circulation model Nucleus for European Modeling of the Ocean version 3.5 (NEMO v3.5). We used the global configuration with a horizontal resolution of 2° longitude by a mean resolution of 1.1° latitude using a tripolar orthogonal grid. The vertical resolution is 10m for the top 100m, decreasing to a resolution of 500m at 5km depth, and a total of 30 vertical z-levels (Madec, 2013). The ocean is described as a fluid using the Navier-Stokes equations and a nonlinear equation of state (Madec, 2013). NEMO v3.5 explicitly calculates vertical mixing at all depths using a turbulent kinetic energy model and sub-grid eddy induced mixing. The model is interactively coupled to a thermodynamic sea-ice model (LIM version 2; Timmermann et al., 2005).

The temporal (t) evolution of zooplankton concentration (Z_j), including the jellyfish PFT, is described through the formulation of growth and loss rates as follows:

$$\frac{\partial Z_j}{\partial t} = \sum_k g_{F_k}^{Z_j} \times F_k \times MGE \times Z_j - \sum_{k=1}^{4} g_{Z_j}^{Z_k} \times Z_k \times Z_j - R_{0°}^{Z_j} \times d_{Z_j}^{T} \times Z_j \qquad (1)$$

$$growth\ through\ grazing - loss\ through\ grazing - basal\ respiration$$

$$- m_{0°}^{Z_j} \times c_{Z_j}^{T} \times \frac{Z_j}{K^{Z_j} + Z_j} \times \sum_i P_i$$

$$- mortality$$

For growth through grazing, $g_{F_k}^{Z_j}$ is the grazing rate by zooplankton Z_j on food source F_k and MGE is the growth efficiency. For loss through grazing, $g_{Z_j}^{Z_k}$ is the grazing of other zooplankton on Z_j. For basal respiration, $R_{0^\circ}^{Z_j}$ is the respiration rate at 0°C, T is temperature, d_{Z_j} is the temperature dependence of respiration ($d^{10} = Q_{10}$). Mortality is the closure term of the model, and is mostly due to predation by higher trophic levels than are represented by the model. $m_{0^\circ}^{Z_j}$ is the mortality rate at 0°C, c_{Z_j} is the temperature dependence of the mortality ($c^{10} = Q_{10}$) and K^{Z_j} is the half saturation constant for mortality. $\sum P_i$ is the sum of all PFTs, excluding bacteria, and is used as a proxy for the biomass of predators not explicitly included in the model. More details on each term are provided below.

2.1.1. PFT Growth

Growth rate is the trait that most distinguishes PFTs in models (Buitenhuis et al., 2006, 2013a). Jellyfish growth rates were compiled as a function of temperature from the literature. In previous published versions of the PlankTOM model, growth as a function of temperature (μ^T) was fitted with two parameters:

$$\mu^T = \mu_0 \times Q_{10}^{\frac{T}{10}} \tag{2}$$

where μ_0 is the growth at 0°C, Q_{10} is the temperature dependence of growth derived from observations, and T is the temperature (Le Quéré et al., 2016). Jellyfish growth rate is poorly captured by an exponential fit to temperature. To better capture the observations, the growth calculation has now been updated with a three-parameter growth rate, which produces a bell-shaped curve centred around an optimal growth rate at a given temperature (Fig. 2 and Table 2). The three-parameter fit is suitable for the global modelling of plankton because it can represent an exponential increase if the data support this (Schoemann et al., 2005). The growth rate as a function of temperature (μ^T) is now defined by; the optimal temperature (T_{opt}), maximum growth rate (μ_{max}) at T_{opt}, and the temperature interval (dT):

$$\mu^T = \mu_{max} \times exp\left[\frac{-(T - T_{opt})^2}{dT^2}\right] \tag{3}$$

The available observations measure growth rate, but the model requires specification of the grazing rate (Eq. 1). Growth of zooplankton and grazing (g^T) are related through the gross growth efficiency (GGE):

$$g^T = \frac{u^T}{GGE} \tag{4}$$

GGE is the portion of grazing that is converted to biomass, which was obtained from the literature (Moriarty, 2009).

2.1.2. Jellyfish PFT Grazing

The food web, and thus the trophic level of PFTs is determined through grazing preferences. The relative preference of jellyfish zooplankton for the other PFTs was determined through a literature search (Colin et al., 2005; Flynn and Gibbons, 2007; Malej et al., 2007; Purcell, 1992, 1997, 2003; Stoecker et al., 1987; Uye and Shimauchi, 2005). The dominant food source was mesozooplankton (specifically copepods), followed by proto-zooplankton and then macrozooplankton (Table 3). 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 (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, but not necessarily actively. The ephyrae stage of scyphozoans are likely to have a higher clearance rate of autotrophs, due to their smaller size, but this will have a minimal effect on the overall preferences and the biomass consumed. Table 3 shows the relative preference of jellyfish for its prey assigned in the model, along with the preferences of the other zooplankton PFTs. The preference ratios are weighted using the global carbon biomass for each type, calculated from the MAREDAT database, following the methodology used for the other PFTs (Buitenhuis et al., 2013a; Le Quéré et al., 2016).

2.1.3. Jellyfish PFT Respiration

Previous analysis of respiration rates of jellyfish found that temperature manipulation experiments with Q_{10} values of >3 were flawed because the temperature was changed too rapidly (Purcell, 2009; Purcell et al., 2010). In a natural environment, jellyfish gradually acclimate to temperature changes which has a smaller effect on their respiration rates. Purcell et al. (2010) instead collated values from experiments that measured respiration at ambient temperatures, providing a range of temperature data across different studies. They found that Q_{10} for respiration was 1.67 for *Aurelia* species (Purcell, 2009; Purcell et al., 2010). Moriarty (2009) collated a respiration dataset for zooplankton, including gelatinous zooplankton, using a similar selectivity as Purcell et al. (2010) for experimental temperature, feeding, time in captivity and activity levels. Jellyfish were extracted from the Moriarty (2009) dataset, which also included experiments on non-adult and non-Aurelia species medusae, unlike the Purcell et al. (2010) dataset. The relationship between temperature and respiration is heavily skewed by body mass (Purcell et al., 2010). The data was thus normalised by fitting it to a general linear model (GLM) using a least squares cost function, to reduce the effect of body mass on respiration rates (Ikeda, 1985; Le Quéré et al., 2016).

$$GLM = log_{10}RR = a + b\ log_{10}BM + c\ T \qquad (5)$$

$$cost\ function = \sum \left(\frac{R^T_{GLM} - R^T_{obs}}{R^T_{obs}}\right)^2 \qquad (6)$$

Where *RR* is the respiration rate, *BM* is the body mass, and *T* and R^T are the observed temperature and associated respiration rate. The parameters values were then calculated using $R_0 = e^a$, and $Q_{10} = (e^c)^{10}$, where e is the exponential function. The resulting fit to data is shown in Fig. 3. The parameter values for respiration used in the model are given in Table 4. Macrozooplankton respiration values are also given in Fig. 3 and Table 4, to provide a comparison to another zooplankton PFT of the most similar size available.

2.1.4. Jellyfish PFT Mortality

There is limited data on mortality rates for jellyfish and to use mortality data from the literature on any zooplankton group some assumptions must be made (Acevedo et al., 2013; Almeda et al., 2013; Malej and Malej, 1992; Moriarty, 2009; Rosa et al., 2013). These assumptions are: that the population is in a steady state where mortality equals recruitment, reproduction is constant and that mortality is independent of age (Moriarty, 2009). All models with zooplankton mortality rates follow these assumptions. In reality the mortality of a zooplankton population is highly variable. Steady states are balanced over a long period (if a population remains viable), reproduction is restricted to certain times of year and the early stages of life cycles are many times more vulnerable to mortality. Despite these assumptions, with the limited data on mortality rates, the larger uncertainty lies with the data rather than the assumptions (Moriarty, 2009). The half saturation constant for mortality (K^{Z_j} in Eq. 1) is set to 20 μmol C L^{-1} the same as other zooplankton types, due to the lack of PFT specific data. In the small amount of data available and suitable for use in the model (16 data points from two studies) mortality ranged from 0.006 – 0.026 per day (Acevedo et al., 2013; Malej and Malej, 1992). Applying the exponential fit to this data gave a mortality rate at 0°C ($m^{Z_j}_{0°}$ in Eq. 1) of 0.018 per day. Sensitivity tests were carried out from this mortality rate due to low confidence in the value.

Results from a subset of the sensitivity tests are shown in Fig. 4. The model was found to best represent a range of observations when jellyfish mortality was increased to 0.12 per day. The fit to mortality for the data ($\mu_0 = 0.018$) and the adjusted mortality ($\mu_0 = 0.12$) is shown in Fig. 3. Mortality rate values closer to 0.018 per day allowed jellyfish to dominate macro- and mesozooplankton, greatly

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reducing their biomass (Fig. 4 and Fig. 5). Low jellyfish mortality also resulted in higher chlorophyll concentrations than observed, especially in the high latitudes (Bar-On et al., 2018; Fig. 4 and Fig. 5; Buitenhuis et al., 2013b). The adjusted mortality rate used for PlankTOM11 may be accounting for several components missing from experimental data including the impact of higher trophic level grazing in the Avecedo et al. (2013) study, which in copepods is 3-4 times higher than other sources of mortality (Hirst and Kiørboe, 2002), the greater vulnerability to mortality experienced during the early stages of the life cycle and mortality due to parasites and viruses, especially during blooms (Pitt et al., 2014).

PlankTOM11 uses a mortality rate for jellyfish that is much higher than the limited observations (Fig. 4 and Fig. 5). Lower jellyfish mortality is likely to be more representative of adult life stages, as jellyfish experience high mortality during juvenile life stages, especially as planula larvae and during settling (Lucas et al., 2012). The limited observations of jellyfish mortality are from mostly adult organisms, which may explain the dominance of jellyfish in the model when parameterised with the observed mortality fit. The higher mortality used for this study may be more representative of an average across all life stages. Experimental jellyfish mortality is also likely to be lower than *in situ* mortality due to factors such as senescence post-spawning and bloom conditions increasing the prevalence of disease and parasites and thus increasing mortality (Mills, 1993; Pitt et al., 2014). Using a higher mortality for this study is therefore deemed reasonable.

2.1.5. Additional Tuning

As shown in Eq. 1, there is a component in the mortality of zooplankton to represent predation by organisms not included in the model. The jellyfish PFT is a significant grazer of macrozooplankton and mesozooplankton (Table 3), to account for this additional grazing the mortality term for macrozooplankton and the respiration term for mesozooplankton were reduced compared to model versions where no jellyfish are present (Table 5). Respiration is reduced in place of mortality for mesozooplankton as their mortality term had already been reduced to zero to account for predation by macrozooplankton (Le Quéré et al., 2016).

Following the change to the growth rate formulation (from Eq. 2 to Eq. 3), all PFT growth rates are lower compared to the published version of PlankTOM10 (Le Quéré et al., 2016), but the change is largest for *Phaeocystis*, diatoms, bacteria and protozooplankton (Fig. 2). Further tuning is carried out to rebalance the total biomass among phytoplankton PFTs following the change in formulation. The tuning included increasing the grazing ratio preference of mesozooplankton for *Phaeocystis*, within the limits of observations, and increasing the half saturation constant of *Phaeocystis* for iron. The tuning resulted in a reduction of *Phaeocystis* biomass and an increase in diatom biomass, without disrupting the rest of the ecosystem. Diatom respiration was also increased to reduce their biomass towards observations. Finally, bacterial biomass was increased closer to observations by reducing the half saturation constant of bacteria for dissolved organic carbon.

2.1.6. Model Simulations

The PlankTOM11 simulations are run from 1920 to 2015, forced by meteorological data including daily wind stress, cloud cover, precipitation and freshwater riverine input from NCEP/NCAR reanalysed fields (Kalnay et al., 1996). The simulations start with a 28-year spin for 1920-1948 where the meteorological conditions for year 1980 are used, looping over a single year. Year 1980 is used as a typical average year, as it has no strong El Nino/La Nina, as in Le Quéré et al. (2010). The spin up is followed by interannually varying forcing for actual years from 1948-2015. All analysis is carried out on the average of the last 31-year period of 1985-2015. PlankTOM11 is initialised with observations of dissolved inorganic carbon (DIC) and alkalinity (Key et al., 2004) after removing the anthropogenic component for DIC (Le Quéré et al., 2010), NO_3, PO_4, SiO_3, O_2, temperature and salinity from the World Ocean Atlas (Antonov et al., 2010).

Two further model simulations were carried out in order to better understand the effect of adding the jellyfish PFT. The first simulation sets the jellyfish growth rate to 0, so that it replicates the PlankTOM10 model set up (Le Quéré et al., 2016) but it includes the updated growth formulation and tuning as presented above. It is labelled 'PlankTOM10' in the figures. This simulation is otherwise identical to PlankTOM11 except for the top predator mortality term for meso- and macrozooplankton, which were returned to pre-jellyfish values, to account for the lack of predation by jellyfish. Macrozooplankton mortality was then tuned from this value to account for the change to the growth calculation (Table 5). The second additional simulation is carried out to test the addition of an 11th PFT in comparison to the addition of jellyfish as the 11th PFT. This is done by parameterising the jellyfish PFT identically to the macrozooplankton PFT, so that there are 11 PFTs active, with two macrozooplankton. This simulation is called PlankTOM10.5. Otherwise, these simulations were identical to PlankTOM11.

2.2. JELLYFISH BIOMASS OBSERVATIONS

MARine Ecosystem biomass DATa (MAREDAT) is a database of global ocean plankton abundance and biomass, harmonised to common units and is open source available online (Buitenhuis et al., 2013b). The MAREDAT database is designed to be used for the validation of global ocean biogeochemical models. MAREDAT contains global quantitative observations of jellyfish abundance and biomass as part of the generic macrozooplankton group (Moriarty et al., 2013). The jellyfish subset of data has not been analysed independently yet.

For this study, all MAREDAT records under the group Cnidaria medusae ('true' jellyfish) were extracted from the macrozooplankton group (Moriarty et al., 2013) and examined. The taxonomic level within the database varies from phylum down to species. The data covers the period from August 1930 to August 2008 and contains abundance (individuals/m^3, n=107,156) and carbon biomass (μg carbon L^{-1}, n=3,406). The carbon biomass data are used over the abundance data despite the fewer data available, as they can be directly compared to PlankTOM11 results. Carbon biomass is calculated from wet weight/dry weight conversion factors for species where data records are sufficient (Moriarty et al., 2013). The data were collected at depth ranging from 0 to 2442m. The majority of the data (97%) were collected in the top 200m with an average depth of 44m (± 32m). The original ungridded biomass data were binned into 1^{o}x1^o degree boxes at monthly resolution, as in Moriarty et al. (2013)*,* reducing the number of gridded biomass data points to 849.

In MAREDAT, jellyfish biomass data are only present in the Northern Hemisphere, which is likely to skew the data. Another caveat to the data is that a substantially smaller frequency of zeros is reported for biomass than for abundance. Under-reporting of zero values will increase the average, regardless of the averaging method used. Biomass observations from other global studies (Bar-On et al., 2018; Lucas et al., 2014) are used conjunctly with the global jellyfish biomass calculated here because of the poor spatial coverage.

To compare to the other PFTs within the MAREDAT database, global jellyfish biomass was calculated according to the methods in Buitenhuis et al. (2013b). Buitenhuis et al. (2013b) calculate a biomass range, using the median as the minimum and the arithmetic mean (AM) as the maximum. The jellyfish zooplankton biomass range in MAREDAT was calculated as 0.46 – 3.11 PgC, with the median jellyfish biomass almost as high as the microzooplankton and higher than meso- and macrozooplankton (Buitenhuis et al., 2013b). The jellyfish biomass range calculated here is used to validate the new jellyfish component in the PlankTOM11 model.

3. RESULTS

3.1. JELLYFISH BIOMASS

The global jellyfish biomass estimated by various studies gives a range of results: 0.1 PgC (Bar-On et al., 2018), 0.32 ± 0.49 PgC (Lucas et al., 2014) and 0.46 PgC calculated in this study (Sect. 2.2). Jellyfish biomass in PlankTOM11 is within the range but towards the lower end of observations at 0.13 PgC, with jellyfish accounting for 16% of the total zooplankton biomass (Table 6). When the modelled biomass was tuned to match the higher observed biomass by adjusting the mortality rate, jellyfish dominate the entire ecosystem significantly reducing levels of the other zooplankton and increasing chlorophyll above observations for the Northern and Southern Hemispheres (Fig. 4 and Fig. 5).

PlankTOM11 generally replicates the patterns of jellyfish biomass with observations. High biomass occurs at around 50-60°N across the oceans, with the highest average biomass in the North Pacific (Fig. 6; Lucas et al., 2014). PlankTOM11 also replicates low biomass in the Indian Ocean, and the eastern half of the tropical Pacific shows higher biomass than other open ocean areas in agreement with patterns in observations (Fig. 6; Lucas et al., 2014). The lack of biomass observations around 40°S makes it difficult to determine if the peak in jellyfish biomass in PlankTOM11 at this latitude is representative of reality. The maximum biomass in the southern hemisphere is mostly around coastal areas i.e. South America and southern Australia (Fig. 6). This is expected from reports and papers on jellyfish in these areas (Condon et al., 2013 and references therein; Purcell et al., 2007). A prevalence of jellyfish in coastal areas is apparent (Fig. 6), in line with observations (Lucas et al., 2014), even without any specific coastal advantages for jellyfish in the model (see macrozooplankton in Le Quéré et al., 2016).

Jellyfish are characterised by their bloom and bust dynamic, resulting in patchy and ephemeral biomass. The mean:max biomass ratio of observations (MAREDAT) was compared to the same ratio for PlankTOM11 to assess the replication of this characteristic. The observations give a wide range of ratios depending on the type of mean used. The PlankTOM11 ratio falls within this range, but towards the lower end (Table 7). PlankTOM11 replicates some of the patchy and ephemeral biomass of jellyfish.

Jellyfish biomass in MAREDAT has poor global spatial coverage. The region around the coast of Alaska has the highest density of observations and is used here to evaluate the mean and seasonality of the carbon biomass of jellyfish as represented in PlankTOM11. PlankTOM11 reproduces the observed mean jellyfish biomass around the coast of Alaska (0.16 compared to 0.13 μmol C L^{-1}), but it underestimates the maximum and spread of the observations (Table 8). The spatial patchiness is somewhat replicated in PlankTOM11, although with a smaller variation (Fig. 7). PlankTOM11 replicates the mean seasonal shape and biomass of jellyfish with a small peak over the summer followed by a large peak in September in the observations and in October in PlankTOM11 (Fig. 7). Overall, PlankTOM11 replicates the mean but underestimates the maximum biomass and temporal patchiness of the observations (Fig. 7 and Table 8).

3.2 ECOSYSTEM PROPERTIES OF PLANKTOM11

PlankTOM11 reproduces the main characteristics of surface chlorophyll observations, with high chlorophyll concentration in the high latitudes, low concentration in the subtropics and elevated concentrations around the equator (Fig. 8). PlankTOM11 also reproduces higher chlorophyll concentrations in the Northern Hemisphere than the Southern (Fig. 9), and higher concentrations in the southern Atlantic than the southern Pacific Ocean (Fig. 8). Overall the model underestimates chlorophyll concentrations, as is standard with models of this type (Le Quéré et al., 2016) particularly in the central and northern Atlantic. PlankTOM11 also captures the seasonality of chlorophyll, with concentrations increasing in summer compared to the winter for each hemisphere (Fig. 8).

To assess the effect of adding jellyfish to PlankTOM, two additional simulations were conducted: PlankTOM10 where jellyfish growth is set to zero and PlankTOM10.5 where all jellyfish parameters are set equal to macrozooplankton parameters (Sect. 2.1.6). The two simulations show similar spatial patterns of surface chlorophyll to PlankTOM11, but different concentration levels. PlankTOM11 closely replicates the chlorophyll ratio between the north and south with a ratio of 2.12, compared to the observed ratio of 2.16 (Fig. 9). PlankTOM10 and PlankTOM10.5 underestimate the observed ratio with ratios of 1.57 and 1.96 respectively (Fig. 9). Adding an 11th PFT improves the chlorophyll ratio, however, the regional chlorophyll concentrations for PlankTOM10.5 are a poorer match to the observations than PlankTOM11, especially in the north (Fig. 9). PlankTOM10 overestimates the observed chlorophyll concentration in the south (0.22 and 0.18 respectively; Fig. 9). All three simulations underestimate chlorophyll concentration in the tropics compared to observations (Fig. 9). These simulations further support the suggestion by Le Quéré et al. (2016) that the observed distribution of chlorophyll in the north and south is a consequence of trophic balances between the PFTs.

PlankTOM11 underestimates primary production by 10 PgC y^{-1}, export production and N_2 fixation are within the observational range, and $CaCO_3$ export is slightly overestimated (Table 6).

In PlankTOM11 each PFT shows unique spatial distribution in carbon biomass (Fig. 5). The total biomass of phytoplankton is within the range of observations, but the partitioning of this biomass between phytoplankton types differs from observations (Table 6). PlankTOM11 is dominated by mixed-phytoplankton and coccolithophores, together making up 47% of the total phytoplankton biomass. Diatoms and *Phaeocystis* are the next most abundant and fall within the observed range, followed by Picophytoplankton with around half the observed biomass (Table 6). The observations are dominated by picophytoplankton, followed by *Phaeocystis* and Diatoms (Table 6). The modelled mixed-phytoplankton is likely taking up the ecosystem niche of picophytoplankton. Coccolithophores are overestimated by a factor of 10 and may also be filling the ecosystem niche of picophytoplankton in the model (Table 6).

3.3 ROLE OF JELLYFISH IN THE PLANKTON ECOSYSTEM

Other than jellyfish, macrozooplankton exhibit the largest change in biomass between the three simulations, followed by mesozooplankton (Fig. 10). This is despite the higher preference of jellyfish grazing on mesozooplankton (ratio of 10) than on macrozooplankton (ratio of 5; Table 3), suggesting that the interaction between macrozooplankton and jellyfish is dominated by competition for resources rather than by their mutual predation. Jellyfish and macrozooplankton both preferentially graze on mesozooplankton and protozooplankton. The greatest difference in PFT biomass between simulations occurs in latitudes higher than 30º (Fig. 10). In the tropics, jellyfish have a low impact on the ecosystem due to their low biomass in this region (Fig. 6 and Fig. 10).

The seasonality of the PFTs in each simulation is shown in Fig. 11 for 30-70º north and south, as the regions with the greatest differences between simulations (Fig. 10). In PlankTOM10 macrozooplankton represent the highest trophic level. The addition of another PFT at the same or at a higher trophic level (PlankTOM10.5 and PlankTOM11 respectively) greatly reduces the biomass of the macrozooplankton, through a combination of competition and low-level predation (Fig. 10 and Fig. 11). The addition of jellyfish changes the zooplankton with the highest biomass from macrozooplankton to protozooplankton, in both the north and south (Fig. 11). However, the addition of jellyfish has a small impact on the biomass of protozooplankton (Fig. 11), despite the high prey preference of jellyfish for protozooplankton. The small impact of jellyfish on protozooplankton biomass may be due to trophic cascade effects where jellyfish reduce the biomass of macrozooplankton, which reduces the predation pressure of macrozooplankton on protozooplankton, whilst jellyfish provide an additional predation pressure on protozooplankton. The decrease in predation by macrozooplankton may be compensated for by the increase in predation by jellyfish.

In PlankTOM11 there is a clear distinction between the biomass in the north and south, with higher biomass for each PFT in the north compared to the south (Fig. 10 and Fig. 11). Plankton types have higher concentrations in the respective hemisphere's summer, and a double peak in phytoplankton in the north (Fig. 10 and Fig. 11). PlankTOM10 also has a higher biomass of each PFT in the north compared to the south, but the difference is smaller than that in PlankTOM11 (Fig. 10 and Fig. 11). The key difference between the two models is the biomass of macrozooplankton. In PlankTOM10 macrozooplankton are the dominant zooplankton, especially in late summer and autumn where their biomass matches and even exceeds the biomass of phytoplankton in the region (Fig. 11). In

PlankTOM11 neither macrozooplankton, nor any other zooplankton, come close to matching the biomass of phytoplankton. The largest direct influence of jellyfish in these regions is its control on macrozooplankton biomass.

In PlankTOM11 in the north, phytoplankton display a double peak in seasonal biomass, with a smaller peak in April of 2.4 μmol C L^{-1}, followed by a larger peak in July of 3.2 μmol C L^{-1} (Fig. 11). The addition of jellyfish amplifies these peaks from PlankTOM10 and PlankTOM10.5 (Fig. 11) and from PlankTOM10 (Le Quéré et al., 2016).

4. DISCUSSION

Model results suggest high competition between macrozooplankton (crustaceans) and jellyfish. The growth rate of jellyfish is higher than that of macrozooplankton for the majority of the ocean (where the temperature is less than 25°C) but the mortality of jellyfish is also significantly higher than macrozooplankton, again for the majority of the ocean. In situations where jellyfish mortality is reduced (but still higher than macrozooplankton mortality), jellyfish outcompete macrozooplankton for grazing. Because jellyfish also prey directly on macrozooplankton, the biomass of macrozooplankton can rapidly decrease in a positive feedback mechanism. This sensitivity of the composition of the zooplankton community to the mortality of jellyfish could help explain why jellyfish are seen as increasing globally. A reduction in jellyfish mortality during early life-stages i.e. through reduced predation on planula larvae and juveniles by fish (Duarte et al., 2013; Lucas et al., 2012), could quickly allow jellyfish to outcompete other zooplankton, especially macrozooplankton.

The high patchiness of jellyfish in the observations is partly but not fully captured in PlankTOM11 (Fig. 7 and Table 7). The reasons for limited patchiness include the model resolution of ~2°x1° which doesn't allow for the representation of small-scale physical mixing such as eddies and frontal regions, which have been shown to influence bloom formation (Benedetti-Cecchi et al., 2015; Graham et al., 2001). Physical processes are likely to be more responsible for jellyfish patchiness than behaviours, due to their simplistic locomotion. For example, many jellyfish blooms occur around fronts, upwelling regions, tidal and estuarine regions, and shelf-breaks where currents can aggregate and retain organisms (Graham et al., 2001). A few large individuals of the species *Rhizostoma octopus* (barrel jellyfish) have been found to have the capacity to actively swim counter current and orientate themselves with currents to aid bloom formation and retention (Fossette et al., 2015). However, this active swimming behaviour is not representative across the group and would only move the jellyfish within an area less than the resolution of the model. Furthermore, there is currently insufficient data and an incomplete understanding of such swimming behaviours to include it in a global model.

The maximum biomass of jellyfish in PlankTOM11 is 98.9 μg C L^{-1}, compared to the observed maximum biomass of 156 μg C L^{-1} and the mean:max ratio is within the range of observations although towards the lower end (Table 7). This demonstrates that even without replication of high patchiness, PlankTOM11 still achieved some ephemeral blooms where jellyfish achieved a high biomass.

A key limitation of jellyfish representation in the model is the lack of a life cycle. Many jellyfish alternate between asexual (budding during the polyp stage) and sexual (broadcast spawning) reproduction (Brotz et al., 2012). Temperature cues have been found to trigger budding of ephyrae, increasing the medusa population (Han and Uye, 2010; Lucas and Dawson, 2014). Data on the polyp stage of jellyfish is largely focussed on common species and almost exclusively lab-based, with the patterns observed being locale- and species-dependant. Modelling of jellyfish life cycles is still relatively new, with the focus of previous modelling studies also being locale- and species-dependant (Henschke et al., 2018; Schnedler-Meyer et al., 2018). Higher temperature within PlankTOM11 increases the growth rate, which translates into increased biomass if there is sufficient food, thus providing a representation of an increasing medusa population. The inclusion of jellyfish life cycles into PlankTOM11 would be a large undertaking, outside the scope of this study. The aim of this study was not to reproduce small-scale blooms, but rather to assess at the large and global scale the influence of jellyfish on the plankton ecosystem and biogeochemistry.

There is currently no coastal advantage for jellyfish included in the model, as there is for macrozooplankton, which have a coastal and under-ice advantage for increased recruitment (Le Quéré et al., 2016). Introducing a similar coastal advantage for jellyfish could introduce an element of life cycle benefits i.e. the increased recruitment and settlement of planula larvae onto hard substrate in coastal regions and also ephyrae released from nearshore systems may benefit from being in nearshore waters (restricted there by mobility and current-closure systems) in much the same way as for other neritic planktonic taxa (Lucas et al., 2012).

Jellyfish in PlankTOM11 are parameterised using data largely from temperate species, because this is the majority of the data available. This may explain some of the prevalence of jellyfish in PlankTOM11 at mid- to high-latitudes and the lower biomass in the tropics. Experimental rate data for a wider range of jellyfish species from a wider range of latitudes is required to address this bias. Another limitation of jellyfish representation in the model is the lack of body size representation. Most biological activity is from small individuals, while most of the biomass is from large individuals. The size distribution of body mass in jellyfish is particularly wide compared to other PFTs (Table 1), so representing jellyfish activity by an average sized individual could well skew the results.

Trophic interactions explain the improvement of spatial chlorophyll with the introduction of jellyfish to the model (PlankTOM10 to PlankTOM10.5 to PlankTOM11), especially the North/South ratio. The three simulations have identical physical environments, with the influence of jellyfish as the only alteration, so any differences between the three can be attributed to the ecosystem structure. Jellyfish are the highest trophic level represented in PlankTOM11, with preference for meso-, followed by proto-, and then macrozooplankton. However, the largest influence of jellyfish is on the macrozooplankton, because the grazing pressure on mesozooplankton from macrozooplankton is reduced, and the grazing on protozooplankton by macro- and mesozooplankton is reduced, while the grazing pressure from jellyfish on both meso- and protozooplankton is increased. The combined changes to macrozooplankton and jellyfish grazing pressure counteract to reduce the overall change in grazing pressure. The top down trophic cascade from jellyfish on the other zooplankton also changes some of the grazing pressures on the phytoplankton, which translates into regional and seasonal effects on chlorophyll.

3.5 CONCLUSION

Jellyfish have been included as a PFT in a global ocean biogeochemical model for the first time as far as we can tell at the time of writing. The PlankTOM11 model provides reasonable overall replication of global ecosystem properties and improved surface chlorophyll, particularly the north/south ratio. The replication of global mean jellyfish biomass, 0.13 PgC, is within the observational range, and in the region with the highest density of observations PlankTOM11 closely replicates the mean and seasonal jellyfish biomass. There is a deficit of data on jellyfish carbon biomass observations and physiological rates. Monitoring and data collection efforts have increased over recent years; we recommend a further increase especially focussing in less-surveyed regions and on non-temperate species.

Jellyfish exert control over the other zooplankton, with the greatest influence on macrozooplankton. Through trophic cascades jellyfish also influence the phytoplankton. PlankTOM11 is a successful first step in the inclusion of jellyfish in global ocean biogeochemical modelling. The model raises interesting questions about the sensitivity of the zooplankton community to changes in jellyfish mortality and calls for an investigation in interactions between macrozooplankton and jellyfish. Future model development could include an exploration of the life cycle, coastal advantages, and higher resolution ocean physical processes to enhance patchiness.

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Table 1. Size range and descriptions of PFT groups used in PlankTOM11. Adapted from Le Quéré et al. (2016).

Name	**Abbreviation**	**Size Range μm**	**Description/Includes**
Autotrophs			
Pico-phytoplankton	PIC	0.5 – 2	Pico-eukaryotes and non N_2-fixing cyanobacteria such as Synechococcus and Prochlorococcus
N_2-fixers	FIX	0.7 – 2	Trichodesmium and N_2-fixing unicellular cyanobacteria
Coccolithophores	COC	5 – 10	
Mixed-phytoplankton	MIX	2 – 200	e.g. autotrophic dinoflagellates and chrysophytes
Diatoms	DIA	20 – 200	
Phaeocystis	PHA	120 – 360	Colonial Phaeocystis
Heterotrophs			
Bacteria	BAC	0.3 – 1	Here used to subsume both heterotrophic Bacteria and Archaea
Protozooplankton	PRO	5 – 200	e.g. heterotrophic flagellates and ciliates
Mesozooplankton	MES	200 – 2000	Predominantly copepods
Macrozooplankton	MAC	>2000	Euphausiids, amphipods, and others, called ‘macrozooplankton’
Jellyfish zooplankton	JEL	200 – >20,000	Cnidaria medusa, ‘true jellyfish’

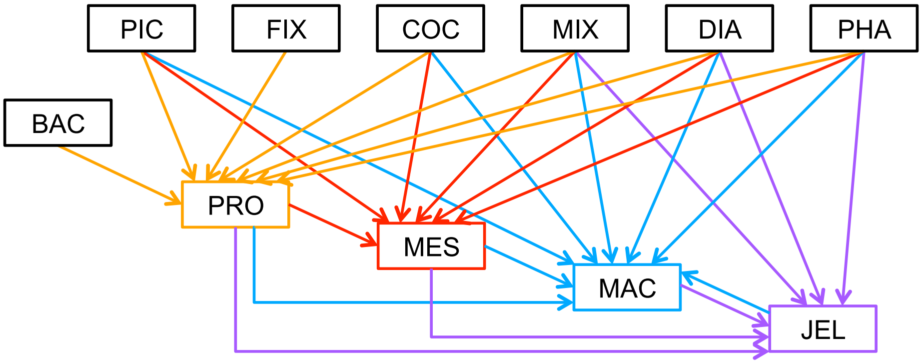

Figure 1. Schematic representation of the PlankTOM11 marine ecosystem model (see Table 1 for PFT definitions). The arrows represent the grazing fluxes by protozooplankton (orange), mesozooplankton (red), macrozooplankton (blue) and jellyfish zooplankton (purple). Only fluxes with relative preferences above 0.1 are shown (see Table 3).

Table 2. Parameters used to calculate PFT specific growth rate with three-parameter fit (Eq. 3) in PlankTOM11.

PFT	**μ_{max} (d^{-1})**	**T_{opt} (°C)**	**dT (°C)**
FIX	0.2	27.6	8.2
PIC	0.8	24.8	11.2
COC	1.0	20.4	7.4
MIX	1.1	34.0	20.0
PHA	1.4	15.6	13.0
DIA	1.3	23.2	17.2
BAC	0.4	18.8	20.0
PRO	0.4	22.0	20.0
MES	0.4	31.6	20.0
MAC	0.2	33.2	20.0
JEL	0.2	23.6	18.8

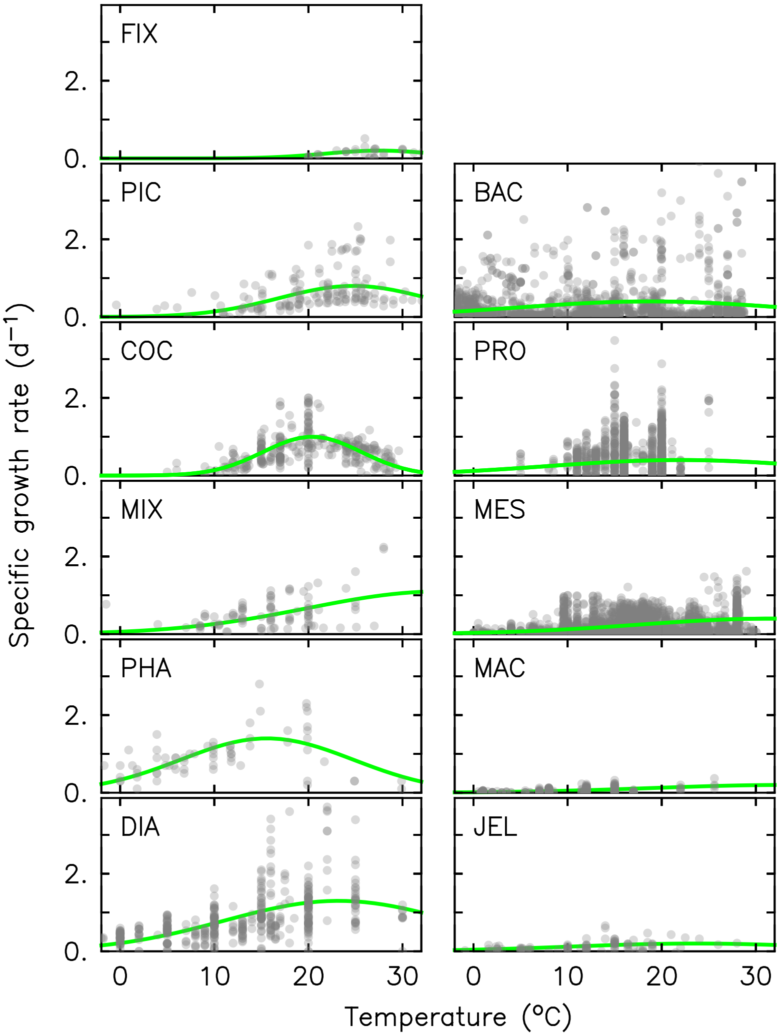

Figure 2. Maximum growth rates for the 11 PFTs as a function of temperature from observations (grey circles). The three-parameter fit to the data is shown in green, using the parameter values from Table 2. For full PFT names see Table 1.

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Table 3. Relative preference, expressed as a ratio, of zooplankton for food (grazing) used in PlankTOM11. For each zooplankton the preference ratio for diatoms is set to 1.

PFT	PRO	MES	MAC	JEL
Autotrophs				
FIX	2	0.1	0.1	0.1
PIC	3	0.75	0.5	0.1
COC	2	0.75	1	0.1
MIX	2	0.75	1	1
DIA	1	1	1	1
PHA	2	1	1	1
Heterotrophs				
BAC	4	0.1	0.1	0.1
PRO	0	2	1	7.5
MES	0	0	2	10
MAC	0	0	0	5
JEL	0	0	0.5	0
Particulate matter				
Small organic particles	0.1	0.1	0.1	0.1
Large organic particles	0.1	0.1	0.1	0.1

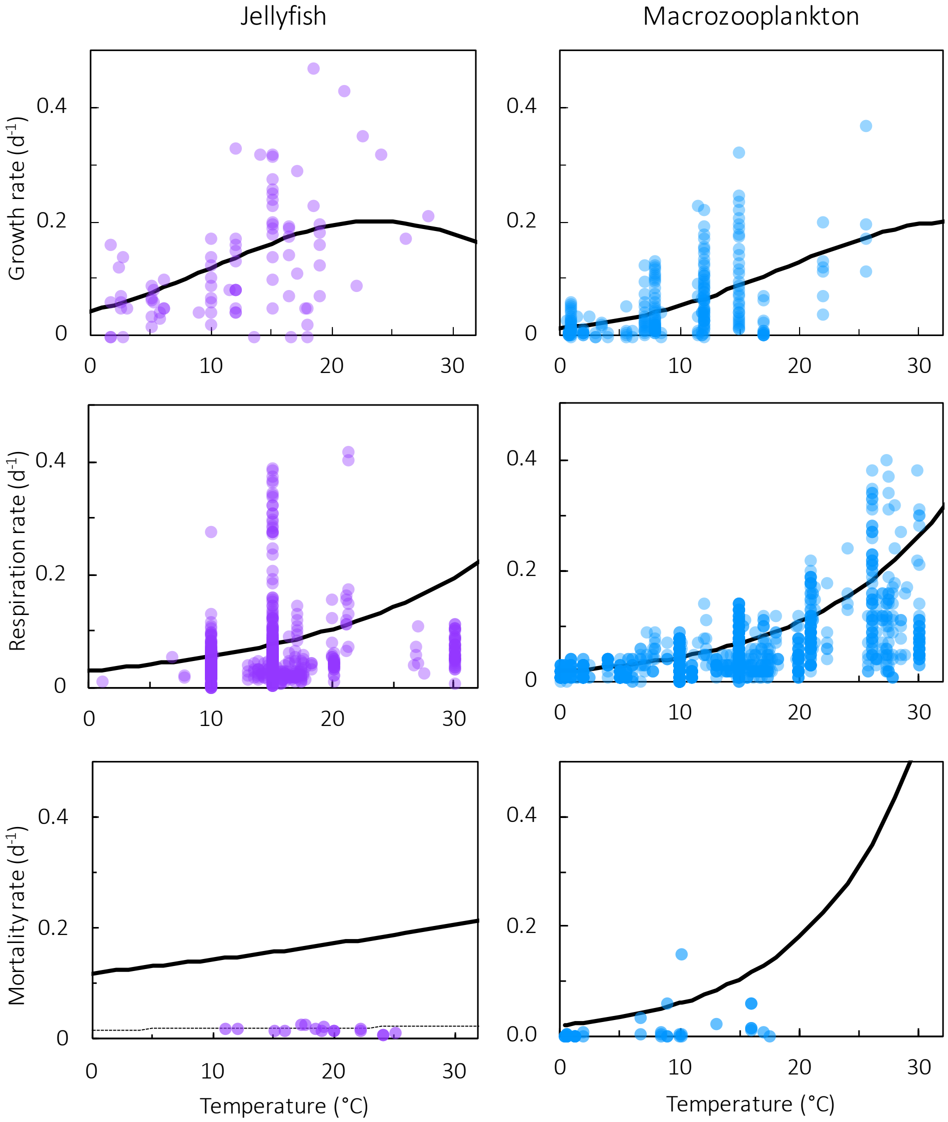

Figure 3. Maximum growth rates (top), respiration rates (middle) and mortality rates (bottom) for jellyfish (left; purple) and macrozooplankton (right; blue) PFTs as a function of temperature. The fit to the data is shown in black, using the parameter values from Table 2 and Table 4. Growth rates are the same as shown in Fig. 2, on a different scale. For jellyfish mortality the thin dashed line is the fit to data and the solid line is the adjusted fit (Table 4).

Table 4. Temperature dependent rates of respiration and mortality for macro- and jellyfish zooplankton. Where μ_0 is the rate at 0°C and Q_{10} is the temperature coefficient (Eq. 2).

Parameters	**JEL**		**MAC**	
	μ_0 (d^{-1})	**Q_{10}**	**μ_0 (d^{-1})**	**Q_{10}**
Respiration	0.03	1.88	0.01	2.46
Mortality	0.12	1.20	0.02	3.00

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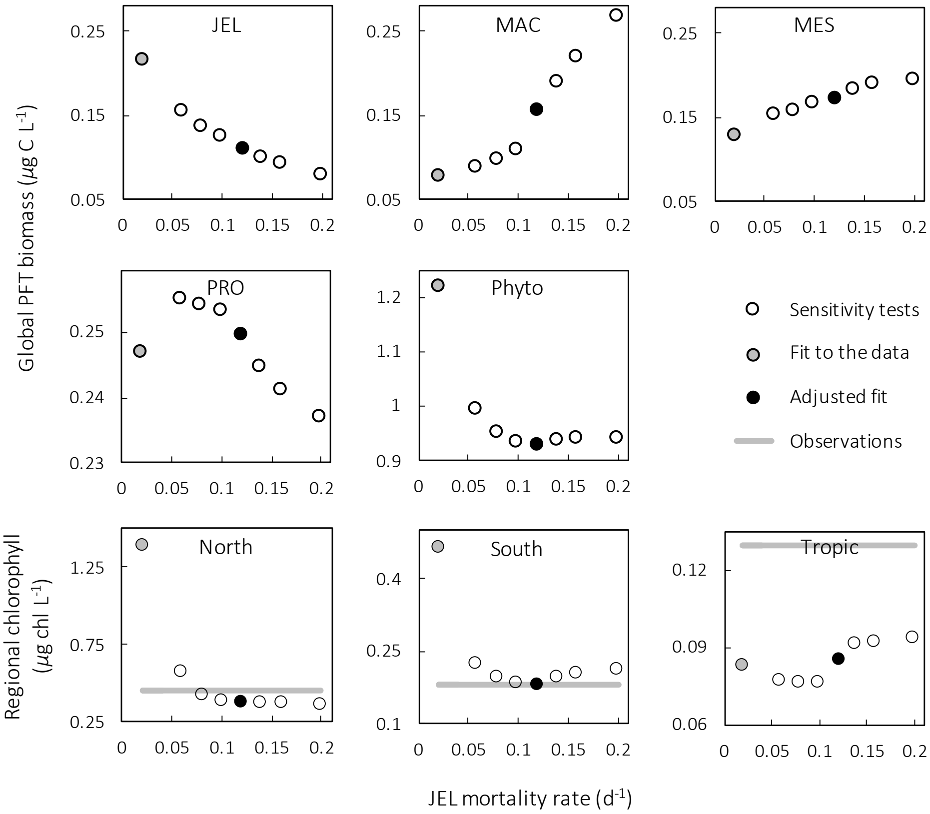

Figure 4. Results from sensitivity tests on jellyfish mortality rates. The adjusted fit simulation used for PlankTOM11 is shown by the black filled circle and the fit to the data simulation is shown by the grey filled circle; global mean PFT biomass (μg C L^{-1}) for 0-200m depth (top - middle), regional mean surface chlorophyll concentration (μg chl L^{-1}; bottom). For the regional mean chlorophyll the observations are calculated from SeaWiFS. All data are averaged for 1985-2015, and between 30º and 55º latitude in both hemispheres: 140-240ºE in the north and 140-290ºE in the south (see Fig. 8). Phyto is the sum of all the phytoplankton PFTs.

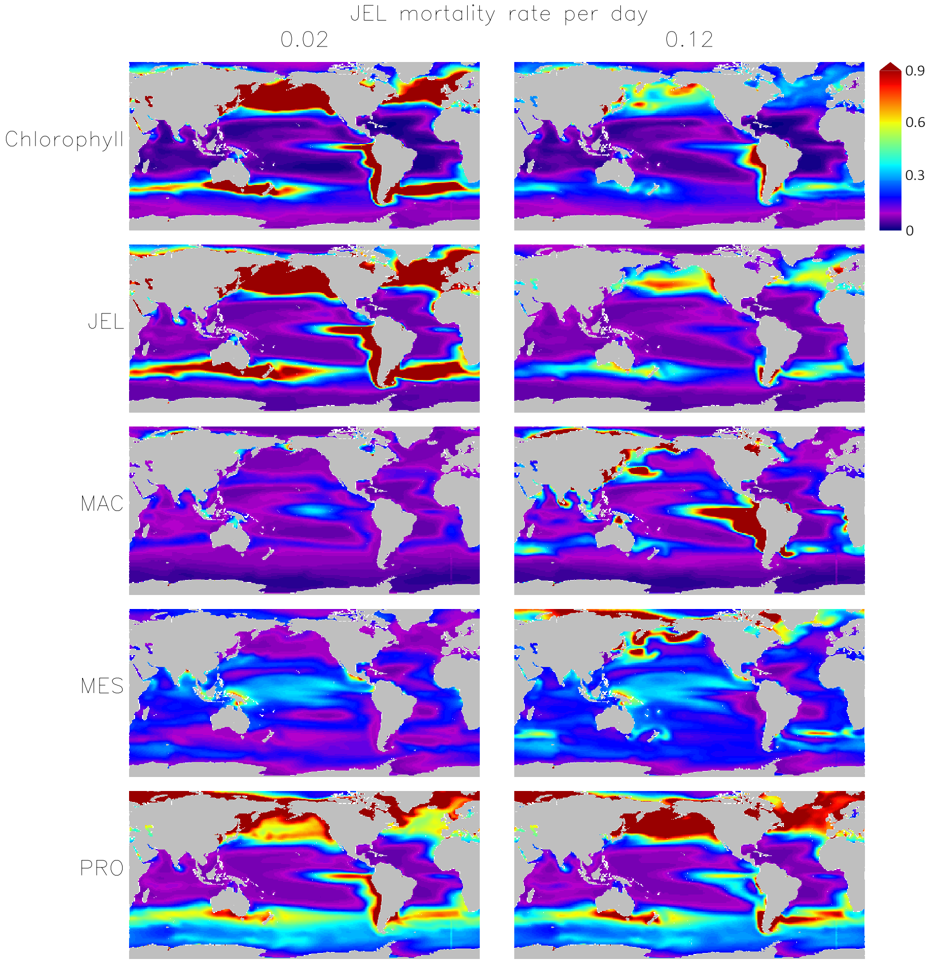

Figure 5. Annual mean surface chlorophyll (μg chl L^{-1}) and zooplankton carbon biomasses (μg C L^{-1}) of JEL, MAC, MES and PRO for adjustment of JEL mortality for the simulation with 0.02 mortality/d^{-1} (left) and the adjusted fit simulation with 0.12 mortality/d^{-1} (right) used in PlankTOM11. Results are shown for the surface box (0-10 meters) and averaged for 1985-2015.

Table 5. Changes to non-jellyfish PFT parameters. PlankTOM10 (2016) is the latest published version of PlankTOM with 10 PFTs (Le Quéré et al., 2016).

Parameters	**PlankTOM10 (2016)**	**PlankTOM11**	**PlankTOM10 (this study)**
MAC mortality	0.020	0.005	0.012
MES respiration	0.014	0.001	0.014

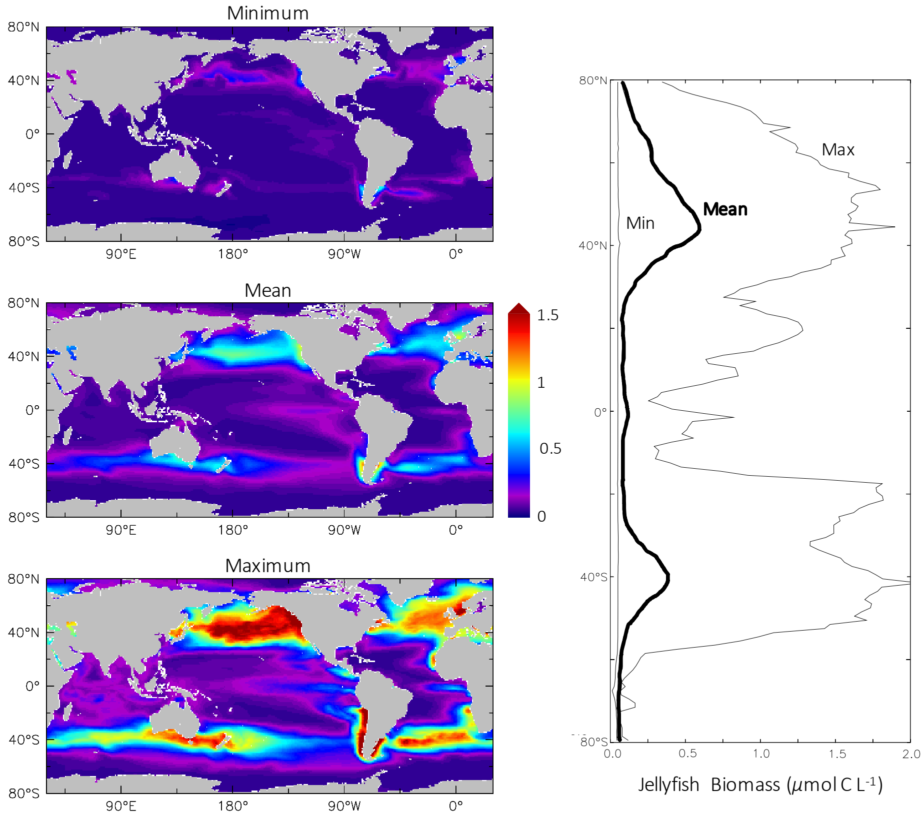

Figure 6. Annual surface carbon biomasses (μmol C L^{-1}) for the jellyfish PFT in PlankTOM11. Results are the mapped monthly minimum (top left), mean (middle left) and maximum (bottom left) from monthly climatologies, and averaged over longitude (right) for the minimum, mean and maximum. All data is for 1985-2015.

Table 6. Global mean values for rates and biomass from observations and the PlankTOM11 and PlankTOM10 models averaged over 1985–2015. In parenthesis is the percentage share of the plankton type of the total phytoplankton or zooplankton biomass. References for observations are given in the appendix. Adapted from Le Quéré et al. (2016).

	PlankTOM11	**PlankTOM10**	**Observations**
Rates			
Primary production (PgC y^{-1})	41.6	43.4	51-65
Export production at 100m (PgC y^{-1})	7.1	7.0	5-13
$CaCO_3$ export at 100m (PgC y^{-1})	1.3	1.2	0.6-1.1
N_2 fixation (TgN y^{-1})	97.2	95.9	60-200
Phytoplankton biomass 0-200 m (PgC)			
N_2-fixers	0.065 (6.1%)	0.075 (7.2%)	0.008-0.12 (2-8%)
Picophytoplankton	0.141 (13%)	0.153 (15%)	0.28-0.52 (35-68%)
Coccolithophores	0.248 (23%)	0.212 (20%)	0.001-0.032 (0.2-2%)
Mixed-phytoplankton	0.263 (24%)	0.268 (26%)	-
Phaeocystis	0.177 (16%)	0.170 (16%)	0.11-0.69 (27-46%)
Diatoms	0.183 (17%)	0.167 (16%)	0.013-0.75 (3-50%)
Total phytoplankton biomass	1.077	1.046	0.412 – 2.112
Heterotrophs biomass 0-200 m (PgC)			
Bacteria	0.041	0.046	0.25-0.26
Protozooplankton	0.295 (36%)	0.330 (32.7%)	0.10-0.37 (27-31%)
Mesozooplankton	0.193 (23%)	0.218 (21.6%)	0.21-0.34 (25-66%)
Macrozooplankton	0.205 (25%)	0.460 (45.6%)	0.01-0.64 (3-47%)
Jellyfish zooplankton	0.129 (16%)	-	0.10-3.11
Total zooplankton biomass	0.823	1.008	0.42 – 4.46

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Table 7. Jellyfish biomass globally from observations (MAREDAT) and PlankTOM11. Three types of mean are given for the observations; Med is the median, AM is the arithmetic mean and GM is the geometric mean. The ratios are all scaled to mean = 1. All units are μg C L^{-1}.

		Mean	**Max**	**Ratio**
Observations	AM	3.61	156.0	1 : 43
	GM	0.95	156.0	1 : 165
	Med	0.29	156.0	1 : 538
PlankTOM11	AM	1.18	98.9	1 : 84

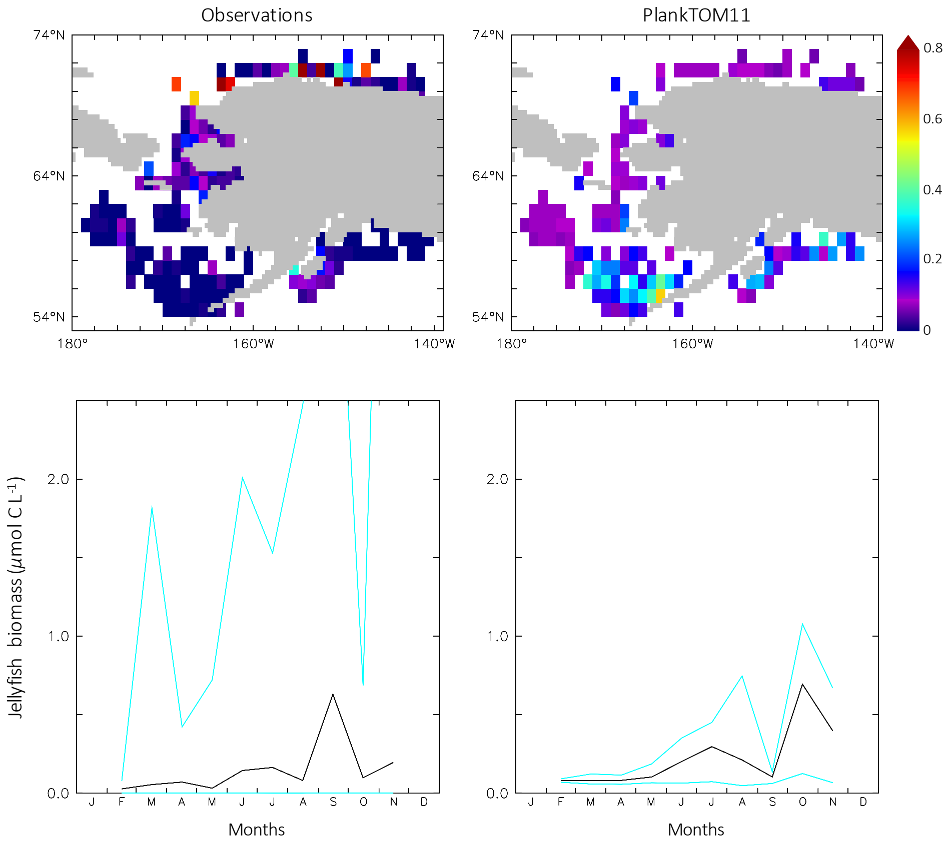

Figure 7. Carbon biomass of jellyfish in μmol C L^{-1} from observations (left) and PlankTOM11 (right) for the coast of Alaska (the region with the highest density of observations). The top panels show the mean jellyfish biomass and the bottoms panels show the seasonal jellyfish biomass, with the monthly mean in black and the monthly minimum and maximum in blue. Observations and PlankTOM11 results are for 0-150m, as the depth range where >90% of the observations occur. No observations were available for January or December.

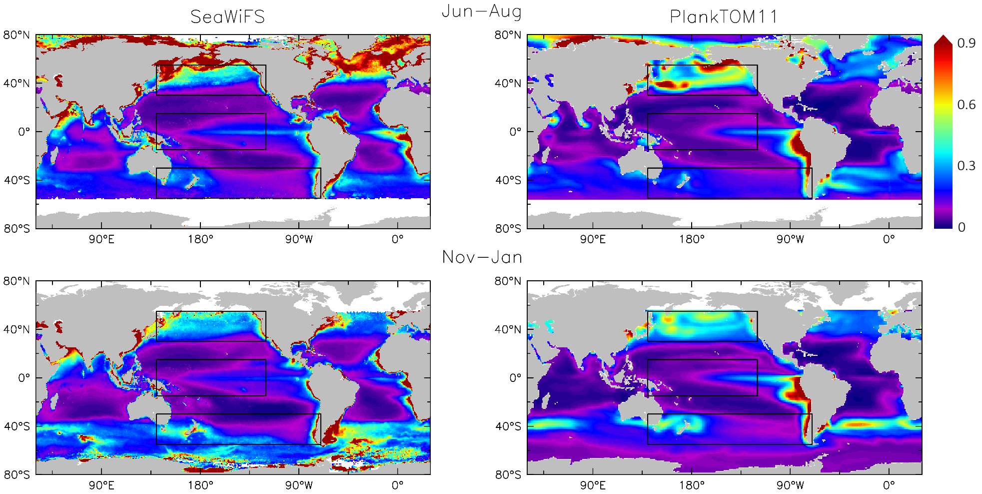

Figure 8. Surface chlorophyll (μg chl L^{-1}) averaged for June to August (top) and November to January (bottom). Panels show observations from SeaWiFS (left) satellite and results from PlankTOM11 (right). Observations and model are averaged for 1997-2006. The black boxes show the North, Tropic and South regions used in Fig. 4 and Fig. 9.

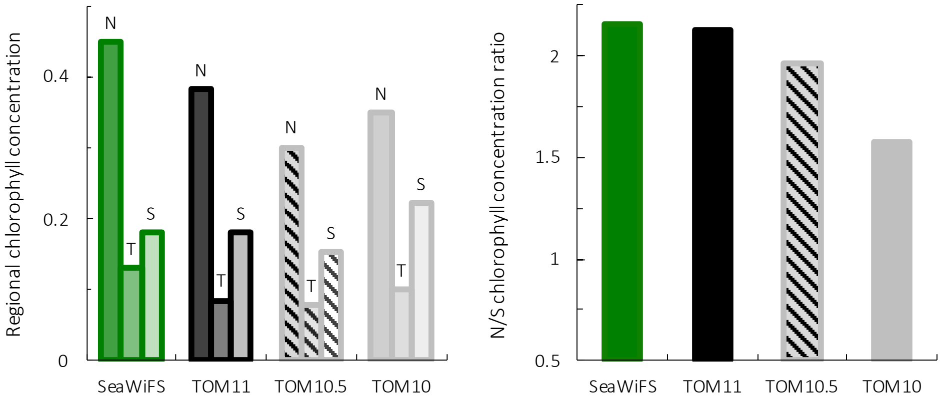

Figure 9. Surface chlorophyll for observations from SeaWiFS satellite, PlankTOM11, PlankTOM10.5 and PlankTOM10. Regional chlorophyll concentration in μg chl L^{-1} (right) for the north (N), tropic (T) and south (S) regions shown in Fig. 8 and the N/S chlorophyll concentration ratio (left). Observations and model are averaged for 1997-2006.

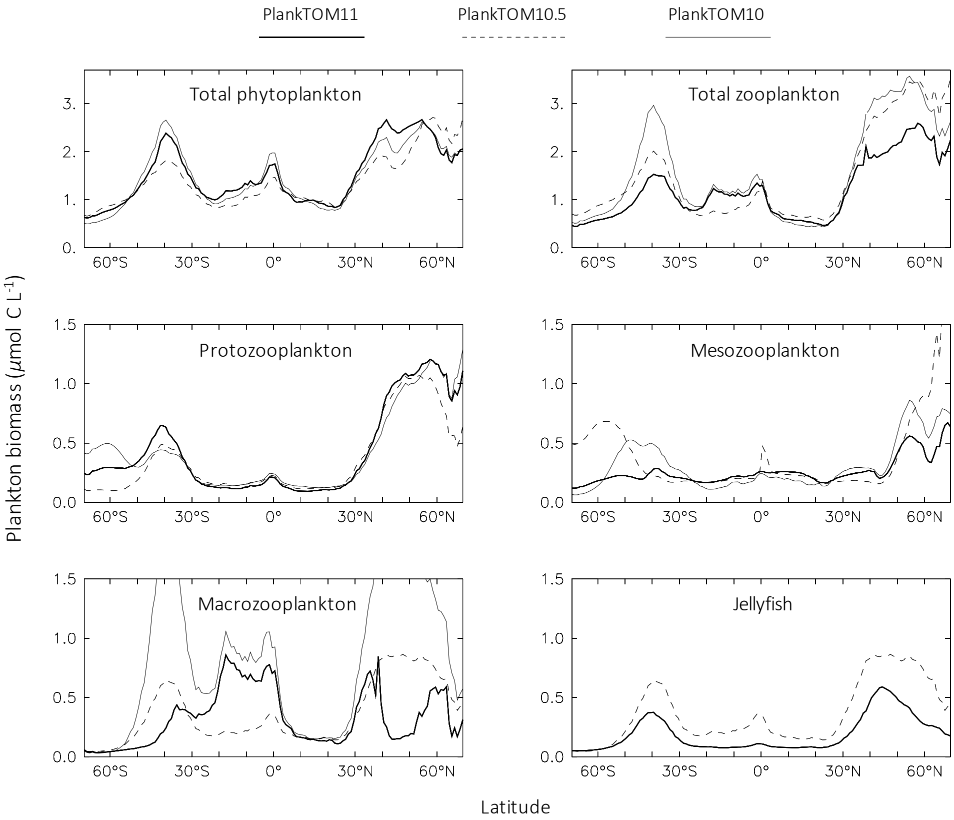

Figure 10. Zonal mean distribution of surface plankton biomass for the PlankTOM11, PlankTOM10.5 and PlankTOM10 simulations. All data are averaged for 1985-2015 for the surface box (0-10m).

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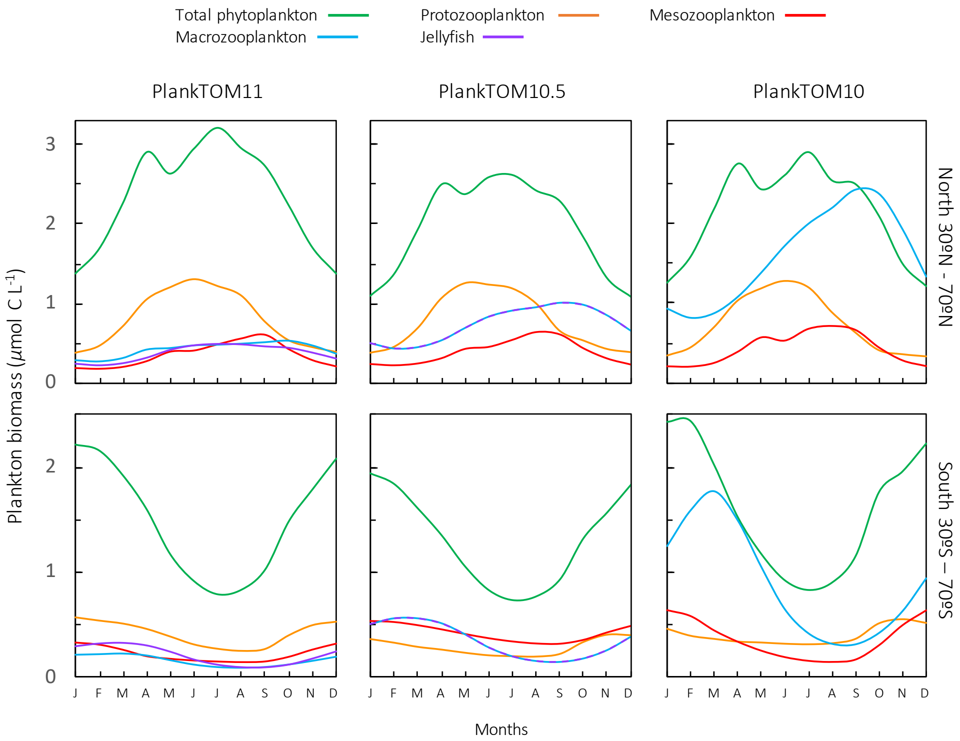

Figure 11. Seasonal surface carbon biomass (μmol C L^{-1}) of total phytoplankton PFTs, protozooplankton, mesozooplankton, macrozooplankton and jellyfish. Panels shown PFT biomass for PlankTOM11 (left), PlankTOM10.5 (middle) and PlankTOM10 (right), for two regions; the north 30ºN - 70ºN (top) and the south 30ºS - 70ºS (bottom) across all longitudes. All data are averaged for 1985-2015 for the surface box (0-10m).

Appendix

Table A1. Global mean values for rates and biomass from observations with the associated references. In parenthesis is the percentage share of the plankton type of the total Phytoplankton or Zooplankton biomass.

	Observations	**Reference for the data**
Rates		
Primary production (PgC y^{-1})	51-65	Buitenhuis et al. (2013b)
Export production at 100m (PgC y^{-1})	5-13	Henson et al. (2011), Palevsky et al. (2018)
$CaCO_3$ export at 100m (PgC y^{-1})	0.6-1.1	Lee (2001), Sarmiento et al. (2002)
N_2 fixation (TgN y^{-1})	60-200	Gruber (2008)
Phytoplankton biomass 0-200 m (PgC)		
N_2-fixers	0.008-0.12 (2-8%)	Luo et al. (2012)
Picophytoplankton	0.28-0.52 (35-68%)	Buitenhuis et al. (2012b)
Coccolithophores	0.001-0.032 (0.2-2%)	O'Brien et al. (2013)
Mixed-phytoplankton	-	-
Phaeocystis	0.11-0.69 (27-46%)	Vogt et al. (2012)
Diatoms	0.013-0.75 (3-50%)	Leblanc et al. (2012)
Heterotrophs biomass 0-200 m (PgC)		
Bacteria	0.25-0.26	Buitenhuis et al. (2012a)
Protozooplankton	0.10-0.37 (27-31%)	Buitenhuis et al. (2010)
Mesozooplankton	0.21-0.34 (25-66%)	Moriarty and O'Brien (2013)
Macrozooplankton	0.01-0.64 (3-47%)	Moriarty et al. (2013)
Jellyfish zooplankton	0.10-3.11	Bar-On et al. (2018), Lucas et al. (2014), Buitenhuis et al. (2013b)

Author Contribution

RMW, CLQ, ETB and SP conceptualized the research goals and aims. RMW carried out the formal analysis with contributions from CLQ and ETB. RW developed the model code with significant contributions from ETB, and RMW performed the simulations. RMW prepared the manuscript with contributions from all co-authors.

The authors declare that they have no conflict of interest.

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