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The role of ecosystem function and emergent relationships in the assessment of global marine ecosystem models: a case study with ERSEM

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GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Abstract

Ecosystem models are often assessed using quantitative metrics of absolute ecosystem state, but these model-data comparisons are disproportionately vulnerable to discrepancies in the location of important circulation features. An alternative method is to demonstrate the models capacity to represent ecosystem function; the emergence of a coherent natural relationship in a simulation is a strong indication that the model has a appropriate representation of the ecosystem functions that lead to the emergent relationship. Furthermore, as emergent properties are large scale properties of the system, model validation with emergent properties is possible even when there is very little or no appropriate data for the region under study, or when the hydrodynamic component of the model differs significantly from that observed in nature at the same location and time.

A selection of published meta-analyses are used to establish the validity of a complex marine ecosystem model and to demonstrate the power of validation with emergent properties. These relationships include the phytoplankton community structure, the ratio of carbon to chlorophyll in phytoplankton and particulate organic matter, the ratio of particulate organic carbon to particulate organic nitrogen and the stoichiometric balance of the ecosystem.

These metrics can also inform aspects of the marine ecosystem model not available from traditional quantitative and qualitative methods. For instance, these emergent properties can be used to validate the design decisions of the model, such as the range of phytoplankton functional types and their behaviour, the stoichiometric flexibility with regards to each nutrient, and the choice of fixed or variable carbon to nitrogen ratios.

GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

1 Introduction

Numerical models of the environment are used frequently for informing policy decisions, for forecasting the impact of climate change, and to obtain a deeper understanding of nature. However, in order for a model to be used for any of these purposes, the model must first be shown to be a valid representation of the system under study. There are two objective strategies available to demonstrate that the model is a valid representation of the system under study. The first strategy is to reproduce the spatial and temporal distributions of historic observations, and the second is to reproduce the functional relationships.

There is a long history of works which demonstrate model validation using static fields, spatial distributions and dynamic variability, including Droop (1973); Fasham et al. (1990); Taylor (2001); Blackford (2004); Allen et al. (2007); Jolliff et al. (2009); Shutler et al. (2011); Saux Picart et al. (2012); de Mora et al. (2013); Kwiatkowski et al. (2014). However, validating a modern ecosystem model using static fields and spatial distributions may give an appropriate assessment of the coupled biogeochemical and hydrodynamic modelled system, but the performance of the ecosystem model may be obscured by deficiencies in the modelled circulation. For instance, the point-to-point analysis described in de Mora et al. (2013) is vulnerable to discrepancies between the model and the observations in the location of important circulation features such as fronts, coastlines or up-welling regions. Validation methods that use historic data are also sensitive to initial conditions and the boundary conditions of the model. These problems are amplified for models with coarse spatial and temporal resolution, such as the monthly mean of a 1° global model. The disentanglement of the performance of the biogeochemical model from that of the physics is a major challenge in marine ecosystem modelling (Holt et al., 2014).

Furthermore, these methods risk compartmentalising the validation of ecosystems and may not cover the interaction of their parts. The ability of a model to represent present day measurements are important, but it does not inform about the models

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

representation of the behaviour of the ecosystem as a whole. Historical static fields may not necessarily validate a model which is subjected to a changing climate due to the scarce availability of long-term time-series datasets.

As a solution to the problem of the absence of data and presence of poorly constrained physics, Holt et al. (2014) wrote “there is a need for metrics that assess the fidelity of the biogeochemical processes independently of the physics”. In that work, they identify one such functional relationship: the link between diatom chlorophyll and total community chlorophyll. They demonstrated that the fraction of the community chlorophyll that originates in diatoms increases with total chlorophyll. In effect, a well known relationship seen in many in situ datasets also appeared in multiple biogeochemical models. This relationship is important because it occurred independently of the hydrodynamic model, and because it reflected the functioning of the modelled ecosystem in a way that would not be visible in a simple point-to-point comparison of ecosystem state.

Many interacting parts of an ecosystem can affect the balance of diatoms chlorophyll against the total community chlorophyll: the diatoms response to nutrients, light and temperature; competition for light and nutrients from other phytoplankton; and the predation on diatoms and other phytoplankton. Each of these interactions between two or more components of the ecosystem are examples of “ecosystem functions”. In the context of marine ecosystem modelling, ecosystem functions are physical, biological or geochemical interactions, processes or relationships that take place within a models framework. Ecosystem function in models can be both explicitly enforced during the model development and tuning, or they can emerge without being explicitly parameterized. The interplay of multiple ecosystem functions often results in the emergence of observable relationships. The link between diatom chlorophyll and total community chlorophyll, as shown by Holt et al. (2014), is an example of such an “emergent relationship”. These emergent relationships can be used to characterise and validate the ecosystem and its functioning. As in the example from Holt et al. (2014), these emergent relationship are important because they occurred independently of the hy-

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

drodynamic model, and because they reflect the functioning of the modelled ecosystem in a way that would not be visible in a simple point-to-point comparison of ecosystem state.

In addition, model validation with emergent properties can be more valuable than a direct comparison of model to experiments, such as primary production bottle measurements. This is because emergent property validation are a large scale test of many combinations of factors, simultaneously testing the model in a wide range of physical and biogeochemical environments.

A selection of historically published large-scale emergent relationships are proposed to illustrate the validation of a complex ecosystem model and demonstrate the power of emergent property validation. The example ecosystem model used here is the European Regional Seas Ecosystem Model (ERSEM), and it is run in a coupled NEMO-ERSEM global hindcast scenario. The emergent relationships shown here are the community structure, the carbon to chlorophyll ratio, the ratio of particulate organic carbon against particulate organic nitrogen and stoichiometric balance.

After this introductory section, Sect. 2 contains a brief description of the circulation model, NEMO, the ecosystem model, ERSEM, and the sea ice model, CICE, used in this study. Section 3 is a non-exhaustive list of examples of ecosystem relationships that have been investigated in the ERSEM ecosystem model. An expanded version of the community structure relationship described by Holt et al. (2014) is included in Sect. 3.1. Section 3.2 shows the ratio of carbon to chlorophyll in phytoplankton and particulate organic matter. Section 3.3 demonstrates how the model reproduces the ratio of particulate organic carbon and nitrogen as described by Redfield (1934); Martiny et al. (2013). Section 3.4 illustrates the internal stoichiometric relationships for ERSEM for each of the nutrient currencies modelled. Finally, Sect. 4 discusses the successes, potential and limitations of these methods.

GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



2 The ERSEM and NEMO models

The European Regional Seas Ecosystem Model (ERSEM) is a lower trophic level biogeochemical cycling, carbon based process model that uses the functional-group approach (Blackford, 2004). The carbon, nitrogen, phosphorus, silicon and iron cycles are explicitly resolved. The pelagic ERSEM model simulates four phytoplankton functional types, three zooplankton functional types, one bacterial functional type and six detritus size classes. It contains variable stoichiometric ratios for each of the plankton functional types. ERSEM can be run in parallel with any one of a range of benthic models of varying complexity, the parametrisation used for this publication uses a simple parametrisation of remineralization where sedimented organic matter is recycled to the water column in inorganic form.

The initial nutrient conditions for nitrate, phosphorus and silicate were taken from the World Ocean Atlas database (Garcia et al., 2010). The initial iron concentrations were zonally averaged interpolations of the iron data from Tagliabue et al. (2012). The iron dust surface deposition climatology was based on Mahowald et al. (2005). The remaining biogeochemical fields were initialised to low concentrations.

In order to be a better representation of nature, marine ecosystem models like ERSEM are typically run in conjunction with an ocean circulation model, such as the Nucleus for European Modelling of the Ocean, NEMO (Madec, 2008). NEMO is a framework of ocean related engines, ocean dynamics, thermodynamics, sinks and sources, and transport. It was designed to be a flexible tool for studying the ocean and its interactions with the other components of the earth climate system over a wide range of space and time scales. The version of NEMO used in this study was version 3.2 and the ocean circulation model was interfaced with the Los Alamos Sea Ice model, CICE (Hunke et al., 2013). CICE has several interacting components: a thermodynamic sub-model, an ice dynamics sub-model, a vertical and a horizontal transport sub-model.

GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The coupled NEMO-ERSEM-CICE models were run simultaneously in the ORCA1 1° global tripolar grid, with 75 fixed depth layers on the UK Met Office super-computing system, MONSooN. The atmospheric boundary conditions were taken from the CORE2 global air–sea flux dataset (Yeager and Large, 2008). The coupled model was run for 117 years, from 1890 to 2007. The initial conditions for the circulation model at 1890 were taken from a 60 year physics-only climatological spin up from a still global ocean. The first 60 years (1890–1950) of coupled NEMO-ERSEM running were spun up using climatological CORE2 forcing. After 1950, the remaining 57 years were run with the inter-annually variable version of the CORE2 forcing.

The simulation was run as part of the iMarNet project: an inter-comparison project of six UK biogeochemical models (Kwiatkowski et al., 2014). The ERSEM model run shown here is an updated parametrisation relative to the ERSEM model data used in that study. A unique requirement of this project was that the six biogeochemical models were run under identical physical conditions, using the same parameters and settings for NEMO, the same computing resource, the same coding framework and the same initial conditions for nutrients. In other words, the physical parametrisations were prescribed according to specific pre-defined settings and no further changes to the physical settings were permitted.

3 Ecosystem function in marine biogeochemical models

In an ideal world, this work would present a comprehensive set of ecosystem functions to validate any given marine ecosystem model. However, models can differ enormously in their complexity, design choices, parametrisations, location and scope, such that each unique model would need to be validated using different set of emergent properties.

The use of emergent relationships and ecosystem functions to validate models works best under certain conditions. The desired scenario is when the historical measured in situ emergent relationship has been observed multiple times with several independent

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

datasets, is valid over large spatial and temporal ranges, and has been reported with a high statistical probability, if fitted to a mathematical function. The ideal scenario regarding the model version of the ecosystem function is that that is is an emergent property of the model, and is not constrained or imposed in anyway. The modelled emergent property should not be a direct extrapolation of the choices made in model design, the emergent property should not be reproduced in the simulation by tuning a small number of parameters, and the model should not be explicitly tuned to match the data.

As emergent relationships are large scale properties of the system, validation with emergence is possible even when there is very little or no appropriate data for the region under study, or when the physical circulation component of the model differs significantly from that observed in nature at the same location and time. This is one of the strengths of the validation with emergent properties method: it can be used to demonstrate ecosystem model quality in the absence of perfectly simulated physical marine environment or extensive local measurements. Nevertheless, it is important that the model and the data originate from similar marine environments. For instance, emergent property validation can not compensate for a catastrophic failure of the hydrodynamic model, nor can it be used to validate the model in regions with unusual and understudied behaviour. However, it is not crucial to match up the exact locations in model and data, as used in the point to point study in de Mora et al. (2013).

A full understanding of the causal nature of the relationship is not a strict requirement in order to be informative. There are many naturally occurring phenomena for which an explicit explanation is not immediately available, but for which the relationship is nevertheless stable. A well known example is the Redfield ratio, (Redfield, 1934; Arrigo, 2005). Unexplained relationships can inform about the validity of some aspect of the model behaviour. Furthermore, if the model could reproduce a natural emergent property in the absence of a causal relationship, then it may be possible to use the model to discover a causal relationship.

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



The emergence of a coherent natural relationship in a simulation is a strong indication that the model has an appropriate representation of the ecosystem functions that create the emergent relationship. If the emergent relationship is not seen in the model, this implies that the ecosystem functions that bring about the emergence are not correctly implemented in the model. If the emergent relationship is present in the model, but breaks down under certain conditions, this means that those conditions are not correctly modelled. Such break down points can be a combination of extreme physical, chemical or biological conditions, and can be used to pinpoint the limitations of the simulation, allowing for powerful and precise criticisms of the model. However, some caution is required as there may also be break down conditions for the emergent property in nature.

The remainder of this section is a non-exhaustive list of the emergent properties that can be used to validate the NEMO-ERSEM iMarNet hindcast. The first emergent property shown here is an extension of the diatom chlorophyll relationship previously described in Holt et al. (2014).

3.1 Phytoplankton community structure

Phytoplankton are often grouped into size or function based classifications. Phytoplankton cell size can influence a range of ecosystem processes, both internally such as nutrient uptake, metabolic rates, physiology and light absorption. At the ecosystem scale, these individual effects combine together to create functional differences in the community primary production, export, the food web, and light and heat absorption by seawater. Phytoplankton function based classifications are also used, and function can influence the classes role in the ecosystem, their preferred nutrient sources, and their production and export rates.

Many marine ecosystem models use a size or function based classification. The phytoplankton classification in ERSEM follows a size and function based classification. There are four plankton functional types (PFT) in ERSEM. Three of the groups are sized based: nanophytoplankton, picophytoplankton and large phytoplankton. The

fourth group, diatoms, are between nanophytoplankton and large phytoplankton in size but include a silicon component. Each PFT has different nutritive affinities and requirements, metabolic rates, and different desirability as a food source for predators.

In both the ecosystem and in the model, the relative abundance of each class is referred to as the community structure. The relative abundance is often measured in terms of chlorophyll, but it also can be gauged in units of cell count, total cell volume, or carbon or nitrogen biomass. The community structure is dependent on a large number of factors, including: the nutritive affinity and nutritional storage capacity of each PFT relative to each nutrient, the desirability as a food source of each PFT for each zooplankton functional type, and local environmental conditions such as light, temperature and nutritive up-welling. In ERSEM, there is no explicit parametrisation of their absolute or relative abundances, it is a property that arises out of a combination of many ecosystem functions.

The relationship between the abundance of each plankton functional type and the total community chlorophyll has been presented repeatedly with data from both high performance liquid chromatography (HPLC) and size fractionated filtration (SFF) measurements. Five examples of this relationship are Hirata et al. (2011); Devred et al. (2011); Brewin et al. (2012, 2014, 2015). Each of these fits is prepared using a different dataset. Hirata et al. (2011) used multiple HPLC databases from around the world. Devred et al. (2011) used chlorophyll and absorption data from the Northwest Atlantic region that was collected between 1996 and 2003. Brewin et al. (2012) used HPLC data in the Indian ocean taken between 1995 and 2007. Brewin et al. (2014) used SFF from the Atlantic Meridional Transect (AMT) cruises in the Atlantic ocean between 1996 and 2012. Brewin et al. (2015) used a aggregation of 16 unique globally distributed databases.

Figure 1 shows the five fits of in situ community structure and the least squared fit of ERSEM to the three-population absorption model of Brewin et al. (2010). For all three panels, the x axes are the total community chlorophyll, and the y axes are the percentage of the total chlorophyll that came from each PFT. The diatom and

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



large phytoplankton functional types are summed together in the left panel. The middle panel shows nanophytoplankton and the right panel shows picophytoplankton. The dashed vertical line indicates a typical detection limit of HPLC and SFF measurements of $0.1 \text{ mg Chl m}^{-3}$. The Devred et al. (2011); Brewin et al. (2012, 2014, 2015) are also fitted to the three-population absorption model, but the Hirata et al. (2011) is fitted with its own community structure model. The difference between the Hirata model and the three-population model is that the Hirata model is a best fit to the data, whereas the three population model is derived based on empirical principles. Despite their differences, these fits have little variability in the overall shape of the fit between datasets and methodologies.

Note that only the fits are shown in Fig. 1, the in situ data itself is not shown, nor is the model data. Showing the fit as a smooth line hides the substantial spread of the in situ data. For instance, the data shown in the widely published Fig. 2 of Hirata et al. (2011) has already been smoothed with a 5-point running mean, and that running mean is further smoothed to the fit line shown in Fig. 1.

Figure 2 is a three panel plot of phytoplankton community structure showing the model data as a logarithmically scaled two dimensional data density histogram in blue-scale. This figure also shows a fit to the model data, and the in situ data fits from Brewin et al. (2015); Hirata et al. (2011). For clarity, the other fits are not shown. For all three panels, the shared x axis is the total community chlorophyll, and the y -axes are the percentage of the total chlorophyll that came from each PFT. The model data is shown as a logarithmically scaled two dimensional data density histogram in blue-scale. The diatom and large phytoplankton functional types are summed together in the top panel. The middle panel shows nanophytoplankton and the bottom panel shows picophytoplankton. The dashed vertical line indicates a typical detection limited of HPLC and SFF measurements. Note that only the fits to the in situ data are shown, the in situ data itself is not shown. The fit to ERSEM, the Brewin 2015 and the Hirata 2011 lines are identical in Figs. 1 and 2.

The combined picophytoplankton and nanophytoplankton chlorophyll, or “piconano” chlorophyll, $chl_{p,n}$, is calculated in Eq. (2).

$$chl_{p,n} = C_{p,n}^m \cdot (1 - \exp(-S_{p,n} \cdot chl)) \quad (2)$$

where $C_{p,n}^m$ is the maximum piconano chlorophyll and $S_{p,n}$ is the initial slope of the exponential function for piconano. The $chl_{p,n}$ function is not shown explicitly in either Fig. 1 or Fig. 2, but is used in the calculation of the nanophytoplankton, diatoms and large phytoplankton functional types community structure.

Unlike chl_p and $chl_{p,n}$, the nanophytoplankton chlorophyll, chl_n , and microphytoplankton chlorophyll, chl_m , are not explicitly fitted. Instead, their contribution to total community chlorophyll are determined from a combination of Eqs. (1) and (2). The nanophytoplankton chlorophyll, chl_n , shown in Eq. (3), is the difference between the piconano group chlorophyll and the picophytoplankton chlorophyll. This is shown in the middle pane of Figs. 1 and 2.

$$chl_n = chl_{p,n} - chl_p \quad (3)$$

The diatoms and large phytoplankton, (together also known as microphytoplankton) chlorophyll, chl_m , are the remainder of the total chlorophyll that is not accounted for by the piconano component. It is calculated is the difference between the piconano chlorophyll and the total chlorophyll. This is shown in the top pane of Fig. 2.

$$chl_m = chl - chl_{p,n} \quad (4)$$

Just to explicitly state the overarching assumption used here, the total chlorophyll, chl , is equal to the sum of the three components functional types chlorophyll.

$$chl = chl_m + chl_n + chl_p \quad (5)$$

Note that the three fits of Fig. 2 are not free to vary independently. For any given value of total chlorophyll on the x axis, the sum of the three populations must be equal

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

⏪

⏩

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

to 100%. Furthermore, the fits are not free to vary to any shape, they are limited by the structure available to Eqs. (1), (3) and (4). Equations (1) and (2) are fitted to the simulated ERSEM data using in the least squares fit. In addition, the fits are most influenced by the high data density regions in this figure. For these reasons, the fits may not appear to match the overall shape of the model distribution, while still being an acceptable fit.

In the top panel of Fig. 2, there is a cluster of points where the diatom and large phytoplankton functional types unexpectedly dominate the community structure at low total chlorophyll. These points account for less than 0.2% of the data, after the cuts described above were applied. Furthermore, they only appear adjacent to the excluded shallow and polar seas. While there is also some evidence of the proportion of large cell increased in the polar regions (Sosik and Olson, 2002), we postulate that it is a combination of multiple factors that creates this excess microphytoplankton. Firstly, in the polar regions there is an abundance of nutrients, and especially silicon, caused by excessive mixing in the physical model. Secondly, the model is parameterized to favour diatoms in low light regions. These factors collude to create an abundance of diatoms and large phytoplankton at low total chlorophyll. When the polar, shallow and inland sea regions are included in the model, the number of points included in these regions of the figure increases. As an example, the fit to the three population model was performed to all the model data from the top 40 m of the surface. The results of this fit are shown in the ERSEM (Top 40 m) column of Table 1. Relative to the Brewin et al. (2015) fit, the fit for this dataset had an overabundance of diatoms and large phytoplankton and an underestimate of picophytoplankton at almost all chlorophyll concentrations. Nevertheless, it is important to stress that the three population community model is an appropriate emergent property for open ocean outside the polar regions.

Similarly, both Figs. 1 and 2 show that the model has a surplus of diatoms and large phytoplankton at low chlorophyll concentrations in this simulation, which coincides with a low proportion of picophytoplankton. It is likely that this fault is caused by the same factors that cause the microphytoplankton PFT to dominate the community in a small

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

of photosynthetic apparatus. For instance, an increase in carbon relative to chlorophyll may be required to maintain fluidity at cold temperature, or low temperature might impose constraints on the enzyme catalytic reactions. Similarly, each plankton functional type responds in a different way to changes in temperature, affecting the community structure, which may in turn influence the carbon to chlorophyll ratio.

While there are many techniques available for measuring total chlorophyll concentration, the direct measurement of phytoplankton carbon biomass is difficult because it requires the mechanical separation of phytoplankton from the other particulate organic matter. Instead, chlorophyll concentration is typically used as a proxy for phytoplankton biomass. For obvious reasons, comparing biomass derived from total chlorophyll to total chlorophyll is not an independent method for obtaining the carbon to chlorophyll ratio. However, it is possible to measure total community chlorophyll and Particulate Organic Carbon (POC) simultaneously and independently.

A meta-study of simultaneous particulate organic carbon and chlorophyll measurements was published in Sathyendranath et al. (2009). The chlorophyll measurements were divided according to two measurement technologies: high performance liquid chromatography (HPLC) chlorophyll, and Turner fluorometer data. The data used was taken from 16 cruises in the Labrador Sea, the Scotian shelf and the Arabian Sea, between 1993 and 2001. Then they used the accumulated data to produce a fit to the following relationship:

$$\text{POC} = m \cdot \text{chl}^p \quad (6)$$

where POC is the particulate organic carbon, chl is the total community chlorophyll and m and p are the fitted parameters.

In order to study the relationship between phytoplankton carbon and total chlorophyll, Sathyendranath et al. (2009) applied the assumption that “at any given chlorophyll concentration, the lowest particulate carbon observed represents the phytoplankton carbon associated with that chlorophyll concentration.” Then, they used a 1 % quartile regression to determine a relationship between the lowest particulate organic carbon

line. The two Sathyendranath et al. (2009) fits of POC to chlorophyll are also shown in as full lines and the two 1 % quartile regression fits representing phytoplankton carbon against chlorophyll are shown as dashed lines. The parameters of these fits are shown in Table 2.

The two 1 % quartile regressions fits are included in Fig. 3 because they indicate a theoretical lower bound for the modelled POC:Chl field. Approximately 3 % of the data fall below the theoretical lower limit indicated by the 1 % Sathyendranath et al. (2009) Turner line. This is an acceptable fraction, as the 1 % quartile regression was an arbitrary cut off point for the minimum POC concentration for each chlorophyll range in the data. However, the data below this line occur in the model only on the edges of the Arctic and Antarctic oceans in the winter. When the entire model domain is included down to 40 m deep, including the arctic and Antarctic and inland and shallow seas, the fraction of data becomes as high as 11 %. This is another indication that either the model has not captured the behaviour of the Polar regions, or the emergent property breaks down in these regions. Unfortunately, Sathyendranath et al. (2009) did not include any data from Polar regions in the winter that could be used to test this hypothesis.

Figure 4 shows the total phytoplankton carbon against total chlorophyll. This figure also shows the model data as a two dimensional density histogram with logarithmically scaled in blue-scale and a least squares fit of the data to Eq. (7). In a modelling analysis, it is unnecessary to apply the 1 % quartile regression, as it is straightforward to extract phytoplankton carbon. Figure 4 also shows the two 1 % quartile regression fits from Sathyendranath et al. (2009) as dashed lines as in Fig. 3. However, the model data shown in this figure is phytoplankton carbon against total chlorophyll; accordingly, the model data and fit are expected to match these dashed lines. As before, the model distribution is the top 40 m of the monthly climatology of the final ten years of the simulation, excluding shallow seas, inland seas and the Arctic and Antarctic oceans. Both the fits and the bulk of the data distribution in this figure coincide with the two Sathyendranath et al. (2009) phytoplankton carbon to total chlorophyll relationship.

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

[Title Page](#)[Abstract](#)[Introduction](#)[Conclusions](#)[References](#)[Tables](#)[Figures](#)[◀](#)[▶](#)[◀](#)[▶](#)[Back](#)[Close](#)[Full Screen / Esc](#)[Printer-friendly Version](#)[Interactive Discussion](#)

This indicates that the modelled phytoplankton may have an appropriate response to temperature, light and nutrients in much of the global ocean.

In Fig. 4, there is a region where the phytoplankton carbon is much less than the Sathyendranath et al. (2009) fit, and this group of data appears to have a different slope. The phytoplankton carbon in the data points are almost entirely composed of diatoms and large phytoplankton, near the polar regions, and account for approximately 2.5 % of the dataset. Similarly to Sect. 3.1, this region highlights that the issues of the abundance of silicate caused by excessive mixing, the favouring of diatoms in low light regions and the relatively low grazing pressure on microphytoplankton from zooplankton at low phytoplankton biomass concentrations. When the polar, shallow and inland sea regions to a depth of 40 m are included in the model, the number of points included in these regions of the figure increases up to approximately 10 % of the dataset.

The carbon to chlorophyll relationship has many knock-on effects in the model: it influences the entire carbon and carbonate cycle. It has a huge impact on the calculation of total global primary production. It also relates to the community structure shown in Sect. 3.1. When the model successfully reproduces the carbon to chlorophyll ratio in a global ocean simulation, this is an indicator that it has a good approximation of the roles of light, temperature and nutrient limitation in each of the plankton functional types. The fact that the model reproduces the natural range of behaviours of the carbon to chlorophyll ratio highlights that the ecosystem model functions appropriately in a range of environments.

3.3 Particulate organic carbon and particulate organic nitrogen

The ratio of carbon to nitrogen in the ocean has long been a historically important measurement, with the ratio first published by Redfield (1934). The interplay of carbon and nitrogen has since been a major component of the modern understanding of ocean biogeochemistry, underlying modern theories of nutrient cycles, nutrient limitation in phytoplankton and stoichiometric variability. The balance of carbon to nitrogen in the

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

ocean has been historically measured in the ratio of carbon to nitrogen in particulate organic matter (POM).

A meta-study of the ratio of particulate organic carbon (POC) against particulate organic nitrogen (PON) was published in Martiny et al. (2013). Their paper used over forty thousands globally distributed POC-PON paired samples from 5383 unique stations in the upper 200 m of the ocean water column. They produced a histogram of the distribution of POC against PON in the global ocean. The power of this figure was that it was a clear demonstration of the discrepancy between a modern understanding of the stoichiometric balance of carbon to nitrogen and the canonical Redfield ratio. Instead of a static Redfield ratio, the observed POC : PON ratio varied between 2 and 20, and the canonical Redfield ratio was closer to the median of the dataset than to the mean or the mode.

The POC : PON histogram from Martiny et al. (2013) was reproduced using simulated data in Fig. 5. This figure shows the POC : PON ratio calculated in the model, the POC : PON ratio of the in situ data from Martiny et al. (2013), but also the canonical Redfield ratio. Both the model and the in situ histograms in Fig. 5 were normalised to unity area. A summary of the statistical analysis of Fig. 5 is shown in Table 3. The mode shown in Table 3 was calculated by finding the most populous group after binning the model ratio in bins of width 0.1. The bin widths used to calculate the mode are finer than those shown in Fig. 5.

The POC of the model in Fig. 5 was calculated as the sum of the carbon components of all phytoplankton functional types, all zooplankton functional types and the particulate detritus groups. These are the same groups that were used to calculate POC in Sect. 3.2. The PON was calculated as the sum of the nitrogen components of the same groups. An artificial detection limit of $0.1 \mu\text{mol m}^{-3}$ was applied to the modelled PON component of the ratio. The model data was a monthly climatology of the final ten years of the simulation (1997–2007), excluding the Arctic ocean and all model data below 200 m. Unlike the data selections of Sects. 3.1 and 3.2, the Antarctic domain, inland seas and shallow seas are included in this data. This is because the Martiny

GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

et al. (2013) dataset does not contain any measurements from the Arctic Ocean, but it does include many data from the Southern Ocean, inland seas and shallow seas.

In nature as in models, particulate organic matter is usually composed of a combination of phytoplankton, zooplankton and detritus. Experimentally, particulate organic matter (POM) is typically measured as all organic matter over a certain size that can accumulate in a filter. In ERSEM, POM is the sum of the all four phytoplankton functional types, all three zooplankton functional types, and the particulate detrital fields. Each phytoplankton functional type has an internal variable stoichiometry and the ability to accumulate a luxury buffer of nitrogen. The micro-zooplankton and heterotrophic nanoflagellates also have variable stoichiometry that follows from their food source. The mesozooplankton has fixed stoichiometry and exudes the excess nitrogen back into detritus. There are six detritus size classes in ERSEM: three dissolved and three particulate classes, but the dissolved organic matter fields did not contribute to the POM shown here. The three particulate detritus classes include carbon, nitrogen and phosphorus currencies, and all three also have a silicon and/or an iron component. None of the detritus fields have any limitations on their stoichiometric variability. This means that the models POC : PON ratio can vary according to local conditions and predation, and the overall particulate organic matter stoichiometry in ERSEM is not susceptible to tuning via a small number of parameters. In order for all of these interlocking and competing components to reproduce the POC : PON ratio variability in the global ocean, it requires all the phytoplankton functional types, zooplankton functional types and detrital fields to be balanced and healthy.

In addition to those fields included in the POC and PON fields, ERSEM includes a bacterial component. The bacterial component of the model compete for nutrients with the phytoplankton, are predated by zooplankton, but do not contribute to particulate detritus.

While the model captures the mode of the in situ data, it does not capture the range of observed POC : PON ratios or the shape of the distribution seen in the data. The model underestimates the frequency of POC : PON ratios in the tails below 5 or more

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

than the Redfield ratio. It is possible that some of this difference is due to spatial bias and uneven sampling of the in situ data. In that case, it may be possible to capture more of the shape of the Martiny et al. (2013) data by sub-sampling the model data to match the distribution used to produce their data. However, the model data shown here is a monthly mean of a 1° by 1° square of ocean. The variability seen when taking an instantaneous measurement of the concentration in a bottle of seawater will always be more extreme than the mean value of a 1° by 1° square of ocean. Secondly, in this work, we attempt to validate the models ecosystem function over a large scale without the use of point-to-point matching.

The model's narrow POC : PON distribution is reflected in its the standard deviation(0.61), which is much lower than that seen in data (2.46). However, the standard deviation of a Gaussian distributions decreases with increasing number of data. Although the POC : PON is clearly not a Gaussian distribution, the difference in sample size may partially explain the difference in standard deviation. While the Martiny dataset is composed of approximately 40k data, a monthly climatology of a 1° model contains more than 21 million points even after removing land points, masked deep water and Arctic data points. However, the range of stoichiometric variability seen in measured POC : PON data is underestimated in the model.

Furthermore, there are precisely zero model data with a POC : PON ratio below 4.3 or above 16.5. The model does a better job of capturing the excess POC relative to PON than it does capturing the excessive PON. This behaviour is linked to the fixed maximum luxury buffer of nitrogen relative to carbon in all the phytoplankton functional types. This maximum nitrogen buffer translates to a fixed minimum value of the POC : PON ratio, which is maintained as it cascades through the trophic levels. On the other end of the scale, there is a minimum requirement of nitrogen to carbon, below which the phytoplankton are nitrogen limited and do not grow.

Despite these limitations, the ERSEM simulation was very successful at reproducing the mode of the POC : PON ratio of Martiny et al. (2013). The means that a the most common values in the model data are the same as the most common values in

the POC : PON ratio data. The reproduction of the mode of the dataset by the ERSEM model is a strong indication that the most common behaviour of the POC : PON relationship is appropriately simulated.

3.4 Intracellular elemental stoichiometry

5 Stoichiometry in marine ecosystem modelling is the balance of each element in organisms and in the ecosystem. As mentioned previously, Redfield observed co-variability in the concentrations of dissolved nitrate and phosphate in seawater, (Redfield, 1934). While further co-variation has since been observed, considerable variability in the balance of elements in particulate organic matter and intracellular material has also been
10 observed, (Martiny et al., 2013). The ratio of each element against carbon has been shown to vary significantly between region, taxa, ecosystem role and physiological status, (Moore et al., 2013). The co-variability of nutrients and carbon in the ocean is closely linked with many important metrics of ecosystem behaviour, such as primary productivity, community structure, export and growth rates, and nutrient limitation.

15 Despite the significance of marine nutrient cycles, co-limitation by two or more nutrients is still poorly understood, and appears infrequently in models, (Moore et al., 2013). Furthermore, variable stoichiometry and co-limitation are required features in order to represent the spatial distribution of nutrient limitation. ERSEM is one of the few models that does implement variable stoichiometry. In addition to its carbon cycle, ERSEM resolves four nutrient cycles: nitrogen, phosphorus, iron, and silicon. All
20 four nutrients can become limiting or co-limiting for any given phytoplankton functional type, with the exception that only the diatoms interact with silicon. In addition, nitrogen, phosphorus and iron uptake and limitation in ERSEM are based on the Droop model (Droop, 1973), which uses the internal nutrient concentration to carbon ratio rather than
25 external inorganic nutrient concentrations to determine phytoplankton behaviour. The silicate limitation and uptake for diatoms is computed from the external availability of dissolved silicate, based on Michalis–Menten kinetics, (Johnson and Goody, 2011).

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

In their meta-study, Moore et al. (2013) compiled multiple datasets of simultaneous measurements of particulate organic carbon and nutrients. To visualise this data, they presented a comparison of the ratio of each element against carbon. For each nutrient, they plotted the typical organic nutrient:carbon ratio on the x axis against the typical inorganic nutrient:carbon ratio on the y axis. Figure 6 shows a version of this figure produced using the four ERSEM nutrients. This figure shows the model distribution with mean of the model data in circular markers, and the typical in situ value and observed range from Moore et al. (2013) in square markers with black bars.

The organic component of Fig. 6 was calculated as the ratio of particulate organic nutrient to particulate organic carbon for each nutrient. The POC was calculated in the same way as in Sects. 3.2 and 3.3: where POC is the sum of the carbon components of all phytoplankton functional types, all zooplankton functional types and the particulate detritus groups. The particulate organic nitrogen, phosphorus and iron were calculated as the sum of the nitrogen, phosphorus and iron components of the same groups. Although ERSEM includes four pelagic silicon fields (diatom silicon, inorganic silicate, and medium and large particulate detrital silicon), the calculation of particulate organic silicon follows the methods of Moore et al. (2013), and only uses the silicon component of diatoms.

As previously described, the modelled ratio of particulate organic nutrient to carbon can vary according to local conditions such as light, temperature and predation. For all of these interlocking and competing components to reproduce the stoichiometric variability of the global ocean, all phytoplankton functional types, zooplankton functional types and detrital fields and their interactions need to be parameterized sensibly. The overall particulate organic matter stoichiometry in ERSEM is not susceptible to tuning via a small number of parameters.

Furthermore, the nutrient cycles of carbon, nitrogen, phosphorus and iron are also influenced by the bacterial loop. The bacterial biomass does not contribute their biomass to the calculation of particulate organic matter used here, but the bacterial functional type competes with the phytoplankton for the inorganic nutrients except dissolved iron

and is an additional food source for zooplankton. This variable stoichiometry bacterial functional type contributes to the flexibility of ERSEM. The bacteria also compete with the zooplankton to scavenge non-silicon particulate detritus. In addition, the bacterial group only excretes to labile and semi-labile detrital fields.

The inorganic component of the model data was taken directly from the output of the simulation. The dissolved inorganic carbon (DIC) cycle in the model is described in Artioli et al. (2012). There are no explicit limitations of the upper or lower limits of inorganic nitrogen, phosphorus or silicon in the model. However, there is a soft cut off for iron at 0.6 nM to take into account for hydroxide precipitation (Aumont et al., 2003) and a firmer upper limit of 2 nM to take into account for the saturation concentration.

The minimum, maximum and mean values of each ratio against carbon in Fig. 6 are shown in Table 4. This table includes the “typical” Moore et al. (2013) data mean and range, and the data from the model run. Moore et al. (2013) did not include any measure of variability in the inorganic data; the inorganic range shown in Fig. 6 and Table 4 was included here as another test of the model. The variability in the inorganic axis is due to the co-variability in the dissolved inorganic carbon and the dissolved inorganic nutrient. However, the range of variability in DIC is usually of order 15 %, but dissolved inorganic nitrogen, phosphorus, iron and silicon can vary by several orders of magnitude. This means that most of the variability in the *y* axis is usually due to the nutrient, not the DIC. Here, this variability is estimated using the Moore et al. (2013) “typical” value for the DIC, and the minimum and maximum values of the nutrients contribution to the Nutrient to DIC ratio were taken from data from the World Ocean Atlas (Garcia et al., 2010) for nitrogen, phosphorus and silicon, and GEOTRACES for Iron (Henderson et al., 2007). This means that the ranges are not the most extreme values ever recorded, but rather the most extreme ratio of inorganic nutrient to DIC seen on a climatological global scale.

Furthermore, the range of variability in the organic nutrient:carbon ratios might not reflect the most current knowledge. The Moore et al. (2013) “maximum and minimum values will typically correspond to nutrient replete or limited cultures respectively and

**Ecosystem function
and emergent
relationships in
marine ecosystem
models**

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

ranges could potentially be extended through observations of other taxa and growth conditions.” For instance, Moore et al. (2013) cite an observed maximum phytoplankton quota of 0.169 for the ratio of nitrogen to carbon, but Martiny et al. (2013) has observed data all the way down to their cut off of 0.5. (Note that Martiny et al. (2013) showed C : N instead of N : C, so their lower cut off value is 2.0 in Fig. 6.) Also, note that the model data does not show any density distribution, only presence/absence. The presence/absence model data in Fig. 6 is extracted from the top 40 m of the global model between 1997 and 2007 and excludes the shallow seas, inland seas and the Arctic and Antarctic oceans. The model data was not further sub-sampled to match the sampling locations of the in situ data. This data has monthly time resolution and is not climatologically averaged.

The ratio of nitrogen to carbon is shown in blue in Fig. 6. The model captured the mean organic ratio, but had a wider range of values than that quoted in the Moore et al. (2013) work. However, as mentioned earlier, the maximum value of this ratio has been extended from 0.169 to 0.5 when included the Martiny et al. (2013) results. The model underestimated both the mean inorganic ratio and the range of variability in the inorganic N : C ratio. The model appears to have a fixed lower limit of dissolved inorganic nitrogen that is higher than the minimum nitrogen observed in nature. The inorganic nitrogen in the model never gets as depleted as observed in reality. This is a problem with the model parametrisations that has also been seen in Sect. 3.3 which will need to be addressed in future parametrisations.

The mean organic phosphorus:carbon ratio is overestimated the model, but the mean inorganic P : C ratio is underestimated. The range of the inorganic and organic P : C ratios were underestimated by the model relative to the Moore et al. (2013) data. However, both the organic and inorganic phosphorus in the model show a wide range of behaviours, reflecting those seen in nature. Similarly to the nitrogen, the lower limit of dissolved inorganic phosphorus in the model is higher than the minimum inorganic phosphorus:carbon ratio observed in nature. The inorganic phosphorus in the model never gets as depleted as observed in reality. However, the inorganic range shown in

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

figure has no indication of the frequency or locations of such low concentrations. The dataset clearly illustrated the effect of external resource limitation: as the inorganic ratio decreases, the organic ratio also decreases, indicating that the phytoplankton become increasingly nutrient stressed in low phosphorus environments.

The ERSEM model has four pelagic silicon fields: diatom silicon, inorganic silicate, and medium and large detritus silicon. The C:Si ratio in Moore et al. (2013) and in Fig. 6 are strictly limited to diatoms; there are no quotas associated with silicon in other components of the ecosystem. The modelled ratio of silicon to carbon, shown in purple in Fig. 6, captured the range of variability in the inorganic version of the ratio. As only diatom silicon are included in this figure and ERSEM has very little variability in the silicate stoichiometry for diatoms, there is no variability in the organic component for silicate. Also, there is only a very slim range of Si:C ratios allowed in the model, so the nutrient stress effect seen in the phosphorus:carbon ratio is not seen in the silicon:carbon ratio in this figure. Instead of becoming silicon-stressed, the community structure changes to disfavour diatoms.

The organic iron:carbon has a deficit in the model, relative to the same ratio in Moore et al. (2013): the model underestimated the mean organic ratio by an order of magnitude. However, the Fe:C ratio is the only inorganic nutrient:carbon ratio where the model captured the measured in situ range.

While there is an atmospheric iron source from dust, the model does not include any atmospheric, riverine or hydrothermal sources of nitrogen, silicon or phosphorus. The nitrogen, silicon and phosphorus shown in this paper have been circulated, consumed and recycled for more than 100 simulated years and the relationship between organic and inorganic nutrients, and nutrients against carbon are still all representative of nature. On the other hand, the iron cycle is nudged towards what is observed in nature by an climatological surface deposition, and through hydroxide precipitation and saturation removal of excess iron. This means that arguably the distribution of inorganic iron is not an emergent property of the model, but rather a tuned outcome. These nudges are needed because the iron cycle in ERSEM is much less complex than that seen in

a nature. An example of a more natural iron model is Tagliabue et al. (2009), which has three bio-available forms of iron and two complexed forms of iron. Despite this, as the inorganic Fe:C ratio decreases, the organic ratio also decreases, indicating that the phytoplankton become increasingly nutrient stressed in low iron environments.

Anthropogenic nutrient loading is expected to increasingly influence nutrient cycles in the ocean and this may lead to shifts in the nutrient balance, (Paerl, 1997). Unfortunately, this model does not include any anthropogenic nutrient loading, or indeed any flux of riverine nutrients, and the dust deposition is forced with an annual climatology.

Overall, this figure informs us about the relationship between the inorganic and organic component of the stoichiometric balance. Effectively, it illustrates whether nutrient limitation and nutrient stress are parameterized in a way that reflects nature. Much of the modelled organic matter appears to be iron poor and phosphorus rich relative to nature. The model never captures the lowest dissolved inorganic nitrate, phosphate, or silicate concentrations. It might be expected that the model will produce a wider range of quotas than the historic datasets as the ocean is vastly under-sampled relative to the model. On the other hand, the model is the mean of a 1° by 1° patch of ocean, and the data is typically the mean of a one litre bottle, which would imply less variability in the model. Furthermore, some of the in situ data may originate in coastal datasets which have a higher spatial variability than would be seen in a coarse global model.

4 Discussions

It has been shown that the ERSEM global hindcast successfully reproduced many natural behaviours of the ecosystem. Each of these behaviours has covered a different aspect of ecosystem function, and when combined together they illustrate the power of model validation with emergent properties and ecosystem function. Many of the features seen here would not be visible in a flat comparison of model to data.

First, it was shown in Sect. 3.1 that the model captures the natural balance of phytoplankton abundance between the four PFTs. This means that the combination of the

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

nutrient affinity, growth rates, photosynthetic behaviour and predation rates ecosystem functions were appropriate to bring out a natural emergent community structure. This method was limited to the top 40 m of the surface ocean, and the relationship breaks down in Arctic waters in the model. Hints of the breakdown of the community structure appear in the in situ data, but are seen clearly in the model. It became clear that the large phytoplankton and diatom functional types are in excess at low chlorophyll concentrations in the modelled community structure. In addition, the picophytoplankton chlorophyll as a fraction of the community behaves much more like the empirical fit to data seen in Hirata et al. (2011) than like the three-population model of Brewin et al. (2010).

Together, the particulate organic carbon to chlorophyll and phytoplankton carbon to chlorophyll ratios from Sect. 3.2 demonstrate that the phytoplankton biomass forms an appropriate fraction of the particulate organic matter. This means that the balance of producers to the rest of organic matter, including zooplankton and detritus, is similar to nature over the range of observed total community chlorophyll. This figure also helped identify some unusual behaviour from the diatom and large phytoplankton functional types. As in Sect. 3.1, the abundance of silicate caused by excessive mixing, the favouring of diatoms in low light regions and the relatively low grazing pressure on microphytoplankton from zooplankton at low phytoplankton biomass concentrations were suggested as causes of this discrepancy.

The ratio of particulate organic carbon to particulate organic nitrogen in Sect. 3.3 illustrates that the carbon to nitrogen balance matches with the historic distribution of measurements. While the model did not reproduce the standard deviation or the tails of the distribution seen in data, the ERSEM simulation was particularly successful at reproducing the mode of the POC : PON ratio. The most common values in the modelled POC : PON ratio are the same as the most common values in the in situ measurement of POC : PON. It was postulated that some of the difference was due the decrease of Gaussian distributions standard deviation with increasing sample size. The ability to reproduce this ratio from the combination of four phytoplankton functional types, three

zooplankton functional types and 3 classes of particulate organic detritus, all of which have variable stoichiometry (except mesozooplankton), is a strong indication of the validity of model.

The stoichiometric variability of particulate organic matter against inorganic ratio of nutrient to DIC from Sect. 3.4 inform that the range of behaviours present in the model match those measured in situ. The nutrients in the model do not typically become as sparse as those seen in nature, apart from iron. The nitrogen, silicon and phosphorus shown in this model have been circulated, consumed and recycled for more than 100 simulated years and the natural relationship between organic and inorganic nutrients, and natural relationships between nutrients and carbon have survived through to the end of the run. The iron cycle is nudged towards nature by an appropriately parameterized climatological surface deposition, and is also a healthy, if somewhat artificial, representation of nature. An interesting feature of this dataset is that as the inorganic ratios of Fe : C and P : C decrease, their organic counterpart also decreases, indicating that the phytoplankton become increasingly nutrient stressed in low nutrient environments.

Combined together, these relationships have informed about community structure and balance of C : Chl in phytoplankton, the ratio of POC : PON in particulate organic matter, the stoichiometric flexibility of POM and dissolved inorganic nutrients. While some selection cuts have been necessary to reduce the impact of nonphysical behaviour, the combination of the relationships can be used to validate the ecosystem model without relying on the model to reproduce an historic measurement at exactly the right place and time. It compliments validation methods, such as the point to point, that may not function in an inappropriately parameterized physical ocean model.

While it has since expanded beyond its original remit, the European Regional Seas Ecosystem Model was originally built as a model for simulating temperate shelf seas. This work has demonstrated that many of ERSEM's design choices and parameterisation are still appropriate in a global context. Furthermore, these relationships were

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

not explicitly parameterized in model development; all of them arise naturally out of a combination of many other well understood natural behaviours.

The combination of these well known phenomena have allowed a test of the majority of the modelled fields throughout the surface ocean. However, these relationships do not cover all aspects of the model. They do not inform about the food web such as the balance of zooplankton and detritus functional types to each other and to the phytoplankton functional types, or about the bacterial or benthic communities in the model. Also these relationship do not cover important fluxes such as primary production, air sea flux gas exchange, or export from the surface or bacteria growth efficiency.

In order to get a better validation of the ecosystem functions of the bacterial class, this would require more measurements of the ratio of primary production to bacterial production. Alternatively, the bacterial growth efficiency could be used to gauge the model's bacterial behaviour.

The models grazers biomass were implicitly included in the POC : PON, POC : Chl and the stoichiometric relationships. However, there are no metric included here to study the zooplankton by themselves. The authors are not aware of a stable metric for describing the community structure of grazers.

These emergent relationships were selected to reduce the impact of spatial biases, but these relationships may still be influenced by uneven in situ data spatial and temporal coverage. This bias could potentially be resolved by using a point to point analysis for the emergent properties, however this may limit the scope and the power of the emergent property validation. These emergent properties also require the assumption that the property can be extended to cover the entire ocean. Some emergent properties have not been tested in shallow or Polar seas, and may not hold across all marine environments.

GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

5 Conclusions

Ecosystem relationships are coherent structures, patterns and properties that are observed to be robust in nature and can be reproduced by a sufficiently complex model. They allow us to demonstrate how natural behaviour emerges from the model. As they are well established functional relationships that hold true over large regions of the global ocean, they are a valuable tool for validating ecosystem model in data sparse regions.

As ecosystem functions arise independently of physical conditions of the ocean, they can be used to demonstrate model quality in the case when the physical features of a sea are not co-located in the model and in nature.

Most importantly, ecosystem functions are the only way to demonstrate the models capacity to represent ecosystem function, as opposed to quantitative metrics of absolute ecosystem state. Many of the features shown here would not be visible in a flat comparison of model to data. For these reasons, ecosystem functions are a critical tool for the validation of marine ecosystem models.

Code availability

The ERSEM model is available under the GNU Public License version 3 (GPL3). Interested parties are encouraged to register at the Shelf Seas Biogeochemistry home page, www.shelfseasmodelling.org, to register in order to download and use the model for their own purposes.

The analysis toolkit used in this work is available from the author upon request under the terms of the Revised Berkeley Software Distribution (BSD) 3-clause license.

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GMDD

8, 6095–6141, 2015

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

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5

GMDD

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Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures



Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Table 1. Parameters of the fits to the three population absorption model for the Brewin et al. (2015), and for ERSEM. Two fits to ERSEM are shown: the first is the fit to the ERSEM dataset excluding the polar, shallow and inland seas, and the second includes all these regions to a depth of 40 m. The parameters are: $C_{p,n}^m$: maximum piconano chlorophyll, $S_{p,n}$ is the slope for piconano chlorophyll, C_p^m is the maximum picophytoplankton chlorophyll and S_p is the slope for picophytoplankton.

	Brewin et al. (2015)	ERSEM	ERSEM (Top 40 m)
$C_{p,n}^m$	0.77	0.345	0.742
$S_{p,n}$	1.22	2.147	0.799
C_p^m	0.13	0.061	0.289
S_p	6.16	10.56	1.168

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 2. The parameters of the particulate organic carbon to total chlorophyll and phytoplankton carbon to chlorophyll fits to the Eqs. (6) and (7).

	Sathyendranath et al. (2009) HPLC	ERSEM Turner	
Particulate Organic Carbon			
<i>m</i>	180 ± 2	157 ± 2	145
<i>p</i>	0.48 ± 0.014	0.45 ± 0.013	0.51
Phytoplankton Carbon			
<i>n</i>	79*	64*	66
<i>q</i>	0.65*	0.63*	0.72

* These values were calculated using a 1 % quartile regression.

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 3. Statistics to describe the POC : PON distribution as reported by Martiny et al. (2013), compared to the result of this study and to the canonical Redfield Ratio.

	Martiny et al. (2013)	Redfield	ERSEM
Mean	7.06	6.63	5.93
Mode	5.9		5.8
Median	6.5		5.84
SD	2.46*		0.61

* This standard deviation was not included in the original publication; it was calculated based on their dataset.

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion



Table 4. Table showing the typical, minimum and maximum organic and inorganic ratios against carbon for Moore et al. (2013) and for the ERSEM simulation.

		Moore et al. (2013)	ERSEM
Mean Organic	N : C	0.13	0.17
	P : C	0.008	0.02
	Si : C	0.13	0.14
	Fe : C	6.1×10^5	5.4×10^6
Range Organic	N : C	[0.05, 0.17 (0.5*)]	[0.09, 0.21]
	P : C	[0.001, 0.026]	[0.006, 0.039]
	Si : C	[0.08, 1.01]	[0.13, 0.15]
	Fe : C	$[2.1 \times 10^6, 2.6 \times 10^4]$	$[1.5 \times 10^6, 3.5 \times 10^5]$
Mean Inorganic	N : C	0.013	0.0008
	P : C	0.00089	0.0002
	Si : C	0.044	0.0053
	Fe : C	2.4×10^7	2.8×10^7
Range Inorganic	N : C	$[8.9 \times 10^8, 0.02]$	$[5.0 \times 10^5, 0.012]$
	P : C	$[8.9 \times 10^8, 0.01]$	$[2.8 \times 10^6, 0.0008]$
	Si : C	$[1.7 \times 10^7, 0.06]$	$[5.4 \times 10^6, 0.036]$
	Fe : C	$[8.7 \times 10^9, 2.6 \times 10^6]$	$[6.8 \times 10^9, 2.4 \times 10^6]$

* indicates values from Martiny et al. (2013) which were not taken into account in Moore et al. (2013).

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

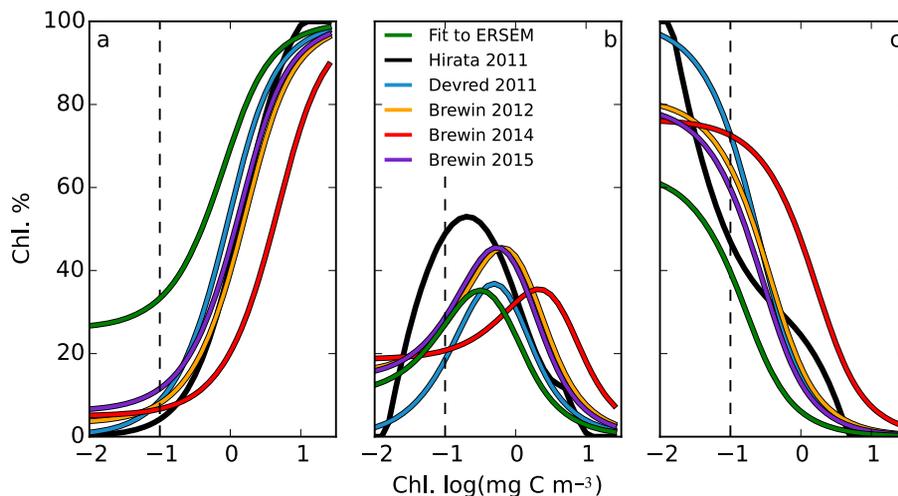


Figure 1. Phytoplankton community structure for all fits including the fit to ERSEM. The panes labelled a, b and c are diatoms and large phytoplankton, nanophytoplankton and picophytoplankton, respectively. The least squared fit of the three-population absorption model to ERSEM is shown as a green line. The other coloured lines are the five fits from (Hirata et al., 2011; Devred et al., 2011; Brewin et al., 2012, 2014, 2015). The dashed vertical line indicates a typical detection limit of HPLC and SFF methods.

[Title Page](#)
[Abstract](#)
[Introduction](#)
[Conclusions](#)
[References](#)
[Tables](#)
[Figures](#)
[◀](#)
[▶](#)
[◀](#)
[▶](#)
[Back](#)
[Close](#)
[Full Screen / Esc](#)
[Printer-friendly Version](#)
[Interactive Discussion](#)

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

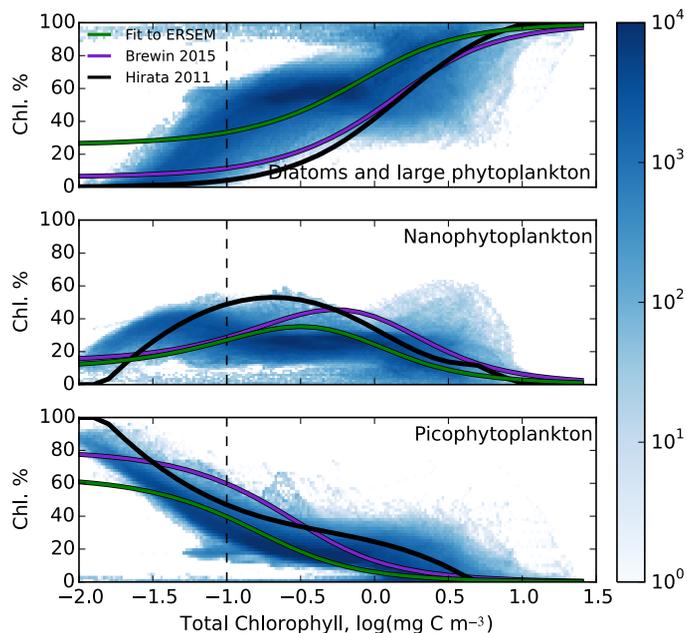


Figure 2. Phytoplankton community structure. The model data is shown as the logarithmically scaled two dimensional data density histogram in blue-scale. A least squares fit of the model data to the three-population absorption model of Brewin et al. (2010) is shown as a full green line, and the fit of historic in situ data to the three-population absorption model from Brewin et al. (2015) is shown in a purple line. A fit to data from Hirata et al. (2011) is shown in a black line. The dashed vertical line indicates a typical detection limited of HPLC and SFF methods.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

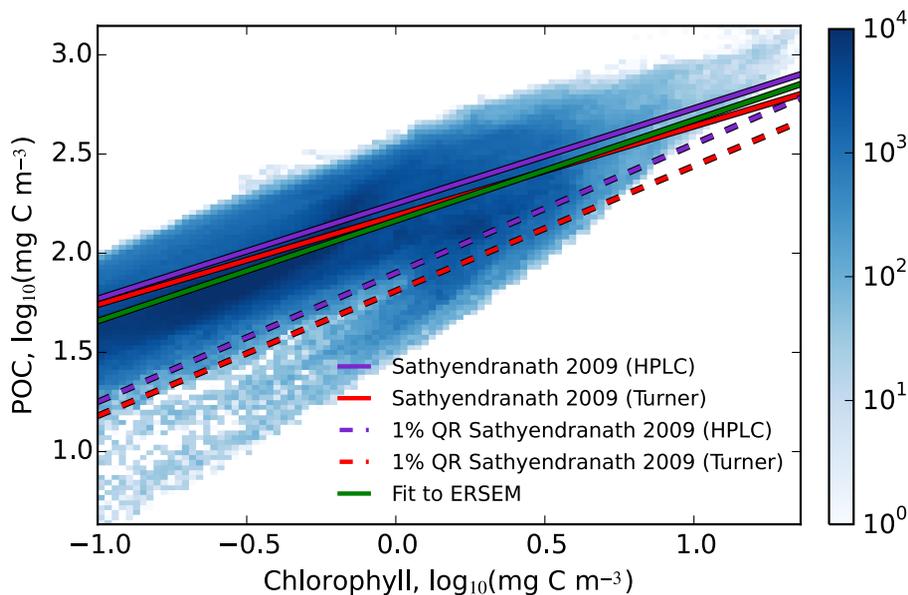


Figure 3. The ratio of particulate organic carbon to total chlorophyll. The model data is shown as the logarithmically scaled two dimensional data density histogram in blue-scale. The full lines indicate the two Sathyendranath et al. (2009) fits to data, and a fit of the model to Eq. (6). The dashed lines show the two 1% quartile regression fit from the data and they indicate a theoretical lower bound for the modelled POC:Chl field.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

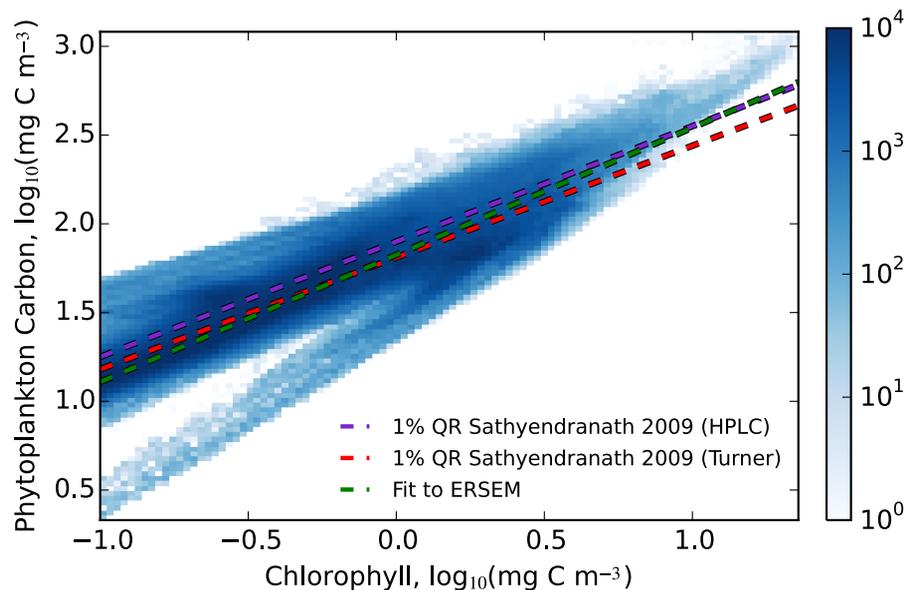


Figure 4. The ratio of phytoplankton carbon to total chlorophyll. The model data is shown as the logarithmically scaled two dimensional data density histogram in blue-scale. The dashed lines show the fit to data, a fit of the model to Eq. (7), and the results of the two 1 % quartile regression from Sathyendranath et al. (2009).

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion

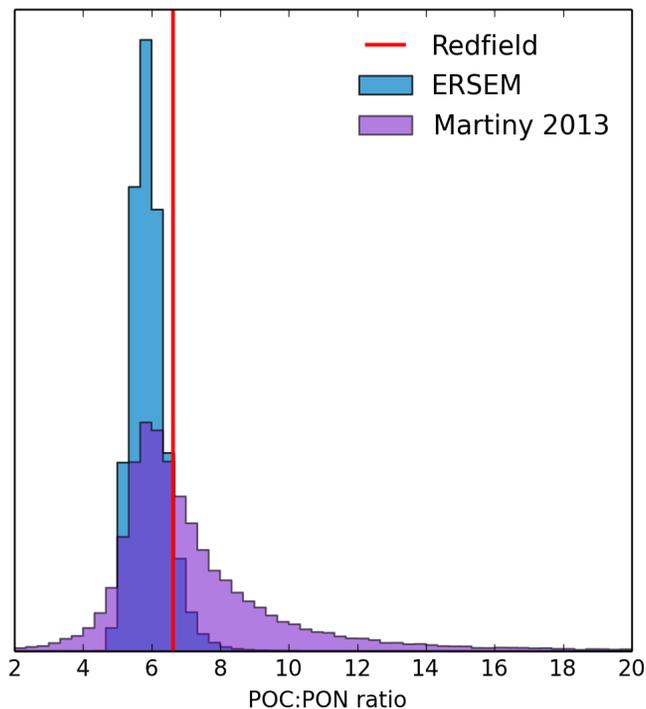


Figure 5. The ratio of Particulate Organic Carbon to Particulate Organic Nitrogen in the Martiny et al. (2013) in situ dataset and in the model. The Redfield ratio is also shown as a red vertical line. The model data was taken from a monthly climatology of the top 200 m of the final ten years of running, excluding the Arctic ocean. Both the ERSEM and the Martiny et al. (2013) histogram were normalised to unity area.

Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

Title Page	
Abstract	Introduction
Conclusions	References
Tables	Figures
◀	▶
◀	▶
Back	Close
Full Screen / Esc	
Printer-friendly Version	
Interactive Discussion	



Ecosystem function and emergent relationships in marine ecosystem models

L. de Mora et al.

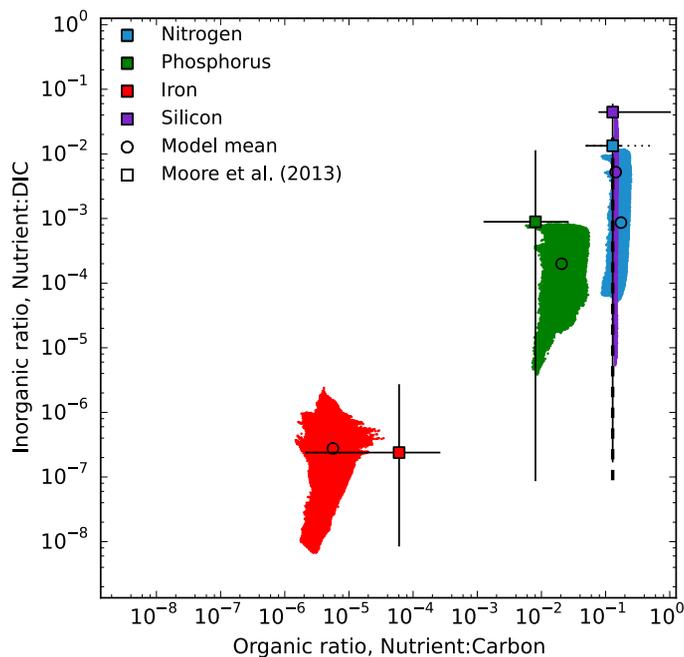


Figure 6. A comparison of the ratio of each modelled nutrient to carbon ratio in organic matter against the dissolved inorganic nutrient to carbon ratios. This figure shows a colour coded distribution of the modelled nitrogen, phosphorus, iron and silicon to carbon ratios. The model distribution means are indicated by circular markers, and the typical in situ value and observed range from Moore et al. (2013) are shown as square markers with bars.

Title Page

Abstract

Introduction

Conclusions

References

Tables

Figures

◀

▶

◀

▶

Back

Close

Full Screen / Esc

Printer-friendly Version

Interactive Discussion