How predictable is plankton biogeography using statistical learning methods?

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**Abstract**

Plankton play an important role in marine food webs, in biogeochemical cycling, and in moderating Earth’s climate. Their possible responses to climate change are of broad scientific and social interest; yet observations are sparse, and mechanistic and statistical methods yield diverging predictions. Here, we evaluate a statistical learning method using output from a 21st Century marine ecosystem model as a ‘ground truth’. The model is sampled to mimic historical ocean observations, and Generalised Additive Models (GAMs) are used to predict the simulated plankton biogeography in space and time. Predictive skill varies across test cases, and between functional groups, and errors are more attributable to spatiotemporal sampling bias than to sample size. Overall, the GAMs yield poor end-of-century predictions. Given that statistical methods are unable to capture changes in relationships between variables over time, we advise caution in their application and interpretation, particularly when modelling complex, dynamic systems.
Testing the skill of a species distribution model using a 21st Century virtual ecosystem.

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Key Points:

\begin{itemize}
\item We build a correlative species distribution model to predict the global plankton biogeography of a trait-based ecosystem model
\item Predictive skill varies across test cases, with functional group, and spatiotemporally, with poor end-of-century performance
\item Key sources of uncertainty are traced to sampling biases in observations, and the temporal variability in target-predictor relationships
\end{itemize}

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Abstract

Plankton play an important role in marine food webs, in biogeochemical cycling, and in Earth’s climate; yet observations are sparse, and predictions of how they might respond to climate change vary. Correlative species distribution models (SDM’s) have been applied to predicting biogeography based on relationships to observed environmental variables. To investigate sources of uncertainty, we use a correlative SDM to predict the plankton biogeography of a 21st Century marine ecosystem model (Darwin). Darwin output is sampled to mimic historical ocean observations, and the SDM is trained using generalised additive models. We find that predictive skill varies across test cases, and between functional groups, with errors that are more attributable to spatiotemporal sampling bias than sample size. End-of-century predictions are poor, limited by changes in target-predictor relationships over time. Our findings illustrate the fundamental challenges faced by empirical models in using limited observational data to predict complex, dynamic systems.

Plain Language Summary

Marine plankton communities play a central role within Earth’s climate system, with important processes often divided among different ‘functional groups’. Changes in the relative abundance of these groups can therefore impact on ecosystem function. However, the oceans are vast, and samples are sparse, so global distributions are not well known. Statistical species distribution models (SDM’s) have been developed that predict global distributions based on their relationships with observed environmental variables. They appear to perform well at summarising present-day distributions, and are increasingly being used to predict ecosystem changes throughout the 21st century. But it is not guaranteed that such models remain valid over time. Rather than wait 100 years to find out, we applied a statistical SDM to a complex virtual ocean, and trained it using virtual observations that match real-world ocean samples. This allows us to jump forward to the end-of-century to test the accuracy of our predictions. The SDM performed well at qualitatively predicting ‘present day’ plankton distributions but yielded poor end-of-century predictions. Our case study emphasises both the importance of environmental variable selection, and of changes in the underlying relationships between environmental variables and plankton distributions, in terms of model validity over time.

1 Introduction

Plankton underpin global ocean food webs and fisheries, mediate marine biogeochemical cycles, and affect climate (Fenchel, 1988; Falkowski et al., 2008; Marinov et al., 2008; Guidi et al., 2016; Hutchinson, 1961). Their global biogeography interacts with the ocean’s inventory of nutrient elements, and its capacity to sequester CO\textsubscript{2} (Cermeño et al., 2008; Guidi et al., 2009; Fuhrman, 2009; Falkowski et al., 1998). Understanding present and possible future biogeographic patterns of plankton communities is therefore a key component of marine microbial research. These biogeographic patterns are affected by numerous environmental factors, including supplies of nutrients and light, ambient temperature, grazing pressure, physical circulation and water column structure, and the seasonality and variability of these drivers (Tittensor et al., 2010; Rutherford et al., 1999; Graff et al., 2016). Despite substantial efforts by observational oceanographers e.g. (Lombard et al., 2019), the vastness of the global ocean and the challenges of measuring complex microscopic plankton communities makes data-limitation inevitable.

Species distribution models (SDMs) (sometimes interchangeably referred to as ecological niche models) have been widely used to predict biogeographic distributions and fundamental niche parameters in terrestrial ecosystems, and have seen a recent surge of popularity in marine ecosystem context (Flombaum et al., 2020; Righetti et al., 2019; Benedetti et al., 2021; Melo-Merino et al., 2020). While mechanistic variants exist, the
most popular implementations of SDM seek to identify the relationships between known
geographic distributions of species’ and sets of environmental variables. These relation-
ships that are typically used by SDM developers to characterise biogeography in terms
of where a species could, or could not, occur (Melo-Merino et al., 2020). Correlations are
extracted using a variety of empirical methods, from classical statistics to bleeding-edge
machine-learning (ML), or a hybridised ensemble thereof. For example, one might seek
to characterise the relationships between measures of plankton concentrations (e.g. cell
counts, gene markers or biomass) and simultaneously measured environmental factors
(e.g. temperature, Chl-a, nutrient concentrations). The fitted model can then be used
together with satellite or large synthesis database measurements to make diagnostic pre-
dictions of plankton. When the resulting SDM performs well relative to the measured
datasets, predictions of species presence/absence or concentrations are then scaled glob-
ally, e.g. see (Tang & Cassar, 2019; Barton et al., 2013; Irwin et al., 2012; Agusti et al.,
2019).

However, a series of assumptions and uncertainties are incorporated into correla-
tive SDMs, many of which go unchallenged or inadequately addressed by SDM devel-
opers. While an exhaustive overview of these assumptions and uncertainties is beyond
the scope of the current work (see (Wiens et al., 2009) for a thorough assessment), some
are especially pertinent to marine microbial biogeography. For example, we cannot be
certain that the environmental variables included in the model are a true and complete
reflection of species’ niche requirements’, or whether some excluded or as-yet-unmeasured
dimensions might better account for the observed distributions. Additionally, it is dif-
ficult to separate correlation from causation in such complex, dynamic and highly-coupled
systems. Our model might highlight sea surface temperature (SST) as the primary driver
of abundance; yet it remains possible that separate factors coupled to SST – perhaps un-
derwater solar radiation penetration or nutrient supply rates – are instead more directly
linked to abundance. Thus, in this scenario, and adopting the terminology of (Holder
& Gnanadesikan, 2021), the relationship between SST and abundance might be described
as ”apparent” while the relationship between underwater solar radiation and abundance
as ”intrinsic”. This disconnect between cause and effect can be further complicated by
trade-offs in the choice of empirical model used to build the SDM, see e.g. the inverse
relationship between predictive skill and interpretability in machine learning models (Carvalho
et al., 2019).

There is a growing body of research that builds correlative SDMs on a variety of
statistical and machine learning models, and uses them to predict global plankton bio-
geometry from sparse observational data, both in the present day, and many decades
into the future, e.g. (Righetti et al., 2019; Ibarbalz et al., 2019; Flombaum et al., 2020;
Benedetti et al., 2021). Some of the results generated by such models have been highly
novel and surprising, and have diverged significantly from those generated using other
methodological approaches, such as trait-based mechanistic models e.g. (Ward et al., 2014;
Dutkiewicz et al., 2009, 2014; Cabré et al., 2015). This is particularly true of predict-
ing end-of-century distributions. For instance, the neural-network-derived correlative SDM
developed in (Flombaum et al., 2020) predicts an increase in picophytoplankton biomass
in the future subtropical oceans, in direct contrast to mechanistic ecosystem models in
e.g. (Dutkiewicz et al., 2013; Marinov et al., 2010). While it is not possible to comment
on which particular modelling regime best approximates the global oceans of 2100, iden-
tifying and addressing potential sources of error would be beneficial for improving ac-
curacy and guiding interpretation.

Thus, the goal of the current work is to investigate the effects of known assump-
tions and uncertainties that are ‘baked into’ correlative SDMs, at a time when their us-
age is seeing an explosion of interest. To achieve this, we set up an idealised testbed to
assess the predictive capabilities of an SDM built on Generalised Additive Models (GAMs)
(Hastie & Tibshirani, 1986) using the output from a mechanistic global scale ecosystem
model, the ‘Darwin’ model (Dutkiewicz et al., 2021), as a ‘ground truth’. To explore the
effect of spatiotemporal biases in real-word observational datasets, Darwin model out-
puts are sampled in space and time to mimic historical ocean measurements, and also
randomly. The resulting SDM is then evaluated in its ability to capture the virtual ocean’s
emergent biogeography in the present day ‘spatial predictions’ and by the end-of-century
‘temporal predictions’. Our experiment is thus designed to generate insights into the fun-
damental limitations of correlative SDMs, applied in the current context, as a function
their core assumptions and uncertainties.

At the outset, we stress that our intention here is not to raise a false dichotomy
whereby one particular methodological approach is pitted against another to decide a
‘winner’. Nor are we making any claim as to the accuracy of the Darwin model in its abil-
ity to faithfully predict plankton abundance and diversity in the real ocean. Rather, the
following case study is designed to assess how a correlative SDM might fare in predict-
ing a complex but well-understood microbial ecosystem (see e.g. (Dutkiewicz et al., 2020))
embedded in a dynamic, self-consistent model of the Earth’s ocean through time.

2 Materials & Methods

We performed a suite of tests using a widely applied implementation of GAMs (Servén
& Brummitt, 2018) as our SDM and the Darwin model, a dynamic marine microbial ecosys-
tem model coupled to an Earth system model ((Dutkiewicz et al., 2021), (Sokolov, 2005)).

Our decision to use GAMs as the empirical framework underlying our correlative SDM
was informed by the work of (Righetti et al., 2019), who demonstrated that GAMs per-
form comparably to Random Forest and Generalised Linear Models in a range of rele-
vant predictive tasks, while offering a higher degree of both interpretability and flexi-
bility. Additionally, GAMs are of intermediate complexity between classical statistical
regression models, and more sophisticated machine learning methods, which arguably
makes them both accessible and potentially attractive to a wide range of researchers. Nonethe-
less, we note that we could have selected any one of a wide variety of statistical or ma-
chine learning algorithms, each with their own unique pros and cons.

To train the GAMs, we sample the Darwin model at the same places and times as
in a large ocean measurement dataset used for similar purposes (Martiny & Flombaum,
2020). The resulting GAMs SDM is then used to predict Darwin model plankton bio-
geography. To quantify how spatiotemporal bias in the training dataset affects predic-
tive skill, we train an additional set of GAMs using a dataset of the same size, but sam-
ped uniformly randomly across the virtual ocean’s surface, and uniformly randomly over
the same period of time. To quantify the effect of training set sample size on predictive
skill, we generate 54 additional random-sample training sets, in 18 different sample sizes.
We evaluate the ability of the SDM to predict the global biogeography of the different
plankton functional groups in the simulation, both during the 22-year period over which
measurements were taken (i.e. spatial extrapolation), and during the last 22 years of the
21st century (i.e. both spatial and temporal extrapolation).

2.1 Numerical Model Simulation

The Darwin model ecosystem used here includes 51 plankton populations across
7 functional groups (2 prokaryotes (pro), 2 pico-eukaryotes (pico), 5 coccolithophores (cocco),
5 diazotrophs (diazo), 11 diatoms (diatom), 10 mixotrophic dinoflagellates (dino) and
16 zooplankton (zoo)). Individual populations correspond to different size classes within
functional groups, with all size classes covering a range of 0.6–2425 µm equivalent spheri-
cal diameter. Functional groups have distinct allometric relationships for growth, graz-
ing, and sinking parameters (see (Dutkiewicz et al., 2020)). The model ecosystem is em-
bedded within the Massachusetts Institute of Technology Integrated Global System Model
(IGSM) (Prinn, 2013; Sokolov, 2005) which includes modules for the physics, chemistry,
and biogeochemistry of the atmosphere, land and ocean. The ocean component has a
2°×2.5° resolution grid and 22 vertical layers (10m thickness at surface to 500m at bot-
tom). The simulation is forced with observed greenhouse gas emissions from 1860−1990
and then with a high emissions scenario that is analogous to the IPCC’s Representative
Concentration Pathway 8.5, from 1990 − 2110. This perturbation results in ∼3°C sea
surface temperature warming by 2100, sea ice retreat, increased stratification, and an
altered overturning circulation. The IGSM has been used to examine changes in marine
biogeochemistry and ecology in previous studies (e.g. (Dutkiewicz et al., 2013) but with
a simpler version of the ecosystem model. The current more complex ecosystem has also
been used in previous studies, but only for the present day’s ocean (Dutkiewicz et al.,
2021; Sonnewald et al., 2020; Kuhn et al., 2019). This model and previous model val-
idation for the present day demonstrates that the output compares well with observa-
tions along both axes of size and functional type (e.g. (Dutkiewicz et al., 2021, 2020)).

2.2 Ecosystem and Environmental Variables

Surface-level plankton abundance data and environmental parameters were extracted
from Darwin simulation outputs, where surface in this context refers to the 10m thick
surface grid box. The ecosystem data contains 51 separate plankton biomasses, arranged
into seven functional groups (as described above). A number of environmental variables
have frequently been integrated into correlative SDMs to predict abundance and diver-
sity, and have thus been included here. They are: sea surface temperature (SST), pho-
tosynthetically active radiation (PAR), phosphate (PO$_4$), nitrate (NO$_3$), silicate (Si) and
iron (Fe). We sampled both the plankton abundance data and the environmental pre-
dictor variables from the 3586 spatiotemporal cells that encompass the representative
ocean measurement coordinates, and from the 3586 randomly selected spatiotemporal
cells. Note that the model simulation used for the current analysis nominally starts in
1991 and extends to 2100. As such, we sample the model output from the beginning of
1991 to the end of 2012 and consider this as a substitute to 1987−2008 in this context.
This is justified because the Darwin model’s internal variability does not match real-world
interannual variability in terms of timing, though does capture the magnitudes (e.g. there
are El Niño events, but these do not occur in the same years as the real ocean). To val-
idate predictions, we also consider whole-ocean surface data over the same period, and
for the final 22 years of the simulation, from 2079 − 2100.

2.3 Building the Correlative SDM

Although GAMs have considerable flexibility in how their core components are se-
lected, we used the standard ‘LinearGAM’ model of the freely available PyGAM pack-
age (Servén & Brummitt, 2018). LinearGAM incorporates a Gaussian distribution func-
tion with an identity link function, and fits predictor functions using penalised B-splines.
In combination, these components impose smoothness to prevent over-fitting, and en-
able the automatic fitting of nonlinear relationships. For an initial set of results, we set
the number of permitted splines to 20 for each predictor variable. We note that our re-
sults are not sensitive to the choice of this parameter (see ‘Model Comparison & Sen-
tsitivity Tests’). At the outset, we attempted to resolve and make predictions for indi-
vidual plankton tracers, but the resulting models proved to be highly unstable, so we in-
stead choose to proceed by summing the abundance data for each functional group, and
training GAMs accordingly. The resulting partial dependency plots were examined for
unexpected behaviours, or any clear indications of over or under-fitting. The resulting
GAMs SDM was then used to make predictions for the global surface ocean plankton
biomasses during 1987-2008 and 2079-2100.
2.4 Model Comparison & Sensitivity Tests

We define presence/absence as modelled biomass being above/below a cutoff threshold (10^{-5} \text{ mmol C/m}^3), but find that patterns in the resulting predictions are not sensitive to the choice of this threshold (Table S4).

The $R^2$ value of the GAMs predictions against the ‘ground-truth’ simulation values is given as $R^2 = 1 - \frac{SS_{res}}{SS_{tot}}$, where $SS_{res}$ is the residual sum of squares and $SS_{tot}$ is the total sum of squares. While $R^2$ is a widely-used statistic in regression analyses, it does not by itself provide a complete picture of goodness of fit. We therefore also examine the mean and median relative differences, defined here as $X_{me} = \frac{\text{mean predicted} - \text{mean actual}}{\text{mean actual}}$ and $X_{md} = \frac{\text{median predicted} - \text{median actual}}{\text{median actual}}$, as an indicator of bias. We also consider the false positive and false negative fractions, i.e. the fraction of grid cells where the GAMs incorrectly predict, respectively, present and absent biomass. Finally, we performed the above analyses with the logarithm of biomass concentrations and found that our results were not sensitive to this choice. Overall, we found that coccolithophores yielded the median performance in terms of goodness of fit with respect to spatial extrapolations. As such, this group is featured in the main body of this work, while results for the other six functional groups are reported in the supplements.

GAM sensitivity was investigated by varying the number of splines used in performing the fits; first by halving to 10, and then doubling to 40. While the resulting partial dependency plots revealed a clear change to the smoothness of the fit, as expected, we found that the resulting statistics were not appreciably impacted. To investigate the effect of sample size on the overall predictive power of the GAMs, we vary the number of randomly-sampled cells from a minimum of 100 (reducing to 63 ocean cells), to a maximum of 20,000 (reducing to 11,557 ocean cells), using 18 different test cases. Each sample size test case consists of three independent random samples, with the mean value being reported along with the standard deviation (Figure 4).

We also performed a range of simpler correlation analyses, to build a broader picture of the emergent relationships between functional group biomass and predictors. These act as a visual aid to better understand how these relationships might change in time and space, and as a basic cross-reference for GAMs-derived partial dependence plots of the training sets. We first calculate the Pearson’s Correlation Coefficient ($\rho$) for each functional group-predictor pair, and the Spearman’s Rank Correlation Coefficient ($\rho_s$). Respectively, these popular methods detect the strength of linear associations between variables, and the strength of correlation in monotonic relationships. A commonly used method for addressing skew or capturing scaling relationships is the log-transform, which we apply to all datasets before recalculting $\rho$. However, this method of broadly applying a single transformation is not optimal. A more robust approach would be to examine the distribution of each target-predictor relationship individually, before an appropriate transformation is selected. Nonetheless, even this more optimal method runs the risk propagating transformation uncertainty into the resulting confidence interval.

With these limitations in mind, we also determine correlations using the more recent distance correlations method of (Székely et al., 2007). This technique captures the strength of both linear and nonlinear associations and avoids the need to make assumptions about variable distributions or linearity. We plot the correlation matrices for the main 3586 cell test cases, both measurements-derived and randomly-sampled, in 1987-2008, and at the same locations in 2079-2100. We explore the effect of sample size on the derived correlations by increasing the number of randomly-sampled cells to 12,894, and finally to 25,683 cells.
3 Results

3.1 Spatial Predictions

We first describe the results of predicting plankton biogeography during the historical measurement period (1987 – 2008) (Figure 1). We find that predictive ability varies considerably across functional groups. There are fewer instances of our SDM incorrectly predicting presence (false positive) or absence (false negative) biomass for prokaryotes, picophytoplankton and coccolithophores (16–19% of all location-month pairs) than for diatoms, diazotrophs, and dinoflagellates (26–31%), with zooplankton in between (21%). Where biomass is present and is predicted as such, the SDM’s predictive ability for biomass concentration also varies substantially between functional groups (Figure 2); the SDM accounts for as much as 71% of the variance in biomass (diazotrophs) and as little as 41% (zooplankton). These patterns are reflected also in the mean relative differences and the balanced accuracy.

Patterns of overprediction of biomass occurs across most of the oceans. For prokaryotes, picoeukaryotes, dinoflagellates and zooplankton, this is especially evident in the Arctic (see Figures (c) of S1, S2, S5, S6). For these groups, we also see consistent underprediction in most of the Indian Ocean and in the Eastern Equatorial Pacific. Meanwhile, diatoms are substantially overpredicted in most of the mid- and high-latitudes in the Northern Hemisphere but perform relatively well in the subtropics (Figure S4(c)). Diazotrophs yield the best overall performance, with only a small amount of overprediction in the subtropical Atlantic, and overprediction in the transition zone latitudes poleward of the subtropics (Figure S3(c)).

In general the SDM shows a tendency to overestimate biomass in the spatial predictions regime. Overestimation ranges between 9–21% on average (picoeukaryotes and zooplankton, respectively), with a median overprediction of ≥16%. Despite this, there are some notable instances in the current context where the model performs well. Spatial predictions for coccolithophores, prokaryotes and diazotrophs all yield R^2 values that range between 0.62 and 0.71 (Figures 1(e), S1(e), S5(e)). Diazotrophs fare particularly well in this regime, with a mean overprediction of 10%, an R^2 of 0.71, and the best visual, qualitative match of biogeography overall (although we note that the median overprediction in this case is a substantial 194%) (Figures S3(c) and S3(e)). On the whole, the SDM trained on data from historical measurement locations appear to be able to reproduce qualitative biogeographic patterns from spatial predictions well, but quantitative performance is variable, with a broad tendency towards overprediction. Notably, the greatest predictive errors more often occur in the undersampled regions of the ocean, such as the Arctic and Indian Oceans, but are by no means confined to these regions. For instance in the highly sampled North Atlantic predictions for diatoms and diazotrophs was also poor.

3.2 Temporal Predictions

The SDM’s predictive ability is substantially reduced when extrapolating to the future ocean (see Figures 1 and 2). Rates of false positives and negatives in presence/absence do not uniformly change across functional groups: the cosmopolitan groups whose ranges expand poleward experience the least overall change, increasing by between 3% and 11% in prokaryotes, dinoflagellates and coccolithophores, with a decrease of 5% for picophytoplankton. The SDM’s ability to correctly predict presence/absence is further reduced for the groups with a more confined biogeography, increasing by between 14% and 23% for diazotrophs, zooplankton and diatoms. We see a substantial increase in false negative occurrences for diatoms (to 29%), the group whose biogeographic range contracts most. Where biomass is present and is predicted as such, the SDM’s predictive ability was reduced for all functional groups. In most cases, this reduction is substantial, with the fraction of variance accounted for by the SDM reducing by between 17 and 50%, such
that the prediction for zooplankton is worse than just assuming a globally uniform constant biomass (i.e. $R^2 < 0$). We see a marked increased in mean relative differences compared to the ‘spatial’ predictions, accompanied by a reduction in balanced accuracy for all groups besides diatoms (Figure 2).

Diatoms are the only group for which the fraction of variance accounted for does not decrease substantially, only from $R^2 = 0.59$ to $R^2 = 0.56$ (Figure S4). Thus, the predictive ability for diatom biomass where it is present is not greatly reduced, despite the SDM’s substantial overprediction of the contraction of diatoms’ biogeography. This is not sensitive to varying the absence/presence cut-off value by an order or magnitude in either direction (Table S1).

Spatial patterns of prediction errors of coccolithophores, prokaryotes, picoeukaryotes, dinoflagellates and zooplankton are largely similar to those for the historical period, except the North Atlantic is now underpredicted for all groups besides diazotrophs (Figures 1, S1, S2, S4, S5, S6). Diatom biomass is notably underpredicted in the Southern Ocean and Northern Atlantic (Figure S4). Meanwhile, diazotroph biomass is notably overpredicted throughout the Atlantic Ocean, the Arctic, bands of the subtropical Pacific and Indian Ocean (Figure S3). Excluding diatoms, the overall tendency towards over-prediction is exacerbated for all groups, increasing by 57% for prokaryotes, picoeukaryotes, coccolithophores, and dinoflagellates, by 20% for zooplankton, and by 49% for diazotrophs. Median overpredictions also increase for all groups besides diatoms.

3.3 Model Trained on Randomised Locations

Here we compared the above results with those produced when the GAMs SDM was trained on randomly sampled datasets (Figure 2). Interestingly, the broad spatial patterns of where overprediction and underprediction occurs do not change much when training the SDM on randomly distributed data, as opposed to the ocean observation locations (Figures S8 and S9). Nonetheless, predictive abilities increase, biases are reduced, and balanced accuracy increases in both the spatial and temporal cases (Figure 2). The fraction of variance accounted for by the SDM increases by 2–19% when using random data to predict historical biogeography, but increase from 5–46% when using random data to predict future biogeography. The most notable differences are for prokaryotic, picoeukaryotic, and zooplankton biomass in the future case. The magnitude of the biases also decreases – average biases are within 3–4% in the historical case using random data. The median bias for all groups is still that of overprediction, with most groups in the range of ≥17% compared to ≥30% for measurements-derived predictions. Diatoms and diazotrophs have a markedly higher bias in both measurements-derived and random cases, of ≥194% and ≥162%, and ≥65% and ≥35%. In the future case, using random data reduces biases for all groups, though does not eliminate them. We also found that the predictive ability of the SDM was only weakly dependent on sample size (where sample size here refers to the number of grid cell-month pairs that are sampled)(Figure 4), with predictive ability appearing to plateau with increasing sample size.

The results using random training datasets suggest that historical measurement biases reduce the predictive ability of the SDM more than the sample size of the training dataset. Predictive ability can be improved by subsampling or weighting one’s training dataset to reduce biases in space and time, although the coarse resolution of the Darwin model – and thus reduced variability as a result of correlated observations – relative to the real ocean may contribute to this plateauing effect.
Figure 1: (a) Mean coccolithophore surface biomass (1987 - 2008) from the Darwin model. Red points indicate spatial location of training set datapoints, derived from ocean measurement data. (b) As per 1(a) for the years 2079 - 2100. (c) Relative (percent) difference between mean coccolithophore surface biomass from the Darwin model and the GAMs SDM (1987 - 2008) (d) As per 1(c) for the years 2079 - 2100. For direct visual comparison, we first calculate the 5th and 95th percentile of the relative difference values for both the spatial and temporal predictions, then scale symmetrically to whichever of these values is the greatest, in either direction. (e) Hexagonally binned scatterplot of 1987-2008 GAMs SDM predictions vs 1987-2008 Darwin model. Colorbar shows log-scaled density of observations. Top inset: Fraction of data above the presence/absence threshold (10^{-5} \text{ mmol C/m}^3) (green box), GAMs SDM below threshold (left, light red), Darwin below threshold (bottom, light red), both below threshold (dark red). Bottom inset: The $R^2$, relative difference of the means ($\bar{X}_{\text{me}}$), and relative difference of the medians ($\tilde{X}_{\text{md}}$). (f) As per 1(e) but for 2079-2100. See Supplemental Materials for other functional groups.
Figure 2: Comparing Darwin model ‘true’ biomasses with GAMs SDM predictions for each functional group in 1987-2008 (historical) and 2079-2100 (future), and from measurements-derived and randomly-sampled training sets. Top to Bottom: (a) Relative differences of the means, given by \( \frac{GAM_{\text{mean}} - Darwin_{\text{mean}}}{Darwin_{\text{mean}}} \). (b) Balanced accuracy, given by \( \frac{\text{sensitivity} + \text{specificity}}{2} \). (c) \( R^2 \)

4 Discussion

Broadly, our GAMs-driven correlative SDM demonstrates capability in qualitatively capturing large-scale spatial patterns of plankton biogeography, but struggles to make robust quantitative predictions. This is particularly evident when the model is trained on historical ocean measurement data, and used to predict future plankton biogeography as a response to climate change. The emergent relationships between predictor variables and plankton abundances change spatially, seasonally and over the longer term. This is demonstrated by the variable nature of the partial dependence plots (Figure 3(a)–(b) and Figures S10 and S11), and by the change in correlation strengths identified by each of the independent methods used in generating the correlation matrices (Figure 3(c)–(f) and Figure S12). The correlation matrices offer an especially powerful visual demonstration of these points; we clearly see the change in apparent relationships between biomass and environmental predictors in the measurements-derived sample space, assessed over the same period of time one hundred years into the future (Figure 3(c) and 3(d)). It’s
Figure 3: Changing Relationships: (a) Partial dependence plots of coccolithophore biomass (mmol C/m³) as a function of each predictor, centred around the median (PO₄, NO₃, Fe, Si) in mmol X/m³, SST in °C, SSS in PSU, PAR in E/m²/day). Plotted using data from 3586 Darwin surface ocean cells at measurements-derived locations spanning 1987-2008 (dashed red line) and at the same locations from 2079-2100 (blue line). Grey lines indicate 95% confidence interval for the 1987-2008 case. (b) As per 3(a), but using data from 3586 randomly sampled cells. (c) Correlation heatmap for the measurements-derived training set, 1987-2008, generated using the distance correlations method of (Székely et al., 2007). (d) Difference between correlation strengths derived in 3(b) and those found at the same locations from 2079-2100. (e) and (f) As per 3(c) and 3(d), but for the equivalently-sized, randomly-sampled training set.

important to note that we should expect these differences to be exaggerated in the real world, where the system is significantly more complex.

Additionally, our results also demonstrate how spatial sampling bias can significantly alter the patterns of apparent relationships between environmental predictors and plankton biomass. The association strengths identified in the measurements-derived sample vary considerably from those found in the random sample of equivalent size (see Figure 3(c) vs. 3(e)). Importantly, this finding is robust across a range of sample sizes, where almost identical patterns of correlations are seen in the 3586 cell case as in the 25,683 cell case, as well as across several methods of deriving correlations (see Figure S12). Nonetheless, the spatial patterns of over and under-prediction derived from the GAMs SDM are not merely the result of spatiotemporal measurement biases. We see remarkable agreement in these broad qualitative patterns between the predictions generated from measurements-derived and random samples ((c) and (d) of Figures 1, and S1–6, and Figures S8 and S9). Ocean measurement biases may explain some element of the tendency towards over-estimation of historical biogeography/abundances; perhaps because measurements have more often been made in places with higher than average abundances. In all cases, training the statistical model on a non-biased dataset reduces the severity of over and under-
Figure 4: $R^2$ of GAMs SDM model prediction as a function of sample size. Points are the mean $R^2$ value for coccolithophore predictions from three independent randomly-generated training sets for each of the 18 sample sizes, ranging from $N=63$ to $N=11,557$. Shading is the standard deviation.

prediction, especially for spatial predictions (Figure S8(c) and S9(e)). But the same broad biogeographic patterns remain, indicating that the SDM is failing to effectively capture changes over time, despite its relatively robust performance according to the broad brush strokes of summary statistics (Figure S4(e) and S4(f)).

The fraction of variance that the SDM can account for saturates with sample size well below 100%, perhaps implying a potential ceiling on predictive ability. Nonetheless, a number of optimisations could be implemented to improve predictive skill; potentially in the SDM developed for the current case study, but certainly in real-world applications. First, we note that an unrepresentative training set presence/absence ratio compared to the population can lead to an unreliable representation of presence/absence in the resulting predictions. To avoid this possibility, researchers working with real observational data will sometimes employ resampling techniques (e.g. (Wei & Dunbrack, 2013)) to account for this effect. By contrast, our experimental design permitted us the unusual opportunity of testing our outcomes alongside a range of representative, randomly-sampled datasets spanning the surface ocean. These unbiased samples are representative of the presence/absence ratios of the population, and thus act as a control for our observations-derived test case. Given the broadly similar patterns of over and underprediction found across test cases, we do not employ resampling techniques here, but we encourage their application in real-world settings.

Related also to the more flexible nature of our study in comparison to correlative SDMs built from real-world observations, is the manner in which we approach training, validation and testing datasets. In some cases, machine learning practitioners working with real-world data, and their associated limitations, might reserve a proportion of the
training set for model validation, as well as an independent, but similarly-distributed, dataset for performance testing. A validation set allows for optimisation via the fine-tuning of model parameters, and for the avoidance of over-fitting, while the test set permits evaluation of model skill. Here, we use whole-ocean Darwin Model output as our test set for evaluating overall performance. Given model response to sensitivity tests, and GAM’s natural robustness to over-fitting as a result of predictor function regularisation, we do not explicitly employ a validation set. Model skill could be improved with parameter fine-tuning, especially in the spatial predictions test case. But it is less clear whether fine-tuning for performance using a training set sampled from the Darwin Model ocean of 1987-2008 would improve end-of-century predictions, for reasons that we will return to as this discussion progresses. Additionally, we speculate that our decision to train the GAMs SDM using the entire measurements-derived sample might itself yield improvements relative to splitting the samples into training, testing and validation subsamples.

The median overestimations of the GAMs SDM compared to the Darwin ‘ground truth’, even when using randomly sampled training data, also implies that these predicted abundance distributions are less skewed than the Darwin model distributions, which are, in turn, less skewed than distributions in the the real ocean. That is not to say, however, that all correlative SDMs will yield equivalent outcomes, regardless of the empirical models at their cores. Recent work by (Rudy et al., 2017) demonstrates that empirical methods can reliably extract the underlying mechanistic equations that govern a dynamical system. Similarly, (Holder & Gnanadesikan, 2021) evaluate random forest (RF) and neural network ensembles (NNE) in their ability to resolve the underlying intrinsic relationships between plankton biomass and environmental predictors, from the apparent relationships in the data. They demonstrate variability in predictive skill across different empirical test cases, and find that NNE’s yield overall superior performance; particularly in the case where plankton growth rates respond rapidly to environmental change, as might be expected in many real-world ocean environments. These hybrid methods represent a potential step toward building more skillful and descriptive models.

Although improvements to overall predictive skill might be made through model optimisation techniques, we argue here that the assumptions and uncertainties inherent to correlative SDMs apply fundamental limits to their utility. For instance, although we might feasibly achieve a better fit to the training data, questions still remain as to whether the environmental data included in the model reflect the true and complete niche requirements of the target species’. Even if we were to overcome this issue, using environmental correlates of distribution to predict abundance elsewhere in space and time implies that the distributions in the training data are at equilibrium, such that the niche is ‘fully occupied’. This may not be the case, as an otherwise suitable niche for a given species might have experienced some recent perturbation that temporarily reduces its equilibrium population density.

Empirical methods that extract the intrinsic drivers of plankton abundance and distribution (as derived in laboratory settings) might also yield considerable improvements to predictive capabilities of correlative SDMs. If factors such as spatiotemporal sampling bias and spatial autocorrelation in ocean measurements can also be accounted for, predictive skill might be greatly improved, especially in spatial extrapolations. However, appreciable improvements to multidecadal predictions of how plankton communities might respond to climate change would still not be guaranteed; we cannot assume that a species’ niche envelope is fixed and immutable over time. This is clearly demonstrated in our results; but we should expect the predictive skill of correlative SDMs applied to real world data to yield poorer results still. For instance, there are many more degrees of freedom in real-world interactions between plankton individuals, communities, and the wider ecosystem and environment. In addition to the controlling influence of e.g. nutrient supply rate, physical transport processes and level of top down pressure, plankton are also able to adapt genetically, epigenetically and plastically to change. With
their short generation times and high biodiversity, we might expect that even intrinsic
relationships could change over the course of a century. This is especially likely in such
a dynamic, randomly-perturbed, and far-from-equilibrium environment, where conditions
are ideal for unpredictable emergent phenomena to arise. By contrast, all such elements
within the Darwin Model are simplified by design, and intrinsic relationships are held
steady over time, such that the spatiotemporal variability in apparent relationships seen
here are the product of many fewer sources of complexity, right down to how climate change
proceeds (a known quantity in the Darwin Model, and yet another significant source of
uncertainty in the real world).

We focus here on deriving our SDM using a statistical learning model that, for rea-
sons outlined in Materials & Methods, we believe makes for an excellent case study. Our
investigation has allowed us to better clarify the strengths and limitations of such an ap-
proach, as applied in the current context. Owing to the complexity and ever-changing
nature of the system, some of these limitations could be fundamental and unavoidable,
particularly when extrapolating far beyond the training regime.

Methodologically, the broader approach we have presented of applying an empir-
ical model to output from a numerical model may be useful for addressing a number of
additional questions. These might include evaluating how best to empirically model whole-
ecosystem properties, such as diversity, from observations, or assessing where and when
to make new observations to maximise information content about global plankton bio-
geography. But, as our results here have demonstrated and reinforced, it is important
to be aware of the strengths and limitations of this approach, especially when dealing
with a high degree of complexity over time.

5 Conclusion

In summary, our results suggest that correlative SDMs like the one developed here
can be powerful tools for extrapolating from sparse measurement sets to capture the qual-
itive spatial patterns of plankton biomass in the present-day ocean. However, their pre-
dictions are especially sensitive to the spatiotemporal bias in historical measurements,
and can tend towards overprediction if not properly accounted for. In addition, such mod-
els demonstrably struggle to predict future plankton biomass because the spatial and tem-
poral complexity of the physical, chemical and biological interactions that characterise
the system give rise to a variability that cannot be accurately predicted decades ahead
of time from correlations in contemporary data. The changes in relationship between en-
vironmental variables and the plankton abundances demonstrated in the current work
could be greatly exaggerated in correlative SDMs that tackle the significantly more com-
plex task of predicting real-world plankton biogeography using sparse observational data.

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**Code Availability.** The physical model used here is available through [http://www.mitgcm.org](http://www.mitgcm.org), and the generic ecosystem code is available through [http://www.gitlab.com/jahn/gud](http://www.gitlab.com/jahn/gud). The specific modifications for the setup used here are available via Harvard Dataverse at [http://www.dataverse.harvard.edu/dataverse/](http://www.dataverse.harvard.edu/dataverse/). Note that a more up-to-date version of the ecosystem model used here is available at [http://www.github.com/darwinproject/darwin/](http://www.github.com/darwinproject/darwin/). The code used to process and analyse the data, and to produce the results for this manuscript, is available at [https://github.com/teatauri/stats-biogeo-2021](https://github.com/teatauri/stats-biogeo-2021).

**Data Availability.** The Darwin Model output used in the current study is available at [http://www.dataverse.harvard.edu/dataverse/](http://www.dataverse.harvard.edu/dataverse/). The dataset will have a doi, and will be hosted through the Harvard Dataverse Darwin project site. The extracted and processed Darwin surface data will also be made similarly available.

**References**


Supporting Information for ‘Testing the skill of a species distribution model using a 21st Century virtual ecosystem.’

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Contents of this file:

1. Figures S1 to S13
2. Tables S1 to S4
3. Access to Darwin model output data
4. Access to code used to produce results

Introduction This document accompanies the above mentioned manuscript, wherein we explore the performance of a correlative species distribution model in predicting the plankton biogeography, using the Darwin model as a ‘ground-truthed’ virtual environment. The analyses used to generate the following results are described in the Materials and Methods section of the main text.

Figures S1 to S6 is a complete set of figures, equivalent to Figure (1) in the main text, for all remaining plankton functional groups included in this study.

Figure S7 shows the true/false positives (TP, FP) and true/false negatives (TN, FN) from the GAMs predictions for all functional groups in the four different scenarios: GAMs trained on measurements-derived datapoints versus random datapoints, and spatial-only predictions (historical) versus end-of-century predictions (future). Note that the format of this figure is best understood as a bar plot visualisation of a confidence matrix, such that $TP + FP + TN + FN = 1$.

Figures S8 and S9 are the relative difference maps between Darwin model "true" values and the GAMs SDM predictions for all functional groups, in the historical period (1987-2008) and by end-of-century (2079-2100).
Figure S10 is the partial dependence plots for all functional groups besides Coccolithophores, which are given in the main text. GAMs trained on data within 3586 Darwin surface cells, from the 1987-2008 period, and the 2079-2100 period. These demonstrate how relationships between each predictor variable and the target variable (plankton biomass) change over time, for each functional group.

Figure S11 is equivalent to S10, but for 3586 randomly-distributed cells.

Figure S12 shows the correlations between predictors and functional group biomass within measurement-derived and randomly-distributed samples, of varying sizes, historical and future. Several methods are used for comparison: Distance Correlations, Pearson’s Correlation Coefficient (\( \rho \)), calculated after data are transformed via natural log (\( \rho_{ln} \)), Spearman’s Rank Correlation Coefficient (\( \rho_s \)).

Figure S13 shows the distribution of randomly-selected datapoints (the ocean observation analogue points are included in Figure 1a in the main text).

Table S1 Summary data for a range of sensitivity tests done on varied random sample sizes, from number of cells N=63 to N=11,557, and in predicting both historical and future biogeography.

Table S2 Summary of results for the predictions generated from the main 3586 cell testcases.

Table S3 Proportion of the functional group biomass measurements that were below the absence cut-off, for the 3586 cell training sets.

Table S4 Summary data for a range of sensitivity tests done on how varying presence-absence cut-off by a factory of ten in either direction affects results.

The raw Darwin model output used for this work is available at http://www.dataverse.harvard.edu/dataverse/.

The processed surface (top 10m) ocean ecosystem and physical data for the years 1991-2012 (which we consider equivalent to 1987-2008, for reasons explained in Methods and Materials) and 2079-2100, will also be made publicly available via Harvard Dataverse.
Finally, should the manuscript be accepted, DOIs for all associated code and data will be provided.
Figure S1: (a) Mean prokaryote surface biomass (1987 - 2008) from the Darwin model. (b) As per S1(a) for the years 2079 - 2100. (c) Relative (percent) difference between mean diatom surface biomass from the Darwin model and the GAMs (1987 - 2008) (d) As per S1(c) for the years 2079 - 2100. (e) Hexagonally binned scatterplot of 1987-2008 GAMs predictions vs 1987-2008 Darwin model. Colorbar shows log-scaled density of observations. Top inset: Fraction of data above the presence/absence threshold (10^{-5} mmol C/m^3)(green box), GAMs below threshold (left, light red), Darwin below threshold (bottom, light red), both below threshold (dark red). Bottom inset: The $R^2$, relative difference of the means ($\bar{X}_{me}$), and relative difference of the medians ($\bar{X}_{md}$). (f) As per S1(e) but for 2079-2100.
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Figure S11: Changing Relationships (models trained at random locations): Difference in partial dependence plots of plankton biomass for GAMs trained on data from 1987-2008 (dashed red line) and from 2079-2100 (blue line), for each predictor (PO$_4$, NO$_3$, Fe, Si in mmol X/m$^3$, SST in °C, SSS in PSU, PAR in E/m$^2$/day). From top to bottom: (a) Pro, (b) Pico, (c) Diazo, (d) Diatom, (e) Dino, (f) Zoo.
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