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Portfolio effect and the predictability of natural phytoplankton population dynamics

A Thesis submitted in partial satisfaction of the requirements
for the degree Master of Science

in

Marine Biology

by

Vitul Agarwal

Committee in charge:

Professor Andrew Barton, Chair
Professor Jeff Bowman
Professor George Sugihara

2020

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Chair

University of California San Diego

2020

TABLE OF CONTENTS

Signature Page.....	iii
Table of Contents.....	iv
List of Figures.....	v
List of Tables	vi
Acknowledgements	vii
Abstract of the Thesis	viii
Chapter 1	1
1.1 Title page.....	1
1.2 Abstract.....	2
1.3 Introduction.....	3
1.4 Materials and Methods.....	5
1.5 Results and Discussion.....	15
1.6 Conclusion.....	29
1.7 Acknowledgements.....	30
Appendix.....	31
References.....	33

LIST OF FIGURES

- Figure 1:** Abundance (cells L⁻¹) of three different illustrative phytoplankton taxa showing various dynamics within the community: (A) Phytoflagellates 2µm (B) *Prorocentrum dentatum* and (C) *Paralia sulcata*. There are 10 months of missing data in 22 years, as indicated by the gaps in the time series.....7
- Figure 2:** (A) Abundance (cells L⁻¹) of 5, 50 and 100 randomly grouped species from October 1992 to December 2014, and (B) Mean prediction skill ($\bar{\rho}$) for groups of species ranging in size from 1 to 198 species in the group (red) and their seasonal surrogates (blue).....17
- Figure 3:** Mean prediction skill ($\bar{\rho}$) by group size for the simple model exploring how measurement noise affects predictability (Eq. 1), with three levels of noise (No noise, Low and High noise levels).....19
- Figure 4:** Mean prediction skill ($\bar{\rho}$) by group size for the model resolving variations in growth rate and carrying capacity (Eq. 2-4) with (right column) and without inter-species interactions (left column). The model was run without stochasticity in growth rates (e.g., process noise; top row) and with stochasticity in growth rates (bottom row).....21
- Figure 5:** Mean prediction skill ($\bar{\rho}$) of time series (red) and seasonal surrogates (blue) for (A) Coccolithophores ($N=16$) (B) Diatoms ($N=130$) (C) Phytoflagellates ($N=14$) and (D) Dinoflagellates ($N=37$).....24
- Figure 6:** Mean prediction skill ($\bar{\rho}$) of time series (red) and their seasonal surrogates (blue) for cells with radius (A) <5µm ($N = 68$) (B) 5-12µm ($N = 63$) and (C) >12µm ($N = 67$). Pie graphs at right provide the relative diversity of taxonomic groups within each size-based category (Diat – diatoms, Dino – dinoflagellates, Cocco – coccolithophores, Phyto – phytoflagellates and Other – *Phaeocystis*).....27
- Figure 7:** Mean prediction skill ($\bar{\rho}$) of time series (red) and their seasonal surrogates (blue) for only diatoms of the following radius: (A) <5µm ($N = 44$) (B) 5-12µm ($N = 40$) and (C) >12µm ($N = 46$).....28
- Figure S1:** Abundance (cells L⁻¹) of three noise model taxa with various levels of observational error: (A) No noise (B) Low Noise and (C) High noise. The values for the parameters can be found in Table 131
- Figure S2:** Abundance (cells L⁻¹) of three phytoplankton community model taxa (A) with no noise and inter-species interactions (B) with inter-species interactions and (C) with process noise. The values for the parameters can be found in Table 2.....32

LIST OF TABLES

Table 1: List of model parameters, units and values used in the noise model.....	11
Table 2: List of model parameters, units and values used in the phytoplankton community model.....	14

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ABSTRACT OF THE THESIS

Portfolio effect and the predictability of natural phytoplankton population dynamics

by

Vitul Agarwal

Master of Science in Marine Biology

University of California San Diego, 2020

Professor Andrew D. Barton, Chair

Phytoplankton play important roles in marine food webs and biogeochemical cycles. The ability to understand natural changes in phytoplankton populations are a central goal in biological oceanography; however, the dynamics of phytoplankton populations are often noisy and difficult to predict. The portfolio effect in ecology is a concept that relies on the aggregation of data to reduce the variance of individual populations. We test whether the aggregation of data across multiple species can help improve the predictions of phytoplankton assemblages one month into the future. Using empirical dynamic modelling, we assess the predictability of phytoplankton assemblages in varying group sizes, and show that certain assemblages of phytoplankton species are more predictable in groups rather than as individual species.

Title:

Portfolio effect and the predictability of natural phytoplankton population dynamics

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forecasting; empirical dynamic modeling; predictability; functional groups; Station L4

Abstract

It is difficult to make skillful future predictions about the dynamics of marine phytoplankton populations. Aggregating species abundance data across multiple species to reduce temporal variability (i.e. the portfolio effect) is an approach that has been applied within fisheries restoration, conservation, and monitoring programs in order to reduce noise and examine long-term patterns and trends. Here, we use 22-year time series of 198 phytoplankton taxa from Station L4 in the Western English Channel (1992 – 2014) to test whether and how the portfolio effect can improve predictions of phytoplankton assemblage dynamics. Using a non-parametric framework to assess predictability, we demonstrate that the prediction skill is significantly affected by how species data are grouped into assemblages, the presence of noise, and stochastic behavior within species. We find that predictability one month into the future increases significantly when species are aggregated together into assemblages with more species, compared with the predictability of individual taxa. In contrast, predictability of the dynamics of dinoflagellates and larger phytoplankton ($>12\mu\text{m}$ cell radius) is low overall and does not increase by aggregating similar species together. The presence of noise, such as observational error in data or stochasticity in growth rates, reduces the predictability of individual species more than the predictability of aggregate groups. These findings show the portfolio effect can be used to increase the predictability of certain assemblages of phytoplankton species and has implications for microbial observing campaigns and ecosystem modeling.

Introduction

Phytoplankton play vital roles in marine ecosystems. Because of the importance of phytoplankton dynamics for marine food webs, fisheries, and biogeochemical cycles (Ryther 1969; Falkowski et al. 1998), there is growing interest in making skillful predictions of phytoplankton population dynamics, particularly on seasonal and longer timescales. Phytoplankton communities exhibit considerable variability on rapid (daily to interseasonal) as well as longer-term (interannual to decadal) timescales due to natural and anthropogenic drivers (Chavez et al. 2003; Falkowski and Oliver 2007; Chiba et al. 2012; Edwards et al. 2013b; Barton et al. 2016). This means that predicting ecological dynamics beyond the immediate future is difficult for a broad range of physical, biological, and ecological reasons. The management of living marine resources could be improved with skillful predictions of primary productivity or phytoplankton community structure, in addition to other environmental and biological conditions (Hobday et al. 2016; Tommasi et al. 2017; Marshall et al. 2019).

Anomalies in phytoplankton populations rapidly decorrelate in time and space (Doney et al. 1998). For example, phytoplankton population anomalies in most of the ocean persist for only a few weeks, on average (Kuhn et al. 2019). In contrast, midlatitude sea surface temperature and nutrient anomalies last, on average, a few months to a year or longer (Deser et al. 2003; Kuhn et al. 2019), and may have interannual persistence when subsurface anomalies are re-exposed by deep water column mixing in subsequent years (Deser et al. 2003). Even longer duration, persistent anomalies in temperature are possible due to dominant modes of climate variability and marine heatwaves, for example in the tropical Pacific due to El Niño Southern Oscillation (Deser et al. 2010) and in the North Pacific due to the North Pacific “blob”

in 2013-2015 (Bond et al. 2015). Surface temperature can, in some regions, be predicted skillfully months or even years in advance (Song et al. 2008; Stock et al. 2015; Taboada et al. 2019). Ocean surface chlorophyll and primary productivity may also be predictable, up to years in advance, though the degree of predictability varies strongly in space (Park et al. 2019; Taboada et al. 2019). While prediction skill of the physical and chemical environment, and aggregate measures of primary producers (e.g., chlorophyll and primary production) on intraseasonal and longer timescales is developing quickly (Park et al. 2019), thus far ecological predictions at the population or species assemblage level have received less attention.

In this paper, we test the portfolio effect in ecology as a possible strategy to improve the predictability of phytoplankton assemblage dynamics. In this context, we define assemblage as a group of more than one species. The abundance of the assemblage is the sum of the abundance of the individual taxa within the assemblage. We define predictability as the correlation coefficient between predicted and observed population abundance (in cells L^{-1}) one month into the future. A higher correlation coefficient implies higher predictability. Briefly, the portfolio effect refers to the reduction of variance through the aggregation of data, in this case the abundance of individual phytoplankton species. By examining the system as a whole, rather than through their individual components, the portfolio effect reduces the “noise” generated by non-linear interactions, potentially highlighting broad signals and patterns (Schindler et al. 2015). This concept was first employed in financial investment theory – diversifying investment to a broader selection of securities reduces overall risk (Markowitz 1952). Here we ask: 1) Are single species more or less predictable than groups of species aggregated together?; 2) What factors affect the predictability of phytoplankton

assemblages?; 3) How does assemblage composition affect predictability?; and 4) What are the implications for future studies that attempt to maximize predictive skill?

We use phytoplankton time series data for 198 phytoplankton taxa sampled at the long-term coastal monitoring Station L4 in the Western English Channel (50° 15'N, 4° 13'W) collected between October 1992 to December 2014. Using empirical dynamic modeling (Sugihara and May 1990), we first quantify the predictability of each taxon, defined as the correlation coefficient between predicted and observed population abundance one month into the future. We then aggregate the time series for varying assemblage sizes (e.g., groups of 2, 3, 4, ..., 198) taxa, and assess the assemblage predictability in comparison to the predictability of individual taxa. We examine how predictability at the taxon and assemblage level varies across major functional groups of phytoplankton, including diatoms, dinoflagellates, coccolithophores, and phytoflagellates, as well as across groups of similarly sized phytoplankton. Finally, we develop a simple model resolving species interactions and stochasticity in a community of phytoplankton to understand the mechanisms that explain changes in predictability between individual and groups of taxa.

Materials and Methods

Ecological data from the English Channel

Station L4 is a coastal station located approximately 10 nautical miles off Plymouth, UK and is characterized by summer nutrient depletion with seasonal vertical and horizontal influx of nitrate into the system (Smyth et al. 2010). Water samples were collected on weekly basis (weather permitting) at a depth of 10m using a 10L Niskin bottle, and species were identified by light microscopy using the Utermöhl technique

(Widdicombe et al. 2010a). Although measurements at station L4 are conducted on a roughly weekly basis, phytoplankton data were converted to monthly averages to account for gaps in the data. The dataset includes 198 phytoplankton taxa, including well-defined species (e.g. *Alexandrium tamarense*), but also more broadly-defined groups such as “Phytoflagellates 2µm”, indicating all flagellates with a mean diameter of 2µm (Widdicombe et al. 2010a; Widdicombe et al. 2010b). In this dataset, there were a wide range of phytoplankton species and associated dynamics, from numerically abundant, generic groups like “Phytoflagellates 2µm” (Fig. 1A) to rarely occurring *Prorocentrum dentatum* (Fig. 1B) and seasonally occurring *Paralia sulcata* (Fig. 1C). Some of the most numerically dominant diatom species were *Paralia sulcata*, *Guinardia delicatula* and *Pseudo-nitzschia "delicatissima"*, whereas the most numerically dominant dinoflagellate species were *Karenia mikimotoi* and *Prorocentrum cordatum*.

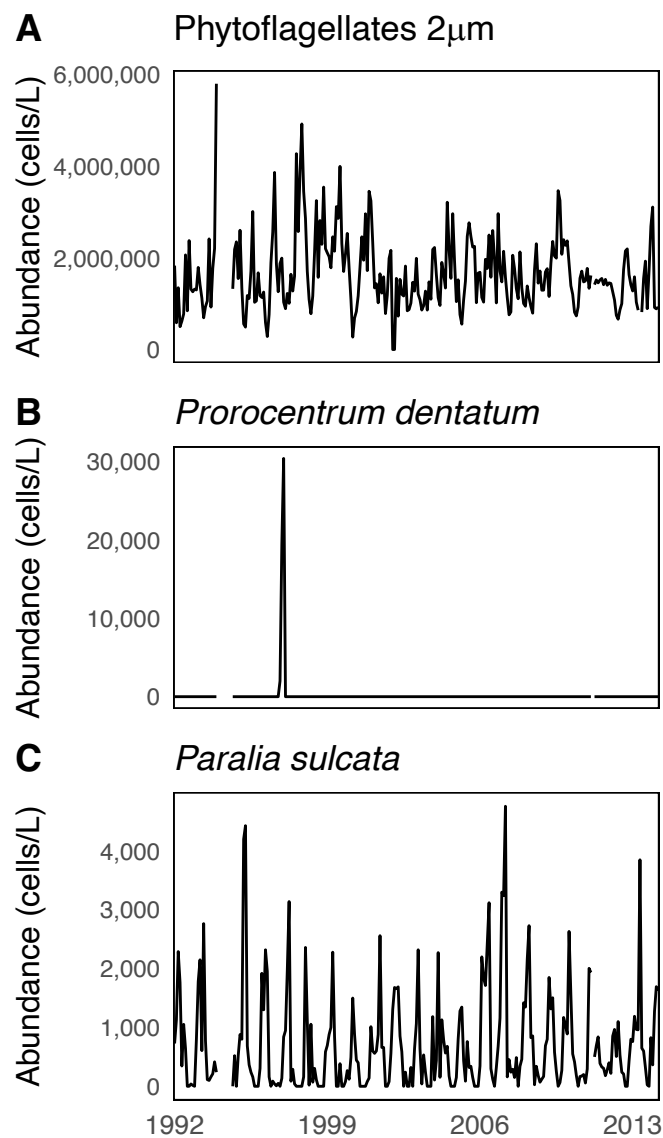


Figure 1: Abundance (cells L⁻¹) of three different illustrative phytoplankton taxa showing various dynamics within the community: (A) Phytoflagellates 2µm (B) *Prorocentrum dentatum* and (C) *Paralia sulcata*. There are 10 months of missing data in 22 years, as indicated by the gaps in the time series.

Group formation

We estimated the predictability of both individual time series and grouped time series created by aggregating multiple time series together (i.e., creating an assemblage of species). By creating groups of species, we explicitly test whether portfolios of species are more predictable than individual species. We grouped taxa together randomly, within the diatom, dinoflagellate, coccolithophore and phytoflagellate functional groups, and by cell size. In the case of grouping species randomly, we selected a random subset of all species for each group size. In the case of functional groups, we followed the same process but limited the selection to only diatoms, dinoflagellates, coccolithophores or phytoflagellates. In the case of grouping by cell size, we created broader categories based on cell radius and randomly selected species within those categories. Each assemblage time series was an arithmetic sum of all the individual species data at each month over time. Since groups were generated from a random subset of all time series, we ran 1000 trials for each group size. Prediction estimates for each group size could then be provided as a mean value ($\bar{\rho}$) and a standard error with 95% confidence intervals.

Empirical dynamic modeling (EDM)

We use empirical dynamic modeling (EDM) to estimate the predictability of both individual and grouped time series. Briefly, EDM is a non-parametric framework for creating predictive models of dynamic systems (Sugihara and May 1990). EDM has been successfully applied to many problems, such as understanding fisheries recruitment (Munch et al. 2018) and testing the nonlinearity of large-scale oceanographic processes (Hsieh et al. 2005). In this study, we employ in-sample

simplex projection to predict phytoplankton assemblage and population dynamics (Sugihara and May 1990).

Takens's theorem suggests that we can reconstruct the dynamical attractor of a system with time lags of a variable of interest (Takens 1981). The number of lags is determined by E , the embedding dimension. Every time-point in a time series for each taxon can then be represented as a set of coordinates in this E -dimensional space $\{x_t, x_{t-1}, x_{t-2} \dots x_{t-(E-1)}\}$, where x_t is the abundance of taxon x at time t , and x_{t-1} is its abundance at time $t - 1$, etc. Following this reconstruction, we can then look at the nearest neighbors of every point and track their movement in time. Future predictions are the weighted average of the trajectory of the nearest neighbors. Prediction estimates are given by ρ ($0 \leq \rho \leq 1$), which is the standard correlation coefficient between observed data and the predicted values based on time series reconstruction. A higher ρ means that predictions a month in advance are more accurate, whereas lower ρ values mean the predictions are less accurate. We next assess whether predictability exceeds what would be expected from seasonal ecological changes.

Phytoplankton in natural ecosystems often respond to seasonal environmental and biological changes. Therefore, we next describe a method for testing whether the predictability we estimate within each population time series exceeds what is expected from seasonality alone. Here we implemented a surrogate test for each time series prediction. Surrogate time series are created in a series of steps: (i) calculate the climatological seasonal cycle for each population or assemblage (i.e., average all the data from all Januaries in the time series to calculate the average January phytoplankton abundance), ii) calculate the residuals, or anomalies, by subtracting the seasonal cycle from each time series, (iii) shuffle the time series of residuals, and iv) add the shuffled

residuals back to the repeating climatological seasonal cycle. The resulting surrogate time series removes the ecological dynamics within the time series but retains the seasonal cycle. We then calculated a ρ value using the simplex methodology described above for this surrogate time series to assess the predictability of the seasonality. A direct comparison of ρ between a time series and its associated surrogates then indicates the strength of our model in predicting actual ecosystem dynamics over seasonal forcing.

Noise modeling

We created a simple model to test how noise added to a time series, for example as measurement error, influences predictability. In the model, the abundance of each species through time ($x_{i,t}$) is a sine function with a species-specific phase shift and time-varying noise added:

$$x_{i,t} = A \cdot \sin(\omega t + \Phi) + A + \gamma^{obs} \cdot \varepsilon_{i,t}^{obs} + \beta_i^{obs} \quad (1)$$

Where $x_{i,t}$ is the abundance of taxon x_i at time t (cells L^{-1}), A is the amplitude (unitless), ω is the frequency of oscillation, Φ is the phase shift (rad), γ^{obs} is the scaling factor of noise (unitless), $\varepsilon_{i,t}^{obs}$ is the observational error (cells L^{-1}) and β^{obs} is an offset (cells L^{-1}) to ensure that $x_{i,t} \geq 0$.

$$\beta_i^{obs} = |\min(\gamma^{obs} \cdot \varepsilon_{i,t}^{obs})|$$

$$\varepsilon_{i,t}^{obs} \sim \mathcal{N}(\mu = 0, \sigma^2 = 1)$$

The amount of observational error in the time series ($\varepsilon_{i,t}^{obs}$) was selected from normally distributed noise and modulated by γ^{obs} . Observational error refers to error associated within the sampling process. In this example, the model resolution is

monthly, and we add noise to each monthly time step. We tested the predictability of 100 species in portfolios (of 1, 2, 3...100 species) with three levels of noise ($\gamma = 0, 0.5$ and 1). The phase shift (\emptyset) allowed for some variability in dynamics across the model species. The values for each of the parameters can be found in Table 1. Sample time series from the model can be found in Fig. S1.

Table 1: List of model parameters, units and values used in the noise model

Symbol	Parameter	Units	Value
\mathbf{t}	time step	months	1
\mathbf{x}_i	abundance of species i	cells L^{-1}	
\mathbf{A}	amplitude of oscillation	-	1
\emptyset	phase shift	rad	$-1 \leq \emptyset \leq 1$
ω	frequency of oscillation	rad month $^{-1}$	$\frac{2\pi}{12}$
γ^{obs}	scaling factor for noise	-	0, 0.5 (low) and 1 (high)
$\epsilon_{i,t}^{\text{obs}}$	observational error for species i	cells L^{-1}	$\sim \mathcal{N}(\mu = 0, \sigma^2 = 1)$
β_i^{obs}	offset to ensure $x_i \geq 0$	cells L^{-1}	$ \min(\gamma^{\text{obs}} \cdot \epsilon_{i,t}^{\text{obs}}) $

Phytoplankton community modeling

We next describe an idealized model of an interacting phytoplankton community that we use sequentially to test how inter-species interactions and stochasticity in vital rates influence predictability for individual and multiple model taxa. The model is based on the Lotka-Volterra competition equations (Lotka 1920). The abundance of species i , x_i (cells L^{-1}), is controlled by the realized population growth rate $r_{i,t}$ (day $^{-1}$), the

carrying capacity $K_{i,t}$ (cells L^{-1}), and the sum of interactions ($\alpha_{i,j}$; *unitless*) with other species (x_j):

$$\frac{dx_i}{dt} = r_{i,t}x_i \left(1 - \frac{\sum_{j=1}^N \alpha_{i,j}x_j}{K_{i,t}}\right) \quad (2)$$

The realized population growth rate and carrying capacity for each species vary through time and are explained below. Each species interacted with only one-fourth the total number of species in the ecosystem and interaction strength was regulated by α . The interaction strength between any two species $\alpha_{i,j}$ was randomly selected from a uniform distribution with limits $\pm\alpha$ and varied on a monthly basis. We created two treatments for interaction strength: (i) $\alpha = 0$ for no interactions between species and, (ii) $\alpha = 0.25$ for strong interactions between species. We limit the number of interacting species to one-fourth the total in order to simulate a community where many but not all species interact directly. Since interactions could be both positive and negative, every species had a minimum abundance of 1×10^{-10} cells L^{-1} through time to prevent extinction.

The carrying capacity of each species ($K_{i,t}$) was controlled by the seasonal cycle without the addition of noise (Eq. 3):

$$K_{i,t} = K \cdot (A \cdot \sin(\omega t) + \delta) \quad (3)$$

$$\delta = A + 0.1$$

The scaling parameter K was constant and equal for every species. We added a small value δ to ensure that $K_{i,t} > 0$. Each species had a basal physiological growth rate μ (day^{-1}) selected from 0.8 to 1.2. To introduce process noise into the system (that is, noise added to the key organism trait in the model), we added randomly generated values of growth rate ε_i^p (day^{-1}) to the seasonal cycle of each species. The values were

selected from a normal distribution $\sim \mathcal{N}(\mu = 0, \sigma^2 = 1)$. We chose to add noise on monthly timescales, assuming that environmental processes that influence growth rates (such as sea surface temperature anomalies) persist for weeks to months (Kuhn et al. 2019). The realized population growth rate for each species (r_i) at time t was a function of the physiological growth rate (μ), the seasonal cycle, and total amount of process noise ($\gamma^p \cdot \varepsilon_{i,t}^p$):

$$r_i = \mu_i \cdot (A_i \cdot \sin(\omega t) + \mu_i + \gamma^p \cdot \varepsilon_{i,t}^p + \beta_i^p) \quad (4)$$

$$\beta_i^p = |\min(\gamma^p \cdot \varepsilon_{i,t}^p)|$$

The parameter γ^p was determined at the start of each experiment. We had two treatments for adding process noise: (i) $\gamma^p = 0$ for no process noise and, (ii) $\gamma^p = 1$ for high process noise. β^p (day^{-1}) is an offset to ensure that $r_i \geq 0$ after the addition of process noise.

The model was run with a time step of 6 hours for 20 years. We aggregated the 6-hourly data to monthly averages to maintain our timescales of prediction and keep our model comparable to L4 monthly-averaged data. Our goal was to check the effects of interaction strength (α) and level of process noise (γ^p) on prediction skill (ρ) and the subsequent change in the portfolio effect for the model ecosystem. Values for each of the parameters in the model can be found in Table 2. Sample time series from the model can be found in Fig. S2.

Table 2: List of model parameters, units and values used in the phytoplankton community model

Symbol	Parameter	Units	Value
\mathbf{t}	time step	hours	6
\mathbf{x}_i	abundance of species i	cells L^{-1}	
\mathbf{A}	amplitude of oscillation	-	1
$\boldsymbol{\omega}$	frequency of oscillation	rad day^{-1}	$\frac{2\pi}{360}$
$\boldsymbol{\alpha}$	limits of interaction strength	-	0 (no interactions) 0.25(strong interactions)
$\boldsymbol{\alpha}_{i,j}$	interaction strength between two species	-	$-\alpha < \alpha_{i,j} < \alpha$
$\boldsymbol{\mu}$	physiological growth rate	day^{-1}	$0.8 \leq \mu \leq 1.2$
\mathbf{K}	carrying capacity scaling factor	cells L^{-1}	30,000
\mathbf{K}_i	effective carrying capacity for species i	cells L^{-1}	
$\boldsymbol{\delta}$	offset to ensure $K_i > 0$	-	$A + 0.1$
\mathbf{r}_i	realized growth rate for species i	day^{-1}	
$\boldsymbol{\gamma}^p$	scaling factor for noise	-	0 (no noise), 1(high noise)
$\boldsymbol{\varepsilon}_{i,t}^p$	process noise for species i	day^{-1}	$\sim \mathcal{N}(\mu = 0, \sigma^2 = 1)$
$\boldsymbol{\beta}_i^p$	offset to ensure $r_i \geq 0$	day^{-1}	$ \min(\boldsymbol{\gamma}^p \cdot \boldsymbol{\varepsilon}_{i,t}^p) $

Results and Discussion

Portfolio effect

Are single species more or less predictable than groups of species?

We find that predictability increases with the number of aggregated species, regardless of taxonomy, and the predictability exceeds what would be expected from seasonality alone. While individual or groups of few species tend to exhibit noisy population dynamics, larger aggregated group sizes tend to exhibit smoother, more repeating annual cycles of abundance (Fig. 2A; this figure shows three illustrative abundance time series with 5, 50, and 100 species added together). In this case, species are aggregated randomly with no regard for their taxonomic grouping. Prediction skill increases with group size for the actual time series and surrogates (Fig. 2B). However, $\bar{\rho}$ is greater for the actual time series than for the seasonal surrogates, suggesting that the predictability is not merely a function of seasonality. The rate of increase in predictability with increasing group size saturates for large groups sizes, possibly pointing to a maximum level of prediction for assemblages of species in this system. We hypothesize that the existence of a maximum could be tied to the presence of noise in our data, originating from a range of sources such as observational error or stochastic environmental influence, which control the overall limits of being able to predict phytoplankton assemblage dynamics.

One implication of this result is that while individual species may not be highly predictable on average, many species aggregated together can be much more predictable. This result appears consistent with empirical studies from aquatic and marine settings (Schindler et al. 2015) as well as theory (Koellner and Schmitz 2006). For example, experimental acidification of lakes has found that species composition

changes markedly while total biomass may not (Schindler 1990; Frost et al. 1995) and that experimental nutrient enrichment across multiple lakes produced contrasting responses in community structure but relatively consistent increases in total biomass (Cottingham and Carpenter 1998). Mutshinda et al. (Mutshinda et al. 2016) found that the total biomass dynamics of diatoms and dinoflagellates at the L4 station in the English Channel were distinct from one another and tied to environmental variations, but that the biomass of individual species within each group was typically less tied to environmental conditions.

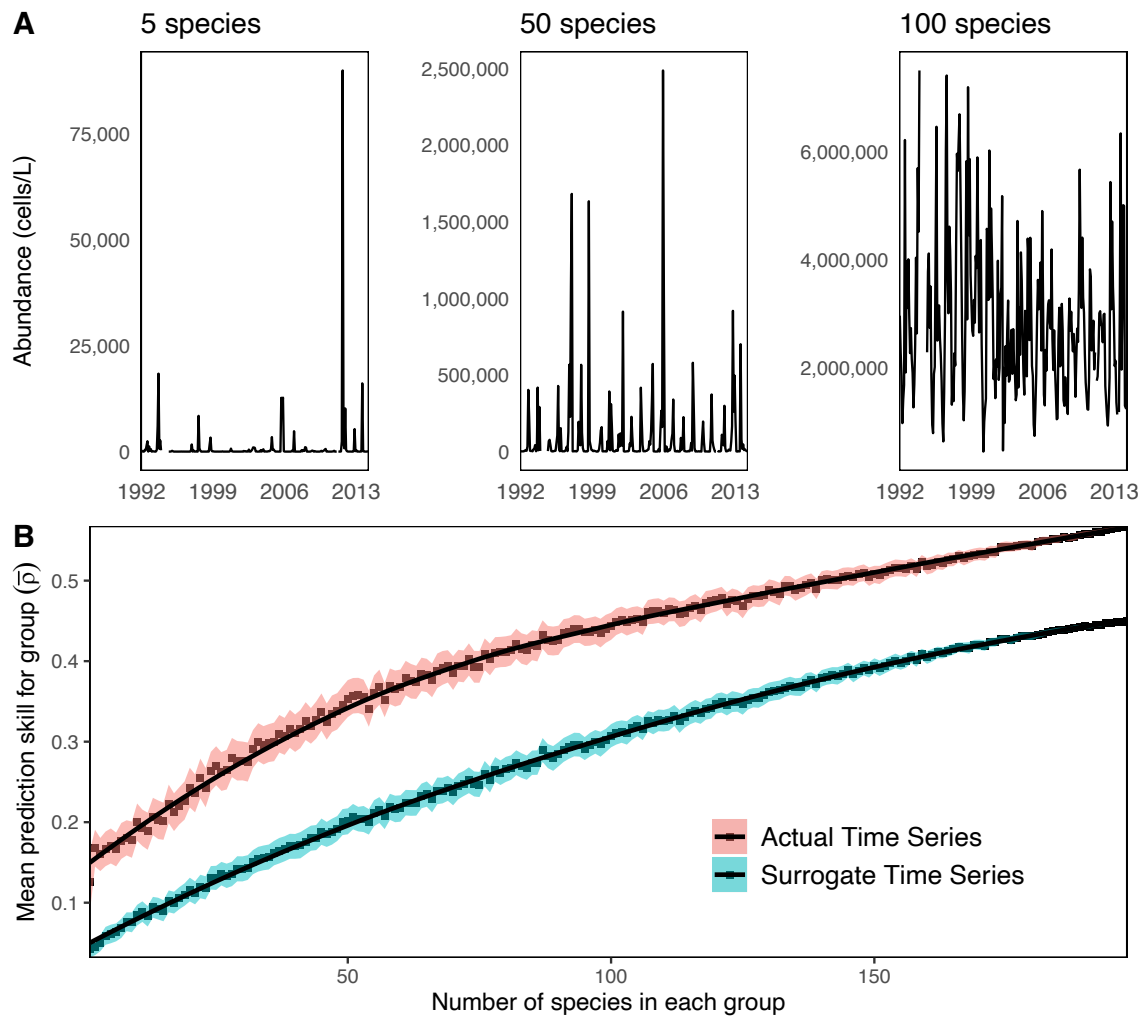


Figure 2: (A) Abundance (cells L^{-1}) of 5, 50 and 100 randomly grouped species from October 1992 to December 2014, and (B) Mean prediction skill (\bar{p}) for groups of species ranging in size from 1 to 198 species in the group (red) and their seasonal surrogates (blue). Each point is the mean of 1000 trials, and the black lines represent local regression fits for both sets of data (actual time series and surrogates). The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$). The confidence intervals narrow with increasing group size because the number of distinct groups of species decreases.

The effect of noise on time series predictions

Using the simple model where species differ only in the timing of their seasonal blooms and noise added to the time series (Eq. 1, Section 2.4), we find that increasing the level of noise decreases the predictability of populations (Fig. 3). In the case where no noise is added to the repeating seasonal cycles of abundance, the system has perfect predictability ($\bar{\rho} = 1$) and increasing the group size does not change predictability. As the noise increases, the maximum prediction skill decreases, and this reduction is particularly evident for the individual time series (Group size = 1) (Fig. 3). In the case of low and high noise (γ of 0.5 and 1, respectively), prediction skill increases with group size, as for the L4 times series data (Fig. 2). The aggregation of multiple time series amplifies the seasonal cycles by diluting the effect of process noise. This is also why the surrogate time series are as predictable as the model time series. These results suggest that noise from a range of sources, including observational error, tends to decrease predictability. The larger the amount of noise added, the larger the group size must be to achieve high predictability.

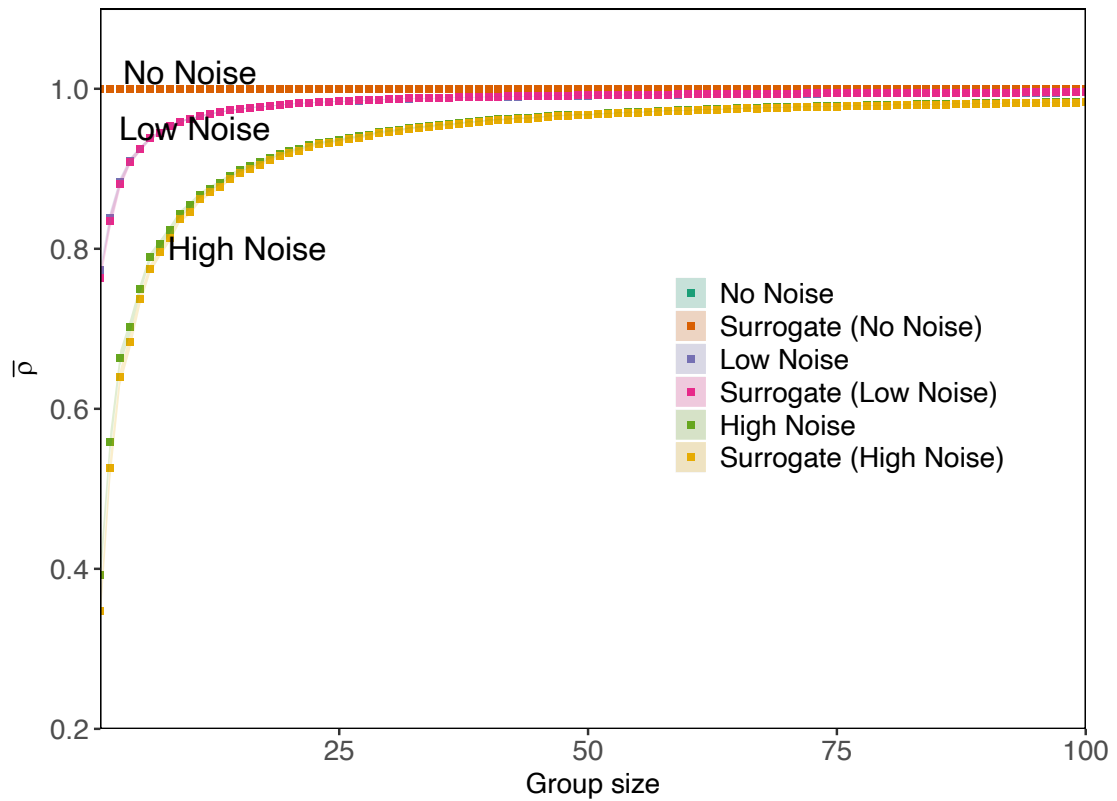


Figure 3: Mean prediction skill ($\bar{\rho}$) by group size for the simple model exploring how measurement noise affects predictability (Eq. 1), with three levels of noise (No noise, Low and High noise levels). Each point is the mean of 100 trials at each group size. The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$). The model predictions overlap with the surrogate predictions because there are no dynamics beyond seasonality in the model.

Species interactions and stochasticity

Using a simple ecological model that resolves species interactions and stochastic variations in growth rates (Equations 2-4, Section 2.5), we examine how interaction strength and stochastic behavior in growth rates influence predictability. In the case where species do not interact ($\alpha = 0$) and there is no stochasticity ($\gamma^p = 0$) in growth rates, the predictability of all groups is perfect ($\bar{\rho} = 1$) and does not increase with group size (Fig. 4A). In the case where there is no stochasticity ($\gamma^p = 0$) in growth rates, but species interact ($\alpha = 0.25$, Fig. 4B), the predictability of individual species is lower than the predictability of aggregated groups. Prediction skill increases with group size and exceeds what would be expected from seasonality alone. In the case with stochasticity in growth rates ($\gamma^p = 1$) but no interactions between species ($\alpha = 0$, Fig. 4C), the predictability of individual species is lower than the predictability of groups and increases with group size. This predictability is also greater than what would be expected from seasonality. We find a similar result in the case with both stochasticity and species interactions ($\gamma^p = 1, \alpha = 0.25$; Fig. 4D). Thus, when stochastic variations in growth rate are uncorrelated across species, the dynamics of individual species may be more difficult to predict than assemblages containing many species. The dynamics of individual species are also more difficult to predict in the presence of inter-species interactions. Because there are many possible factors that influence the growth of phytoplankton in real systems that may be difficult to resolve, and because the interactions between species are in many cases difficult to assess, our results suggest under these conditions predicting single species will be difficult while prediction of assemblages of species may be more skillful.

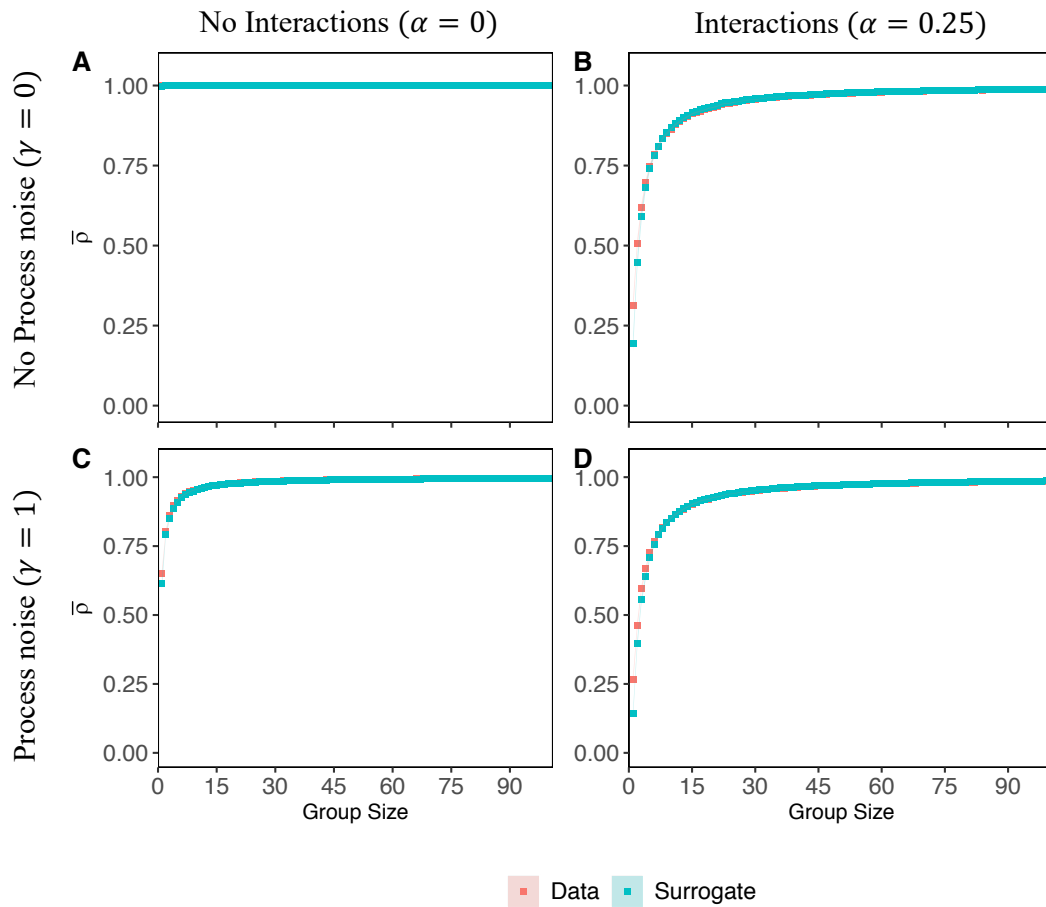


Figure 4: Mean prediction skill ($\bar{\rho}$) by group size for the model resolving variations in growth rate and carrying capacity (Eq. 2-4) with (right column) and without inter-species interactions (left column). The model was run without stochasticity in growth rates (e.g., process noise; top row) and with stochasticity in growth rates (bottom row). Each point is the mean of 100 trials at each group size. The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$).

How does group composition affect predictability?

We also explored whether predictability varied across taxonomic groups of species (e.g., diatoms, dinoflagellates, coccolithophores and phytoflagellates) and across cell size (Figs. 5-6). We first analyze the predictability of diatoms, dinoflagellates, coccolithophores, and phytoflagellates, as these groups are well-represented at the L4 station, with 130, 37, 16, and 14 taxa, respectively. In many applications, taxonomically similar species are analyzed (Widdicombe et al. 2010b) or modeled (Le Quere et al. 2005) collectively rather than on a species level, even though species within groups in many cases have different traits (Edwards et al. 2012; Marañón et al. 2013) and ecological dynamics (Edwards et al. 2013a; Mutshinda et al. 2016). We also separate taxa measured at L4 into three size classes: small ($<5\mu\text{m}$), medium ($5\text{-}12\mu\text{m}$), and large ($>12\mu\text{m}$). The size cutoffs are arbitrary but designed so that each group has a roughly equal number of taxa. Like taxonomic groups, in many cases phytoplankton of similar size are aggregated together in field measurements or satellite algorithms (Hirata et al. 2011). Cell size constrains many important organism traits, such as growth rate and nutrient affinity (Edwards et al. 2012; Marañón et al. 2013), as well as predator-prey interactions (Hansen et al. 1994, 1997) and therefore may provide an additional way of grouping phytoplankton, and drawing out any differences in the portfolio effect that could arise as a result of group selection.

Taxonomy

Mean prediction skill increases with group size for diatoms, coccolithophores and phytoflagellates (Figure 5A-C). Unlike other functional groups, the predictability of dinoflagellates does not increase with group size (Figure 5D). For all the functional groups, there is a clear difference between the predictive skill of time series and predictions based on seasonality alone. Dinoflagellates also have lower maximum predictability at high group size than other groups (lower $\bar{\rho}$ in Fig. 5D compared to others). Why do dinoflagellates apparently differ from other groups in this regard?

Dinoflagellates are a morphologically and physiologically diverse group of phytoplankton (Smayda and Reynolds 2003; Hackett et al. 2004; Brandenburg et al. 2018). They exhibit not just a range of morphology and size-constrained traits, but also large variations in trophic mode, motility, production of allelopathic chemicals, and other traits (Smayda 1997; Stoecker et al. 2017). Since the portfolio effect is not apparent for this group, we believe that dinoflagellate species have dynamics that are independent of each other (i.e. aggregated data is not indicative of a common process on a larger ecological scale). Unlike dinoflagellates, the predictability of both diatoms and coccolithophores increased with group size (Figure 5A-B). A strong portfolio effect for diatoms and coccolithophores might point to common processes or features that link individual species, for example the uptake of silica by diatoms (Hamm et al. 2003). The results suggest that the portfolio effect in ecology is dependent on the process of group selection. A possible implication of these results is that field measurement programs should focus efforts on identifying to species level those phytoplankton, such as the dinoflagellates, for which predictability does not increase with group size. In contrast,

for groups such as diatoms, a coarser level of identification (i.e., to genera) would not limit the utility of the data for making predictions.

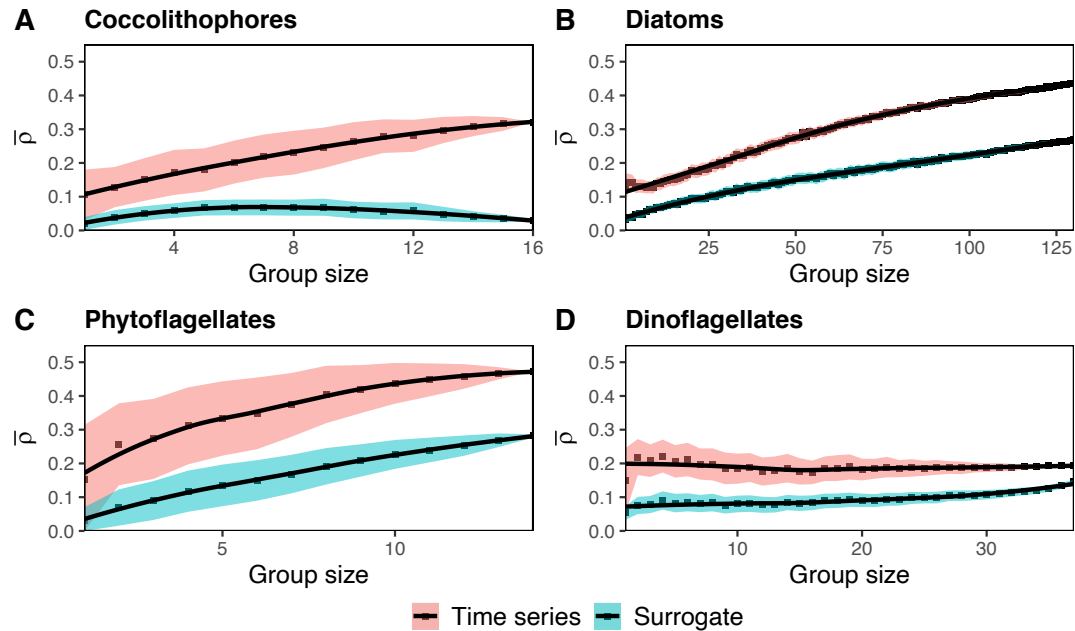


Figure 5: Mean prediction skill ($\bar{\rho}$) of time series (red) and seasonal surrogates (blue) for (A) Coccolithophores ($N=16$) (B) Diatoms ($N=130$) (C) Phytoflagellates ($N=14$) and (D) Dinoflagellates ($N=37$). Each point is the mean of 1000 trials, and the black lines represent local regression fits for both sets of data (actual time series and surrogates). The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$).

Size

Next, we describe how predictability changes across three size bins (<5 μm , 5-12 μm , and >12 μm). For cells in the <5 μm size range, predictability increases with group size (Fig. 6A). The increase with group size is minor for cells in the 5-12 μm size range (Fig. 6B) and negligible for the largest cells (Fig. 6C). The maximum predictability at large group size is lower for the largest compared to the smallest phytoplankton (comparing $\bar{\rho}$ across Fig. 6A-C). A similar result is apparent when we look only within the diatoms (Fig. 7): predictability increases with group size for the smallest diatoms (Fig. 7A) but does not change much for the larger diatoms (Fig. 7B-C). The relative insensitivity of prediction skill to group size among larger phytoplankton may be due to the observation that episodic blooms of phytoplankton are typically dominated by large phytoplankton (Irigoien et al. 2004).

There are several implications of this finding. First, because increasing group size does not lead to increased prediction strength in large phytoplankton (including among diatoms; Fig. 6C, 7C), field measurement programs ideally should continue to measure and identify all species in this size range individually. In order to predict the dynamics of large phytoplankton, each species should be considered independently of each other as it is more important to retain species-specific information. In contrast, for the smallest phytoplankton, skillful predictions of integrated biomass of small phytoplankton might be achieved by measuring a few tens instead of all species (Fig. 6A, 7A). This suggests that numerical models used for ecological prediction and forecasting may need to resolve even more biodiversity among the larger size classes (e.g., Follows et al. 2007; Dutkiewicz et al. 2015). Similarly, for field monitoring programs designed to detect (Widdicombe et al. 2010b) and forecast changes in marine

ecosystems, an ideal sample design might focus taxonomic identification time on the larger taxa but allow some of the smaller, harder to identify groups to be aggregated together.

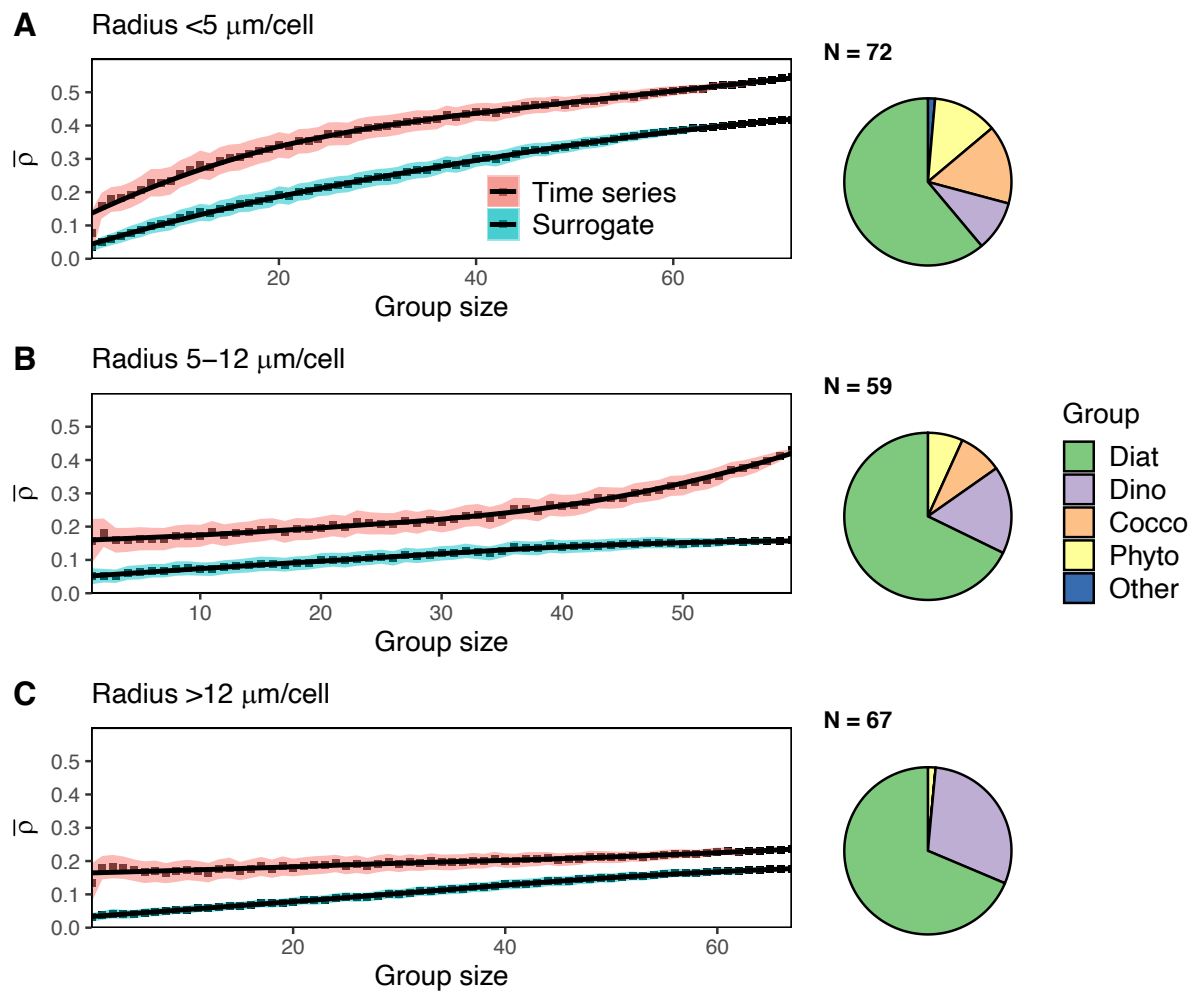


Figure 6: Mean prediction skill ($\bar{\rho}$) of time series (red) and their seasonal surrogates (blue) for cells with radius (A) $<5\mu\text{m}$ ($N = 68$) (B) $5\text{-}12\mu\text{m}$ ($N = 63$) and (C) $>12\mu\text{m}$ ($N = 67$). Each point is the mean of 1000 trials, and the black lines represent local regression fits for both sets of data (actual time series and surrogates). The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$). Pie graphs at right provide the relative diversity of taxonomic groups within each size-based category (Diat – diatoms, Dino – dinoflagellates, Cocco – coccolithophores, Phyto – phytoflagellates and Other – *Phaeocystis*).

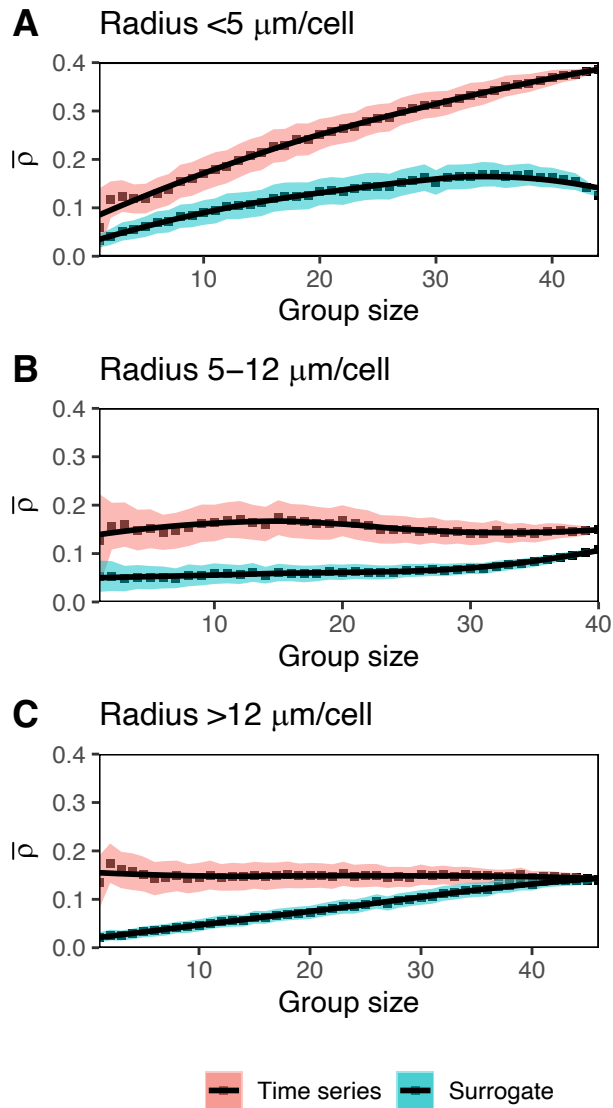


Figure 7: Mean prediction skill ($\bar{\rho}$) of time series (red) and their seasonal surrogates (blue) for only diatoms of the following radius: (A) <5 μm ($N = 44$) (B) 5-12 μm ($N = 40$) and (C) >12 μm ($N = 46$). Each point is the mean of 1000 trials, and the black lines represent local regression fits for both sets of data (actual time series and surrogates). The shaded regions are 95% confidence intervals (defined as $\pm 1.96 \times SE$).

Conclusions

The dynamics of individual phytoplankton populations are noisy and typically difficult to predict. The portfolio effect is an approach that relies on the aggregation of data to reduce variability and identify long-term patterns and trends. By aggregating individual phytoplankton populations into varying assemblage sizes, we used empirical dynamic modeling to assess the predictability of population and assemblage dynamics over monthly timescales. We observed that the presence of noise in data, such as observational error and stochastic environmental influence, reduces the overall predictability of phytoplankton populations. Predictability is also significantly affected by how species are grouped together. Dinoflagellates and large phytoplankton ($>12\mu\text{m}$ cell radius) have lower overall predictability and do not increase in predictability with group size. This could be tied to the differences in dynamics between the individual species. In contrast, aggregating species as coccolithophores, diatoms, and phytoflagellates leads to improved predictability of the composite assemblage abundance time series over individual taxa. Similarly, small phytoplankton ($<5\mu\text{m}$ cell radius) are more predictable in groups than as individual taxa and this predictability exceeds that which we expect from seasonality alone. Field monitoring programs should continue to focus efforts on species-level identification of dinoflagellates and large phytoplankton. In contrast, high predictability of smaller phytoplankton and coccolithophores, diatoms, and phytoflagellates could be achieved by aggregating them together, for example by size fractionating measurements or identifying species only to genus or higher level.

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Chapter 1, in part, has been submitted for publication of the material as it may appear in *Limnology and Oceanography*, 2020, Agarwal, Vitul; James, Chase; Widdicombe, Claire; Barton, Andrew; Wiley Online Library, 2020. The thesis author was the primary investigator and author of this paper.

Appendix

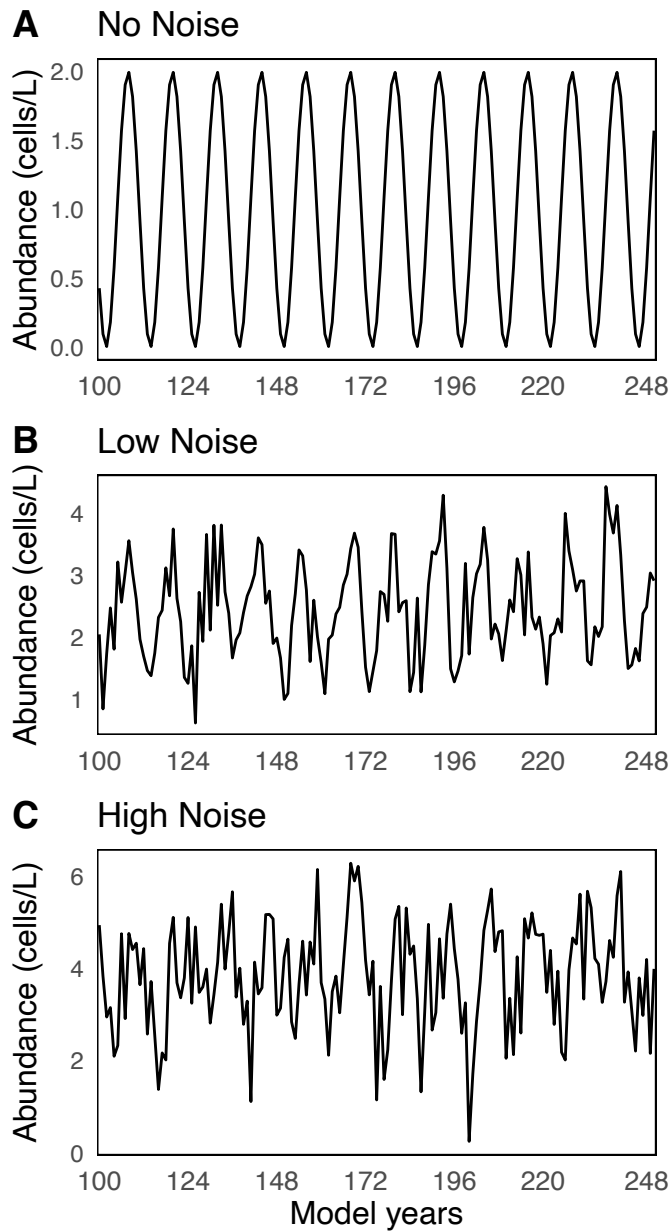


Figure S1: Abundance (cells L⁻¹) of three noise model taxa with various levels of observational error: (A) No noise (B) Low Noise and (C) High noise. The values for the parameters can be found in Table 1.

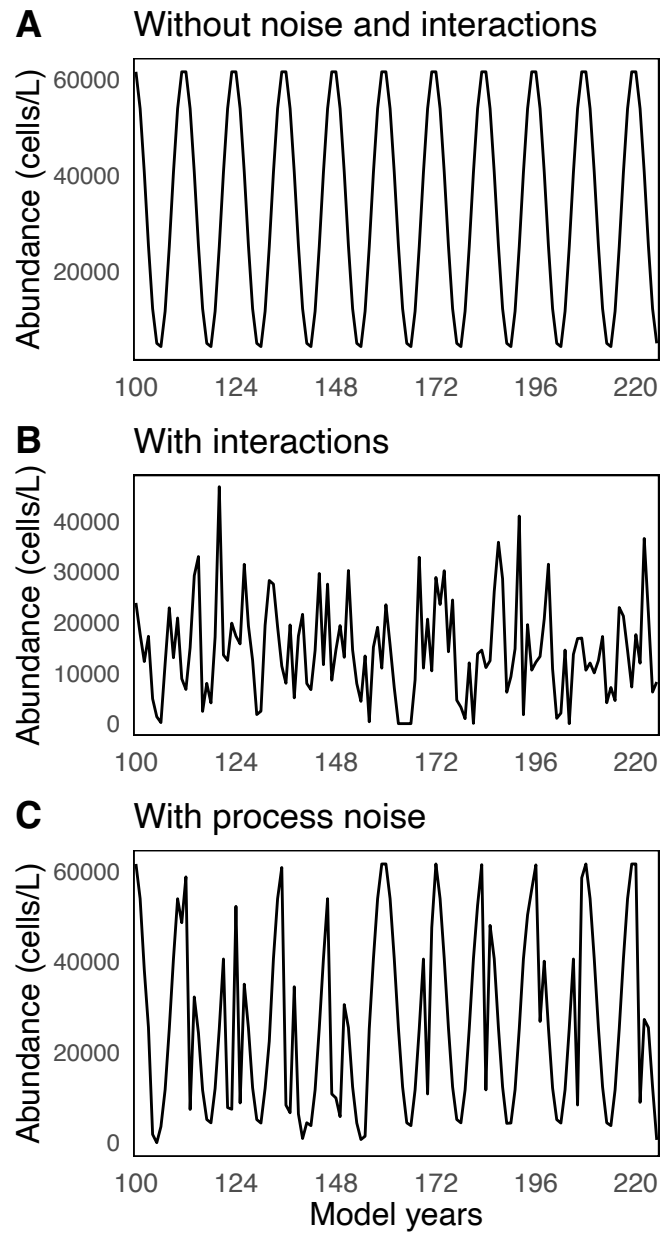


Figure S2: Abundance (cells L⁻¹) of three phytoplankton community model taxa (A) with no noise and inter-species interactions (B) with inter-species interactions and (C) with process noise. The values for the parameters can be found in Table 2.

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