



What explains phytoplankton dynamics? An analysis of the Helgoland Roads Time Series data sets

by

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Terminology	Definition	Chapter
N-limited	If the N: P ratio is below the Redfield ratio (i.e. 16:1), the	Ι
ecosystem	system is N-limited	
P-limited	If the N: P ratio is higher than the Redfield ratio, the system	Ι
ecosystem	is P-limited.	
Carrying capacity	The maximum densities of phytoplankton that can be	II
(<i>K</i>)	supported by a given environment; definition as in plant	
	terrestrial systems.	
Actual carrying	Maximum number of diatom cells that can be supported by	II
capacity (AK)	a given environment in a particular time. For intra-annual	
	and inter-annual cases, each week and year have a value of	
	AK respectively which is calculated based on the	
	environmental conditions of respective week and year.	
Theoretical	The maximum value of AK calculated from intra-annual and	II
maximum carrying	inter-annual cases. Lon-term intra-annual cycle has one	
capacity (TMK)	value of TMK and similarly long-term inter-annual case also	
	has one value of TMK.	
Ecosystem	The deviation of AK from TMK. This deviation provides	II
potential	information on the overall conditions of the system. High	
	deviation of the AK from the TMK means the system has	
	less potentiality for phytoplankton growth and low deviation	
	means the system has high potentiality. The 0 difference	
	between TMK and AK indicates no deviation and this means	
	that AK reached at the TMK of ecosystem.	
Trophic level	Measure of the position of an organism in food web which	II
	starts from 1 which stands for primary producers, trophic	
	level 2 stands for primary consumers that eat primary	
	producers, 3 for secondary consumers, and so on.	
Local variance	Heterogeneity of a value of an observation with respect to	III
	the value of another observation.	
Ecosystem	Heterogeneity of a value of an observation in principal	III

List of terminologies with their definition as used in this thesis

variability	component 1 (PC1; calculated from biotic, abiotic and		
	climatic factors) with respect to the PC1 value.		
Probability of	Probability of a species being present at time $t+1$ which was	III	
species occurrence	absent at time t.		
Probability of	Probability of a species being absent at time $t+1$ which was	III	
species being	present at time t.		
absent			
Probability to "out	Probability of a species to out compete another species.	III	
compete"			
Competitive	The maximum number of coexisting species cannot exceed	IV	
exclusion principle	the number of limiting resources in equilibrium.		
Paradox of	Idea that multiple phytoplankton species may coexist while	IV	
plankton	seemingly only a few resources (i.e. light and nutrients) are		
	limiting.		
Supersaturated	Number of coexisting species is greater than the number of	IV	
coexistence	limiting resources.		
Liebig's law of the	Only a single resource limits species' growth at any given	IV	
mmum	time.		
Synthesizing unit	time. Synthesizing Units (SUs) are generalized enzymes that	IV	
Synthesizing unit (SU)	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two	IV	
Synthesizing unit (SU)	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a	IV	
Synthesizing unit (SU)	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a function of substrate concentrations but of substrate fluxes	IV	
Synthesizing unit (SU)	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a function of substrate concentrations but of substrate fluxes that arrive at the SUs the dissociation rate of the substrate-	IV	
Synthesizing unit (SU)	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a function of substrate concentrations but of substrate fluxes that arrive at the SUs the dissociation rate of the substrate- SU complex to unchanged) substrate and (unbounded) SU is	IV	
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Synthesizing unit (SU) Heteroclinic cycles	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a function of substrate concentrations but of substrate fluxes that arrive at the SUs the dissociation rate of the substrate- SU complex to unchanged) substrate and (unbounded) SU is assumed to be small. A collection of solution trajectories that connects sequences	IV	
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Synthesizing unit (SU) Heteroclinic cycles Favorable growth condition data set Poor growth	time. Synthesizing Units (SUs) are generalized enzymes that follow the rules of classic enzyme kinetics with two modifications: product formation is not taken to be a function of substrate concentrations but of substrate fluxes that arrive at the SUs the dissociation rate of the substrate- SU complex to unchanged) substrate and (unbounded) SU is assumed to be small. A collection of solution trajectories that connects sequences of equilibria, periodic solutions or chaotic invariant sets. Data sets (after splitting the full data set) contain all data for favorable growth conditions i.e. years with anomalies of environmental parameters > 0. Poor growth condition, i.e. years with anomalies of	IV IV V	

ABSTRACT

Phytoplankton is a diverse group of organisms that account for almost 50% of the global primary production. In shallow coastal seas, various factors, such as water depth, current, temperature, nutrients, and predators, control the growth of phytoplankton. This thesis aims to investigate the role of environmental variables in structuring phytoplankton communities at Helgoland Roads, North Sea. It contains a detailed description of long-term changes in nutrients, calculates the phytoplankton-carrying capacity of the German Bight, and explores the response of phytoplankton diversity to environmental changes. Moreover, the importance of different biotic and abiotic factors in explaining the variability of phytoplankton abundance is discussed here.

The German Bight is subjected to changes in nutrients concentrations and therefore it is important to assess how these changes may modify the carrying capacity (K) of the system. The first step is to assess the long-term change in the N: P ratio in the German Bight and then to estimate the phytoplankton K by using the long-term dataset of the Helgoland Roads. The phytoplankton K has been estimated by considering factors that control the growth of phytoplankton in the ocean. The findings show that in the long-term P-limitation increases in the German Bight and the N: P ratio gradually increases from near-shore regions to the offshore ones. Long-term intra-annual and inter-annual mean K are estimated to be 10.13×10^7 cells m⁻³ and 1.30×10^8 cells m⁻³ respectively. Both intra and inter-annual K show variability over time, with inter-annual K showing an overall increasing trend.

The next important step is to understand species diversity in response to environmental changes and their co-existence mechanisms. Based on the Helgoland Roads dataset, these findings show that ecosystem variability is an important predictor of phytoplankton diversity. High diversity is related to low ecosystem variability due to a non-significant relationship between the probability of species occurrence and its absence, a significant negative relationship between the probability of occurrence and the probability to outcompete others, and high species occurrence at low ecosystem variability. A simulation study that uses the species competition model of Dutta et al. (2014) compares it with the Helgoland Roads dataset to show that the coexistence of species is related to periodic changes in species biomass and the variation in interspecific competition and niche configuration. The nonlinear functional response and the position of resource supply within the convex hull of species resource uptake rates are also key factors in this regard.

The third step is to quantify the relative importance of different biotic and abiotic factors in explaining the variability of phytoplankton abundance by using a Bayesian regression model.

The results indicate that biotic factors are more important than the abiotic ones (explaining 9.8% and 7.5% of the phytoplankton variance respectively). For the rest of the year, this trend is reversed, with biotic factors being less influential than the abiotic ones (8.2% and 9.6% respectively). Among the different biotic and abiotic factors, diatom bio-volume and nitrate concentration explain most of the variability in phytoplankton abundance throughout the year (6.5% and 2.1% respectively).

This thesis, for the first time, estimates the phytoplankton K of the German Bight, showing a high degree of variability over time. It also establishes a causal relationship between ecosystem variability and biodiversity; it explains the coexistence of the phytoplankton species in a system limited by multiple resources. In addition, this thesis establishes a pattern of seasonal phytoplankton dynamics in relation to biotic and abiotic factors. Overall, the results of this thesis will expand our understanding of the effect of long-term environmental changes on the dynamics of the phytoplankton community in the North Sea.

INTRODUCTION

The global marine environment is changing rapidly. Significant correlations between changes in the marine environment and phytoplankton species abundance and diversity have been reported (e.g. Aebischer et al. (1990); Beaugrand and Reid (2003). Wiltshire et al. (2015) have identified large changes in phytoplankton species distribution in the North Sea in the last few decades. An increase in the phytoplankton colour index during the mid to late-1980s (Edwards et al. (2001); Reid et al. (1998) changes phenology (Wiltshire and Manly (2004), while changes in species composition are also observed (Beaugrand (2003). Considering all these changes, this thesis aims to analyses the factors influencing the long-term annual and seasonal dynamics of the phytoplankton at the Helgoland Roads Time Series station.

The special interest in phytoplankton in this thesis is motivated by the fact that they are a taxonomically and functionally diverse community; they are the dominant primary producers in the sea and thus the base of the marine food web. Moreover, similar to terrestrial plants, they take up CO_2 and release O_2 , playing a vital role in the global carbon cycle. Through diverse strategies of nutrient uptake and storage phytoplankton affect fluxes of elements in the ecosystem (Falkowski et al., 1998) and serve as a major source of trace gases, such as dimethyl sulphide, that influence climate (Andreae and Crutzen, 1997; Charlson et al., 1987). Since changes in the phytoplankton community structure affect the food web and geochemical cycles, a thorough understanding of phytoplankton dynamics is essential to understand the variability of marine biogeochemical processes, the ecosystem metabolism, and the function of the marine food web. Ecological studies aimed at elucidating the control of various factors on phytoplankton diversity are notoriously difficult, since many factors interact (nutrient abundance, interspecific competition, and predation) to shape the community composition. One practical approach to study changes in phytoplankton communities is to analyse long-term observations of taxonomic and environmental data (Irwin et al., 2012).

The German Bight of the North Sea has been subjected to changes in concentrations and ratios of nutrients due to human activity (Hickel et al., 1993). Since the 1960s this area has been subject to nutrient enrichment, and all countries around the North Sea have agreed on a nutrient reduction strategy during the 1980s (Lenhart et al., 2010). As a consequence, a steady decrease in all nutrients has been measured in these areas since the early 1980s (Hickel et al., 1993). This is also reflected in the Helgoland Roads Time Series dataset (Raabe and Wiltshire, 2008; Wiltshire et al., 2010; Wiltshire et al., 2008). Largescale variability in these ecosystem drivers of the North Sea over the last decades (Wiltshire et al.,

2015) has affected phytoplankton production (Edwards et al., 2001; Reid et al., 1998) and species composition (Boersma et al., 2007). Considering these changes in the ecosystem drivers, one key question is how they may affect the K of the system (Wiltshire et al. (2010). Given the simultaneous fluctuation of many biotic and abiotic parameters, it is difficult to pinpoint the parameters driving a system; although the biotic changes are accompanied by variations in environmental conditions, it is often challenging to establish changes in the causal relationship.

The primary goal of this PhD thesis is to assess the effect of environmental variables on the phytoplankton community using the long-term Helgoland Roads dataset. The major objectives are: (i) to estimate the long-term seasonal and annual phytoplankton K, (ii) to evaluate the response of long-term phytoplankton diversity to ecosystem variability, and (iii) to quantify the relative importance of different biotic and abiotic factors to explain the variability of phytoplankton abundance. Achieving these goals are the subjects of separate papers in this thesis.

The first objective of this PhD thesis is to estimate the long-term seasonal and annual phytoplankton K at the Helgoland Roads Time Series station. Thus, long-term geo-spatial changes in the N: P ratio and its impact on the chlorophyll distribution in the German Bight are shown in Manuscript (MS) I (Chapter I). Changes in the long-term seasonal and annual phytoplankton K are estimated on the basis of the Helgoland Roads Time Series dataset in MS II (Chapter II; (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004), while the relationship between the phytoplankton K and higher trophic levels and their efficacy as a management tool is also established.

The second objective of this PhD thesis is to evaluate the long-term response of phytoplankton diversity to ecosystem variability at Helgoland Roads. MS III (Chapter III) describes the first study on the linkage of ecosystem variability with marine biodiversity at Helgoland Roads. Understanding species coexistence and succession is one of the most important research objectives in community ecology—it attempts to explain how millions of species can be organized into biological communities and how biodiversity is maintained. In MS IV (Chapter IV), phytoplankton species coexistence under simultaneous co-limitation of resources is studied by using a competition model introduced by Dutta et al. (2014).

The final objective of this thesis is to quantify the relative importance of different biotic and abiotic factors in explaining the seasonal variability of phytoplankton abundance at Helgoland Roads. MS V (Chapter V) describes the development of a Bayesian regression model to quantify the relative importance of different biotic and abiotic factors to explain the seasonal variability of phytoplankton abundance at Helgoland Roads.

Study area and data source

For this study, quality-controlled data on phytoplankton species and environmental variables (i.e. nutrients, temperature, salinity, and Secchi depth) have been used from the Helgoland Roads Time Series station.



Figure 3 Geographical location of the study area. The left panel shows the map of northern Europe with a black rectangular box indicating the location of the German Bight. The middle panel shows a close up of the German Bight. The black rectangular box indicates the position of Helgoland. The right panel shows the location of Helgoland Roads Times Series Station (the sampling point is marked as filled black circle) located between the two islands i.e. Helgoland and Düne (Sarker and Wiltshire, 2017).

The Helgoland Roads Time Series Station (54°11.3' N, 7°54.0' E) is located between two islands, Helgoland and Düne (Figure 3), in the North Sea. Long-term monitoring of biological, chemical, and physical parameters has been carried out continuously at Helgoland Roads on a daily basis since 1962 by the Biologische Anstalt Helgoland (BAH) of the Alfred Wegener Institute, Germany, and it is one of the longest and most species-rich aquatic datasets available (Wiltshire and Dürselen, 2004). Water samples are collected from a depth of 1m and preserved for further analysis of nutrients, phytoplankton, and zooplankton. The nutrients (silicate, phosphate, ammonium, nitrate, and nitrite) are measured immediately using the standard colorimetric methods after Grasshoff (1976) on a filtered sub-sample of the water sample (Wiltshire et al., 2010). The phytoplankton sub-sampled from the Helgoland Roads sample is preserved in brown glass bottles using Lugol's solution and counted daily under an inverted microscope at the species level, whenever possible, or otherwise differentiated into defined size classes, by using Utermöhl-settling chambers at the species level (Hoppenrath et al., 2007; Wiltshire and Dürselen, 2004; Wiltshire et al., 2010). The

dominant microalgae in the North Sea are the diatoms. These are also the most reliable in the data sets in terms of data quality control (Wiltshire and Dürselen, 2004) and therefore have been used here. The corresponding zooplankton time series started in 1974, and the samples are collected twice a week (Greve et al., 2004; Wiltshire et al., 2015).

List of manuscripts

This PhD project is composed of five manuscripts and each of these manuscripts represent the one specified aim of the thesis. In Table 1, the list of the manuscript, status and corresponding section number are shown.

Table 1. The manuscripts (MS) presented in the current work.

MS	Manuscript title	Status	Chapter
number			
MS I	Limiting nutrient in the German Bight: A	Ready as manuscript	Ι
	geo-spatial analysis of long-term N: P		
	ratio and chlorophyll integrating multiple		
	in-situ data base		
MS II	Phytoplankton carrying capacity: Is this a	Published in Ocean and	II
	viable concept for coastal seas?	Coastal Management	
MS III	Does ecosystem variability explain	Published in <i>Journal</i>	III
	increase in phytoplankton diversity?	of Sea Research	
	Solving an ecological puzzle with long-		
	term data sets		
MS IV	To share or not to share? Phytoplankton	Under review in	IV
	species coexistence puzzle in a resource-	Ecological Modelling	
	limited ecosystem		
MS V	Explaining seasonal phytoplankton	Manuscript ready to	V
	variability by abiotic and biotic factors in	submit in Journal of	
	a shallow-sea ecosystem	Plankton Research	

CHAPTER I

Limiting nutrient in the German Bight: A geo-spatial analysis of long-term N: P ratio and chlorophyll integrating multiple *in situ* data base

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(Ready as manuscript)

Abstract

Changes in nutrients loadings in coastal and marine ecosystems have an impact on major ecological processes. Much effort has been put into reducing nitrogen and phosphorus loadings into European waters which has resulted in an overall change in the nutrient ratio. In this study, we aimed to assess the long-term geo-spatial change in the N: P ratio in the North Sea. We evaluated the consequent impact of elevated nutrient ratio on the chlorophyll distribution in the German Bight. The historical archives (1981-2010) of in situ winter N: P ratio and chlorophyll data for the German Bight were combined from all possible existing data bases and analyzed on a decadal basis. We found that on the long-term, P- limitation increased in the German Bight. The N: P ratio increases gradually from the nearshore regions to the offshore regions. Over the past decades chlorophyll concentrations have increased in the coastal area. Chlorophyll concentrations are high in coastal waters and decrease gradually towards the open water as the distance increases from the coast. We also found that the N: P ratio is an important predictor of chlorophyll distribution in the German Bight. This study is the first compilation of spatial nutrient limitation and chlorophyll distribution in the German Bight and provides an insight into the influence of long-term nutrients ratio change on chlorophyll distribution.

Key-words: Redfield Ratio, nutrients limitation, river inputs, primary production, North Sea.

Introduction

Phytoplankton takes up nutrients for growth. Nutrients constitute one of the three principal resources (chemicals, energy and to a lesser extent space) required for life (Moore et al., 2013). The relative concentrations of nutrients are potential regulators of phytoplankton community structure as requirements of different species are variable (Mutshinda et al., 2013b). Thus, nutrient composition may change algal growth rate (Goldman et al., 1979; Moore et al., 2013) and net production, and thus induce shifts in species composition (Edmondson, 1970; Howarth, 1988). Therefore, it is important to determine the limiting nutrients of algal dynamics in an aquatic ecosystem.

Generally, in estuarine and coastal ecosystems, nitrogen (N) and phosphorus (P) are the nutrients that most ofen limit phytoplankton growth (EEA, 1999; USEPA, 2001). Some algae also require silicate (essential for diatoms), but this nutrient is in abundance in the ocean and does not normally limit the total amount of algal production. As a result, in marine environments the relationship between nutrient limitation and algal production is often expressed in terms of N and P supply (Elser et al., 2007; Guildford and Hecky, 2000; Hecky and Kilham, 1988).

Based on the measurement from the Atlantic, Pacific and Indian oceans, Alfred Redfield discovered that the ratio of N to P is a nearly constant 16:1 in both phytoplankton biomass and in seawater (Redfield, 1958). This approach of stability in nutrient ratios has provided invaluable information in understanding oceanic ecosystems. For example, the discovery of this constant nutrient ratio laid the foundation in our understanding of natural biogeochemical processes in the ocean (Falkowski and Davis, 2004), and provides insights into nutrient dynamics (i.e. offers information about the limiting nutrient in the aquatic ecosystem) and overall algal production in the ocean (Langenberg, 2014). In addition, the Redfield Ratio can be interpreted as the mid-point between N and P limitation in primary producers, and by applying the Redfield Ratio as a criterion, one can distinguish between P and N deficient ecosystem (Burson et al., 2016; Justić et al., 1995). In general, if the N: P ratio is below the Redfield Ratio, the system is N limited and if the ratio is higher, the system is P limited.

The North Sea is bordered by the industrialized nations. Eutrophication along the European North Sea coast started mainly in the 1950s as increasing amounts of fertilizer were used in modern agriculture (Billen et al., 2005; Loebl et al., 2009; Lotze et al., 2005; Nienhuis, 1992). Based on the fact that the nutrient loads in many European rivers were extremely high from 1950s to the mid-1980s (Loebl et al., 2009), all countries around the North Sea agreed to a reduction of nutrient input 50% between 1985 and 1995 (Skogen et al., 2004).

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Policy measures started in the 1970s and became effective in the 1990s reducing domestic and industrial point sources of phosphorus and nitrogen, and subsequent loads to the North Sea (Brion et al., 2004; Carstensen et al., 2006; de Vries et al., 1998; de Wit, 1999; Nixon et al., 2003). These mitigating measures have resulted in a decrease in total P inputs to the continental coastal waters of the North Sea by 50–70% and N inputs by 20–30% in the period 1985-2002 (Burson et al., 2016; Lenhart et al., 2010; Passy et al., 2013). Data from Pätsch and Lenhart (2011) show that the annual loads of TN and TP from these three rivers (Elbe, Weser and Ems) have declined significantly (p<0.001) from 1981 to 2009 at a rate of 6.02kt/year and 0.39kt/year respectively (Fig. 1). These TN and TP loads from rivers are correlated with the TN and TP concentrations in the German Bight. For example, van Beusekom et al. (2008) showed this correlation for the Wadden Sea and preliminary analyses of the data collected at the Helgoland Roads Time Series station showed that TN and TP loadings from rivers can explain the 53% and 42% variability in TN and TP concentrations. In pre-industrial times, the Atlantic inflow from the north coming in over Scotland into the North Sea was responsible for a significant input of nutrient rich water into the northern North Sea (Edwards et al., 2002; Turrell et al., 1992). However, since the rivers started dumping the nutrients into the North Sea rivers have gained importance as the source of

nutrients inputs of this area. After the mid-1980s, P inputs to the coastal waters of the North Sea were down while N inputs were not down at the same level (Lenhart et al., 2010) which indicates less P content water entered into the North Sea system after the 1980s. This unbalanced nutrients loadings may induce a change in nutrients limitation in the system. We would expect that there is a change in N or P limitation from river to open water as well as a



Fig. 1 Long term variations in TN and TP loadings from Elbe, Weser and Ems rivers into the German Bight based on the data from Pätsch and Lenhart (2011). Solid black and grey straight lines indicate the declining trend in TN and TP from 1980 to 2009 (R^2 =0.50 and 0.66 respectively with p<0.001).

We selected the German Bight of the North Sea for our analysis, since this area has been most clearly subjected to changes in nutrient concentrations and ratios due to human interferences (Hickel et al., 1993). Dissolved nutrients show maxima in winter, when phytoplankton growth is at a minimum (van Bennekom and Wetsteijn, 1990), and in the Southern North Sea algal growth and nutrients uptake on the average starts at the end of winter (Gieskes and Kraay, 1975). Nutrient depletion by uptake makes it difficult to compare the changes in nutrient limitation pattern. To remove this biological noise (nutrient depletion by uptake of nutrients) from the analysis, we restrict our analysis to the winter N: P ratio and chlorophyll distribution.

We know that changes in nutrient limitation may cause major changes in the algal production (Brauer et al., 2012; Tilman, 1982). Therefore, an understanding of the spatial nutrient limitation pattern due to change in riverine loadings and impacts on algal production are important. Spatial nutrient limitation pattern is however still lacking for the German Bight. Our study aims to answer the following questions:

- 1. Is the German Bight nutrient limited?
- 2. What is the spatial dimension of nutrient limitation pattern from the coastal to open water in the German Bight?
- 3. What is the consequence of this nutrient limitation on the chlorophyll biomass in this area?

Materials and methods

Study area

The domain of the study area is located between 53°N–55.50°N and 7° E–9.20° E, and bounded by The Netherlands and Germany to the south. To the east it is bounded by Denmark and Germany. The German Bight is characterized by a complex hydrography resulting from interactions of coastal and Atlantic currents, riverine input, tides, wind and topography (Gowen et al., 1995; Orvik et al., 2001). The hydrography and specifically the salinity of the German Bight are affected by Atlantic inflow from the English Channel

CHAPTER I

(southern boundary) and the Fair Isle Passage (northern boundary) (Wiltshire et al., 2015). Moreover, the position of the estuaries of the main rivers that drain central Europe, favour the accumulation of eutrophying substances in the German Bight in the past and made it the most extensively eutrophied area of the North Sea (Hickel et al., 1993). Strong tides cause turbulent horizontal and vertical exchanges (Becker et al., 1992). The dominant current patterns are from the south to southeast, with an input of coastal waters characterized by a riverine component and associated with the prevailing local hydrodynamic conditions (Scharfe, 2013).The near-surface circulation pattern in the German Bight is permanently changing due to strong tidal currents and the variability of the local wind field (BSH, 2016). When waters move from the deeper North Sea into the German Bight, they become highly turbid due to the suspension of sediments (Wiltshire et al., 2015).

Data sources

The present study is a compilation of nutrients and chlorophyll datasets in the German Bight. Data used for this study are obtained from Biologische Anstalt Helgoland (Raabe and Wiltshire, 2009), The Coastal Observing System for Northern and Arctic Seas (COSYNA), Das Deutsche Ozeanographische Datenzentrum (DOD), Elbe Data Information System (FIS), International Council for the Exploration of the Sea (ICES), Marine Environmental database, German Federal Maritime and Hydrographical Office (MUDAB), KUSTOS program (Coastal Mass and Energy Fluxes-the Land-Sea Transition in the Southeastern North Sea) and World Ocean Database 2013 (WOD13) through direct download from the websites and email enquiries. All available datasets were aggregated to create an exhaustive inventory of the nutrients and chlorophyll distributions in the German Bight. The raw data include longitude, latitude, depth, date and observed parameters value. In this paper, we only use N: P ratio (molar) and fluorometric measurement of chlorophyll concentration.

Data analysis

The database used for this study are N: P ratio and chlorophyll data for the winter (December to February). Due to lack of sufficient N: P ratio data and chlorophyll data for this area before 1981 we analysed chlorophyll only the period from 1981 to 2010. Large scale changes in the North Sea ecosystem are now well established (Boersma et al., 2015; Scharfe, 2013). Edwards et al. (2002) and Weijerman et al. (2005) identified a major shift around 1988 in the North Sea and there is an indication of another possible shift between 1995 to 1998 (Scharfe, 2013; Weijerman et al., 2005).

To investigate the relationship between nutrient limitation patterns and chlorophyll distribution from 1981 to 2010 and emphasizing the major shift in the North Sea ecosystem, we separated whole time period into three time blocks i.e. 1981–1990, 1991–2000 and 2001–2010. The time block 1981-1990 corresponds to the shift around 1988, 1991-2000 corresponds to the shift in the end of 1990s and 2001-2010 represents the ecosystem in recent years.

In order to get a consistent data collection, first we gridded the winter data points for each time block into a 0° 5′ × 0° 5′ grid. To eliminate extreme data, we calculated the mean of all data points inside the grid and eliminated the data whose difference from the grid mean exceeded the standard deviation of that respective grid. The gridded database included data points (Fig. 2) for 1981-1990, 1991–2000 and 2001–2011 which were unique in terms of temporal distribution. We considered 1686, 2640 and 2171 data points for both N: P ratio and chlorophyll for the time blocks 1981-1990, 1991-2000 and 2001-2010, respectively. After gridding, the geospatial tabular data of N: P ratio and chlorophyll were interpolated using kriging method maintaining the same geographic extent. After interpolation, thematic layers of N: P ratios were then classified into three classes i.e. Redfield Ratio (N: P ratio from 15 to 17), N-limited (if the ratio is below the Redfield Ratio) and P-limited (if the ratio is above the Redfield Ratio).

First we investigated geo-spatial changes in the N: P ratio and chlorophyll concentrations in the German Bight for different time blocks, and then we explored the relationships between chlorophyll distribution and the N: P ratio change.



Fig. 2 Distribution of data points in different time blocks.

Results

We analyzed the historical nutrients ratio data in the German Bight to understand how reduction in riverine TN and TP loads has affected nutrient limitation pattern. We structured the result section according to our overarching research questions.

Is the German Bight nutrient limited?

Spatial distributions of N: P ratio (Fig. 3) showed that the German Bight is P-limited. Over the past decades this P- limitation increased in this area.



Fig. 3 Geo-spatial distribution of winter nutrient limitation in the German Bight in three time blocks a) 1981-1990, b) 1991-2000 and c) 2001-2010.

What is the spatial dimension of nutrient limitation patterns in the German Bight?

We found a difference in spatial nutrient limitation from nearshore regions to offshore regions. The N: P ratio increases gradually from the nearshore regions to the offshore regions as the influence of TN and TP loadings (concentration of TN and TP) from river is higher in the coastal water, and this influence decreases with the increase in distance from the coast. Over the past decades in the coastal water N: P ratio was found to be near to/at the Redfield Ratio. In the first time block (1981-1990; Fig. 3a, 4), offshore areas close to the river Ems, Weser and Elbe were found to be P-limited. Spatial distribution of nutrient limitation in the second time block (1991-2000; Fig. 3b, 4) also indicated the P-limitation in the German Bight. Coastal area near to the river Weser and Elbe, and offshore area were found to be Plimited while eastern coast was governed by the Redfield Ratio In the third time block (2001-2010; Fig. 3c, 4), P-limited area expanded compared to the first and second time block. In the first time block 70.4% area were found to be P-limited, and in second and third time block 73.72% and 83% area were found to be P-limited respectively (Fig. 5). In the first time block 24.6% area were governed by the Redfield Ration while 24.14% and 16% area were governed by the Redfield Ration in second and third time block respectively. Only 5%, 2.14% and 1% area were found to be N-limited for the first, second and third time block respectively.



Fig. 4 Increase and decrease in P-limited, Redfield and N-limited area from 1981-2010



Fig. 5 Changes in area with different nutrient limitation pattern in different time blocks

What is the consequence of nutrient limitation on the chlorophyll distribution?

Chlorophyll distribution in the German Bight is shown in Fig. 6. Over the decades chlorophyll concentrations increased in the coastal area. Similar to the N: P ratio, chlorophyll concentration shows difference in spatial distribution. Chlorophyll concentration is high in coastal water and decreases gradually towards the open water as the distance increases from the coast. In first time block (Fig. 6a), offshore area is found with low chlorophyll concentration. Three rivers mouth (Ems, Weser and Elbe) and Sylt- $R\phi m\phi$ Bight have high chlorophyll concentration. Transition zone between offshore area and river mouths including central-eastern coast has intermediate level of chlorophyll concentration. Similar to the first time block, in the second time block (Fig. 6b) offshore area has low chlorophyll

concentration. North-eastern part and surrounding area near to Ems and Weser River have high chlorophyll concentration. In third time block (Fig. 6c), high chlorophyll concentration is found in the eastern part. During this period chlorophyll concentration decreased in Ems and Weser River where higher chlorophyll concentration found in first and second time block.



Fig. 6 Geo-spatial distribution of winter chlorophyll concentration in the German Bight in three time blocks a) 1981-1990, b) 199 1-2000 and c) 2001-2010.

A compilation of geo-spatial database of nutrient ratio and chlorophyll concentration reveals that the German Bight is becoming P-limited and that the eastern coastal area has an increasing trend in chlorophyll concentration. Both N: P ratio and chlorophyll declined with increasing the distance from the land. We incorporated the N: P ratio and spatial location as explanatory variables and chlorophyll concentration as response variable in a linear model i.e. chlorophyll ~ N: P ratio + spatial location, and found that N: P ratio is an important predictor of chlorophyll distribution in the German Bight. We observed the N: P ratio effects on chlorophyll as a function of distance to land (Fig. 7). The model predicted negative effects between 7° N and 8° N, and positive effects between 8° N and 10° N (R²=0.1, p<0.0001). Cumulatively, all these findings suggest that high N: P ratio might responsible for high chlorophyll concentration in the coastal area.

Discussion

We analyzed the long-term geo-spatial changes in nutrients ratio and chlorophyll concentrations in the German Bight by utilizing all possible data sources available to us. Overall P-limitation increased. Off-shore was always found P-limited. Chlorophyll concentrations increased towards the coastal edge. Looking at the effects N: P ratio on chlorophyll concentration as a function of distance to land we found that a high N: P ratio supports high chlorophyll concentrations in the coastal zone.



Fig. 7 Effects of N: P ratio on chlorophyll as a function of longitude. Significant relationship $(R^2=0.1 \text{ and } p<0.0001)$ were estimate as quadratic function of longitudes. Light blue shades in the graph indicate the 95% confidence interval and read dashed line indicate the mean effect (=0) of N: P ratio on chlorophyll.

The Southern Bight of the North Sea has been subject to nutrient enrichment since the 1960s and subsequent nutrient reduction actions since the late 1980s. The impact of these changes on the North Sea system is absolutely far from being identified (Lenhart et al., 2010). Due to different strategies taken to control the riverine P-loads in the Europe, the nutrients loads in the Rhine, Scheldt, Maas, Weser and Elbe decreased (Carstensen et al., 2006; De Jonge et al., 1996; Soetaert et al., 2006; van Beusekom, 2005). The goal for phosphorus reduction has been achieved due to the improvement of municipal treatment plants and replacement of phosphorus by tensides as detergent in washing powder (Behrendt et al., 2000). Currently the phosphorus loadings of the rivers entering the North Sea in the Netherlands have been reduced by more than 50% with respect to 1985 (Troost et al., 2014). Baretta-Bekker et al. (2008) reported that nitrogen loads have not been reduced by the same amounts of phosphorus and reductions of 20–30% were achieved for riverine nitrogen. A stronger decline trend in P compared to N is also observed for the Dutch coastal zone (de Vries et al., 1998), Helgoland (Hickel, 1998; Radach, 1998; Wirtz and Wiltshire, 2005) and Wadden Sea (Philippart et al., 2007). The consequence is the change in N: P ratio in sea water (Fig. 3).

CHAPTER I

The effect of reduction in riverine nutrient input to the system has reflected in our current study. The unbalanced nutrients reduction resulted in nutrient limitation in the German Bight. Long-term spatial analyses of nutrients data indicate that the German Bight is becoming P-limited. Reduction in P loads lead to an increase in the N: P ratio. We found variation in N: P ratio between offshore and coastal waters. In all three time blocks (Fig. 3), P is the limiting nutrient in the offshore area and coastal water is mixture of N-limitation, the Redfield Ratio and P-limitation. Our results show that the gradient of P-limitation increased from coast towards open water. Redfield et al. (1963) also reported that the N: P ratio can depart widely in coastal waters and in the surface of the open ocean. In our analysis we found that coastal zone is P-limited and near to the Redfield Ratio especially for the last two time blocks (figure 3a&b). When the system is P-limited, a reduction in N may shift the system to an N-limited state or to ratios that are closer to the Redfield Ratio. In the Elbe, N dropped only after 1990 (de Wit, 1999; EEA, 1999) and our analysis show a similar trend. In the first time block (Fig. 3a), Elbe is P-limited which is shifted to the Redfield Ratio in the second and third time blocks which is a consequence of drop in N after 1990.

Resource availability is a function of phytoplankton dynamics and thus in order to understand ecosystem a proper insight into nutrient availability is needed (Colijn and Cadee, 2003). Cadée and Hegeman (2002) reported that phytoplankton may respond to elevation in nutrient loads by an increase or decrease in primary production and chlorophyll-a (Chl-a) concentrations.

The N: P ratio in the offshore waters is now well above the Redfield Ratio and indicative of P-limitation. Coastal water was found to be either P-limited or at the Redfield Ratio. In the offshore area, nutrient limitation and the chlorophyll pattern has not changed over the decades. Overall however there is an increased trend in chlorophyll concentrations in the German Bight.

During the 1980s, an increase in the Phytoplankton Colour Index (PCI) was also observed in the North Sea (McQuatters-Gollop et al., 2007). A modelling study by Troost et al. (2014) found though eutrophication has been substantially reduced since 1985, coastal N and chlorophyll concentrations are still higher than those found in 1930.Cadée and Hegeman (1993) found high primary production at the Dutch coast from the beginning of the Eighties to the 90s, although P declined. (Wiltshire et al., 2015) showed a highly significant increase in algal numbers in recent years at the Helgoland Roads Time Series station though P is decreasing.

CHAPTER I

N-limitation of primary productivity has been reported in coastal ecosystems worldwide including the Baltic Sea (Lugus et al. 2004), the Qatar peninsula in the Arabian Sea (Quigg et al. 2013) and many other places as summarized in recent reviews by Howarth and Marino (2006) and Paerl (Paerl, 2009). Lee et al. (1996) reported that, the growth of phytoplankton in the coast is limited mainly by N indicating that P-limitation might not significantly affect the phytoplankton growth. Thus N enrichment or no N limitation can cause of increase of chlorophyll concentrations in estuaries and coastal seas (Howarth and Marino, 2006). We also found similar trend in our analysis. In the coastal edge where N is not a limiting nutrient in the German Bight, chlorophyll concentration is higher compared to offshore area where P is always limiting. Exception is also found in some areas near to the coast with low chlorophyll concentration where P is limiting nutrient. Loebl et al. (2009) and Ly et al. (2014) have provided evidence that in certain areas of the North Sea primary production is limited by phosphorus.

Nutrient limitations of phytoplankton have been experimentally evaluated for a long time. Experimental studies have established how external and internal cellular concentrations of nutrients determine phytoplankton growth rates. However, in natural situations it is difficult to relate the nutrients concentrations and ratio with the phytoplankton production. Moreover, from experimental studies it is difficult to have insights on the impact of historical nutrient changes on the phytoplankton production. Therefore, it is important to analyse historical nutrient data to understand the changes. Here for the first time we used observed data to expose the nature of nutrient limitation on the marine chlorophyll production in the German Bight. So, what have our study found? Is the German Bight nutrient limited? Yes. Over the past decades the German Bight became P-limited. What is the spatial dimension of nutrient limitation patterns in the German Bight? The N: P ratio gradually increases from the coast to open water. What is the consequence of nutrient limitation on the chlorophyll distribution? The chlorophyll production in the Bight is also responding to this change in nutrient ratios. Chlorophyll concentrations are higher in the coastal area and low in the open water zone.

We now understand the consequence of unbalanced nutrient reduction on the aquatic ecosystem of the German Bight. We assume that further removal of P from the system will lead the German Bight to a more P-limitation state or a drop in N loadings may lead the German Bight to a state near to the Redfield Ratio. This positive trend in P deficiency might affect the marine food web. Increased P-limitation can make the mixotrophic dinoflagellates, nanoflagellates and harmful algal species beneficiary (Burkholder et al., 2008) as they can access to alternative P sources. Moreover reduced P in the ecosystem will lower the P content

in phytoplankton, and may offer poor quality food to zooplankton (Sterner and Elser, 2002) and lower the growth rates of zooplankton (Malzahn et al., 2007; Malzahn and Boersma, 2012) which will ultimately effect the fisheries (Malzahn et al., 2007).

CHAPTER II

Phytoplankton carrying capacity: Is this a viable concept for coastal seas?

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Abstract

Carrying capacity estimations for any population of organisms is made in order to determine the maximum population densities that could result under set environmental conditions. Carrying capacity (K) is often used in terrestrial ecosystems to estimate potential plant densities (yields) related to the availability of resources. Here we wanted to see whether a similar concept could be applied to the plants of the ocean: Phytoplankton. Using the Helgoland Roads Time Series data sets, the main focus was on those which control phytoplankton growth in the ocean. We aimed to estimate K and determine whether K is static or variable, evaluated the relationship of phytoplankton K with higher trophic levels. We also provided a guideline to use K as ecosystem management tool. Algorithms were developed to estimate the K based on each controlling factor. A pair-wise comparison matrix was used for weighting the controlling factors and then to integrate the estimated K based on controlling factors to obtain an overall K. Long-term intra-annual and inter-annual mean Kwere estimated 10.13×10^7 cells m⁻³ and 1.30×10^8 cells m⁻³ respectively. Our analyses suggest that K should not be considered as a static permanent value. This is because it is driven by overall environmental conditions and is subject to change when overall environment change. We linked the estimated K to pelagic fisheries data of the North Sea and found that phytoplankton K is correlated with the pelagic fisheries of this area. Our overall conclusion is that phytoplankton K is a viable concept and could be utilized as a valuable management tool.

Key-words: Diatoms, carrying capacity, management, North Sea, Helgoland Roads.

Introduction

Phytoplankton represents a diverse group of primary producers and although it makes up less than 1% of the plant biomass on the earth, it accounts for 50% of global primary production (Field et al., 1998). Being the dominant primary producers in the sea, phytoplankton act at the base of the marine trophic webs (Sterner and Elser, 2002). Phytoplankton abundance as the main food source, governs the abundance of herbivorous zooplankton, which in turn regulates the level of planktivorous. Thus, changes in the abundance of phytoplankton affect both the herbivorous zooplankton and planktivorous fish.

In the oceanic ecosystem phytoplankton dynamics are regulated by both "bottom-up" factors (e.g. light and nutrients) and "top-down" mechanisms (e.g. zooplankton) (Wiltshire et al., 2008). The maximum densities of phytoplankton that can be supported by a given environment could be, as in plant terrestrial systems (Hobbs et al., 1982; Hobbs and Swift, 1985), considered to be a type of phytoplankton carrying capacity (K). It is this potential which we wish to consider in this study.

Carrying capacity estimations for any population of organisms is traditionally made in order to determine the maximum population densities that could result under set environmental conditions. This is often used in terrestrial ecosystems to estimate potential plant species densities (yields) related to the availability of resources. The K of a population is generally dependent on food, shelter, predation and exploitation (Kashiwai, 1995), and similarly a considered phytoplankton K in a marine system could be considered to be directly dependent on the resources important for phytoplankton. In a shallow coastal sea, phytoplankton dynamics are controlled by light availability, temperature, nutrients and zooplankton (Mitchell et al., 1991; Wiltshire et al., 2015) and thus these factors can be used to estimate the phytoplankton K in the coastal seas.

Generally marine food web studies focus on the links between resources (e.g. nutrients) to phytoplankton through zooplankton and to fisheries. Changes at any of these levels will affect any trophic level dependent upon them. Such changes can be anything from pollution mitigation with a reduction in nutrients through to the introduction of a new species into a system. Any change in phytoplankton K might affect the phytoplankton densities which will affect the following tropic levels (i.e. zooplankton and fisheries). The "classical" K concept is based on the idea that once the population of a system has exceeded the K, the population will suffer a crash (Abel and McConnell, 2001). Applying this concept to our study system one can hypothesize that once phytoplankton density exceeds its K, the phytoplankton stock in the system will crash, and in terms of higher trophic levels, this could mean a decrease in

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zooplankton and fish abundance. Considering the importance of phytoplankton to the marine ecosystem and fisheries, we consider K for phytoplankton can be an interesting management tool for marine systems.

Algorithms for *K* estimation have been developed (Moen, 1973; Robbins, 1973) and used to evaluate the quality of ungulate habitat (Bobek, 1977; Wallmo et al., 1977). Some work has been carried out for fisheries (e.g. (Byron et al., 2011; Cross et al., 2011; Dame and Prins, 1997; Perry and Schweigert, 2008; Vasconcellos and Gasalla, 2001)) and environment (Mazaris et al., 2009; Wang et al., 2017). But studies for plankton *K* are very rare i.e. Hopkinson et al. (2013) performed an experimental study. In theoretical studies on phytoplankton, *K* is considered as a constant, which is not often realistic (Safuan et al., 2012). Carrying capacities in nature are variable and many studies have discussed about the importance of time dependent *K* (Banks, 1993). Carrying capacity of a population depends on the physical and biotic environment (Arrow et al., 1995) and thus phytoplankton *K* should not be constant. In our extensive literature search, no studies were found by us for plankton *K* estimation using real data on the long-term taking the phytoplankton requirements of resources into account.

Phytoplankton K indicates the highest potentiality for phytoplankton growth of the ecosystem. Fisheries recruitment is highly related with this highest potentiality and phytoplankton densities in the ecosystem, for example cod recruitment in the North Sea (Beaugrand et al., 2003). Another example is monitoring of ecosystem potentiality using phytoplankton K could help farmers to decide when to sow, maintains, and harvest their marine aquaculture items (for example oyster). Maximum numbers of marine aquaculture farms are also dependent on phytoplankton K. Thus considering the importance of phytoplankton K as a management tool, it is important to estimate phytoplankton K. In addition as theoretical studies consider K as a static permanent value; it is also an exciting scientific question to see if a change in ecosystem variables also changes the phytoplankton K.

Therefore, our aims for this study are to:

- (i) Estimate phytoplankton *K* in the North Sea using the Helgoland Roads Time Series data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004).
- (ii) Work out if *K* can remain constant over the time or changes with a change in environmental variables.
- (iii) Relate phytoplankton K with the higher trophic levels (e.g. with fisheries) and provide information on how to use K as an ecosystem management tool.
Materials and methods

Pelagic data collection

Phytoplankton *K* for the German Bight was estimated by using the Helgoland Roads longterm data sets. The Helgoland Roads Time Series Station (54°11.3' N, 7°54.0' E) is located between two islands, i.e. Helgoland and Düne (Fig. 1), in the North Sea. Long-term monitoring of biological, chemical and physical parameters has been carried out continuously at Helgoland Roads on a work daily basis since 1962 by Biologische Anstalt Helgoland (BAH) of the Alfred Wegener Institute, Germany and is one of the longest and most species rich aquatic data sets available (Wiltshire and Dürselen, 2004).



Fig. 1 Geographical location of the study area. Left panel shows the map of northern Europe with a black rectangular box indicating the location of the German Bight. Middle panel map shows a close up of the German Bight. Black rectangular box indicates the position of Helgoland. Right panel map shows the location of Helgoland Roads Times Series Station (sampling point marked as filled black circle) located between two islands i.e. Helgoland and Düne.

The water samples are taken from the surface (1m depth) as representative of the entire water column, which is generally well-mixed as a result of strong tidal currents (Hickel, 1998). Secchi depth as a measure of water transparency and temperature are measured directly on station. The bucket sample is mixed and sub-sampled into a glass bottle for future analyses of nutrients, salinity and phytoplankton (Wiltshire et al., 2010). This long-term dataset is quality controlled through a careful comparison with data sets from the same water bodies and reference data sets [e.g., BSH (Hamburg), ICES (Copenhagen) and MUDAB (Hamburg)] for the North Sea (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). The pelagic biotic and abiotic data sets are now sufficiently understood with problems, errors and corrections

documented, and can be used as reference data to assess long-term changes in the North Sea (Wiltshire et al., 2010). The nutrients (silicate, phosphate, ammonium, nitrate and nitrite) are measured immediately using the standard colorimetric methods after Grasshoff (1976) on a filtered sub-sample of the water sample (Wiltshire et al., 2010). The phytoplankton sub-sampled from the Helgoland Roads sample is preserved in brown glass bottles using Lugols' solution and counted daily under an inverted microscope to species level, when possible, or otherwise differentiated into defined size classes, using Utermöhl settling chambers to the species level (Hoppenrath et al., 2007; Wiltshire and Dürselen, 2004; Wiltshire et al., 2010). The dominant microalgae in the North Sea are the diatoms. These are also the most reliable in the data set in-terms of data quality control (Wiltshire and Dürselen, 2004) and thus, were those used here. The corresponding zooplankton time series started in 1974 (Greve et al., 2004; Wiltshire et al., 2015). Two nets have been deployed three times a week with a 150- μ m Nansen net and a 500- μ m CalCOFI (Wiltshire et al., 2010). Oblique hauls are made with a Nansen net, whereas the CalCOFI net is towed behind the research vessel (Greve et al., 2004).

Phytoplankton carrying capacity assessment

In this study we defined phytoplankton *K* as the maximum diatom cell densities which can be supported by a given environmental condition at a given time. This *K* is derived from the number sunshine hours, SiO₂ concentration (μ mol/L), PO₄ concentration (μ mol/L), NO₃ concentration (μ mol/L), and the grazing potential of herbivore zooplankton, using the data of the Helgoland Roads Time Series Station. However, a number of other factors i.e. wind speed, current velocity etc. also drive the phytoplankton dynamics which are not considered in our study. This is one of the limitations of our study.

As the first stage of analysis, also mostly done for plant K in terrestrial ecosystems, we estimated diatom K in-terms of sunshine hours, SiO₂, PO₄ and NO₃ (i.e. maximum diatom densities supported by the amount of these resources found in the system) using the following formula:

$$K_m = \frac{N}{M_m} \times S_{mt} \tag{1}$$

In Eq. (1), K_m denotes the *K* in-terms of resource *m*, where m= sunshine hours or SiO₂, or PO₄ or NO₃. $\frac{N}{M_m}$ is a constant which represents the ratio of diatom cell densities (*N*) and amount of resource *m* (M_m) when the molar ratio of nutrients maintain the "Redfield Ratio" (Redfield, 1934) in the ecosystem. This is based on the fact that Redfield (1934) discovered

that when nutrients are not limited at the ecosystem, the molar elemental ratio N: P in most phytoplankton and sea water is 16:1. Diatoms, being silicified organisms, require silicate on top of the other plant nutrients. Brzezinski (1985) sets the "Redfield Ratio" for diatoms as: Si: N: P = 15:16:1. We used this version here. We considered the maximum diatom densities to be the standard *K* when the molar ratio of nutrients in the system reached the "Redfield Ratio". Thus: S_{mt} represents the observed values of resource *m* at time *t*.

The concept we devised for the *K* assessment of phytoplankton for the German Bight is shown in Fig. 2. This came into play for the second step of our analysis. The sunshine hours, SiO_2 , PO_4 and NO_3 were weighted relative to each other, by applying a pair-wise comparison matrix in the context of a decision making process known as the "Analytical Hierarchy Process (AHP)" (Saaty, 1990). Details on AHP method are given as supplementary information of this article (S1). This pair-wise comparison allowed us to determine the relative weight of resources considered for *K* estimation. This weighting of resources also reflects their relative importance for diatom growth. The pair-wise comparison matrix developed for diatom *K* estimation is shown in Table 1.



Fig. 2 Analytical hierarchy schemes for diatom K estimation in the German Bight using the Helgoland Roads Time Series data sets.

In the third step we combined estimated diatom *K* in-terms of sunshine hours, SiO₂, PO₄ and NO₃. In order to do this the *K* for each resource (Eq. 1) as estimated in the first step, was multiplied by their respective weight calculated in a pair-wise comparison matrix (Table 1) in second step of analysis. The product of *K* for each resource and respective weight is then added: $K_{Diatom} = \sum (K_m \times Weight_m)$.

The four resources for diatom K were calculated by Eq. (2).

 $K_{Diatom} = (K_{Sunshine hours} \times 0.07) + (K_{SiO_2} \times 0.24) + (K_{PO_4} \times 0.34) + (K_{NO_3} \times 0.35)$ (2)

As herbivore zooplankton density cannot be ignored because it also affects diatom densities through grazing (Griffin and Rippingale, 2001) we included it in our analyses in the final step. Thus, Eq. (2) is extended to Eq. (3) with herbivore zooplankton effect. This was the product of herbivore zooplankton densities at the time t and, the ratio between average diatoms K (estimated by using equation 2) and average herbivore zooplankton densities.

 $K_{Diatom} = (K_{Sunshine hours} \times 0.07) + (K_{SiO_2} \times 0.24) + (K_{PO_4} \times 0.34) + (K_{NO_3} \times 0.35) + Zooplankton effect$ (3)

Table 1 Pair-wise comparison matrix to assess the relative importance of selected resources for diatom *K* estimation. "Values" represents the pair-wise comparison between each pair of resources (SH=Sunshine hours, Si=SiO₂, P=PO₄, N=NO₃), "Decimal" represents the fractional values of respective paired comparison and "Normalization" represents normalized value of "Decimal". Weight (Wt) of each resource, consistency index (CI), random consistency index (RI) and consistency ratio (CR) were calculated following Saaty (1990).

	Values					Decimal				Normalization				λ_{max}	CI	RI	CR
	SH	Si	Р	N	SH	Si	Р	N	SH	Si	Р	N	-				
SH	1	1/3	1/5	1/5	1	0.33	0.2	0.2	0.71	0.07	0.07	0.07	0.07	4.10	0.03	0.9	0.04
Si	3	1	3/4	3/4	3	1	0.75	0.75	0.21	0.22	0.25	0.25	0.24				
Р	5	3/2	1	1	5	1.5	1	1	0.36	0.34	0.34	0.34	0.34				
N	5	7/4	1	1	5	1.75	1	1	0.36	0.38	0.34	0.34	0.35				
Column sum				14	4.58	2.95	2.95										

For a better understanding of K, we divided the estimated K into two components i.e. "actual carrying capacity" (AK) and "theoretical maximum carrying capacity" (TMK). In addition, we estimated "ecosystem potential" by subtracting AK from TMK. We defined these terminologies (i.e. AK, TMK and ecosystem potential) in table 2.

Terminology	Description						
Actual carrying capacity (AK)	Maximum number of diatom cells that can be						
	supported by a given environment in a particular						
	time. For intra-annual and inter-annual cases, each						
	week and year have a value of AK respectively which						
	is calculated based on the environmental conditions						
	of respective week and year.						
Theoretical maximum carrying	The maximum value of AK calculated from intra-						
capacity (TMK)	annual and inter-annual cases. Lon-term intra-annual						
	cycle has one value of TMK and similarly long-term						
	inter-annual case also has one value of TMK.						
Ecosystem potential	The deviation of AK from TMK. This deviation						
	provides information on the overall conditions of the						
	system. High deviation of the AK from the TMK						
	means the system has less potentiality for						
	phytoplankton growth and low deviation means the						
	system has high potentiality. The 0 difference						
	between TMK and AK indicates no deviation and this						
	means that AK reached at the TMK of ecosystem.						

Table 2 Descriptions of terminologies used in this study.

Results

Long-term intra-annual mean diatom AK (Fig. 3A) was found to be 10.13×10^7 cells m⁻³ with a maximum during week 29 (33.25×10^7 cells m⁻³). This maximum AK is the "theoretical maximum K" (TMK) for intra-annual case. Minimum intra-annual AK was found to be 0.01×10^7 cells m⁻³ during week 51. Mean inter-annual AK was found to be 1.30×10^8 cells m⁻³ (Fig. 3B) with a maximum (i.e. TMK for inter-annual case) of 2.004×10^8 cells m⁻³ in 1994 and a minimum 0.70×10^8 cells m⁻³ in 2011.



Fig. 3 Intra-annual (A) and inter-annual (B) variation of AK at the Helgoland Roads time Series Station. Hollow black circles in both A and B graphs indicate the TMK for intraannual and inter-annual respectively. Box plots represent the mean of intra-annual (A) and inter-annual (B) AK.

Both intra-annual and inter-annual diatom AK at Helgoland Roads showed variability over the time (Fig. 3). Estimated intra-annual AK increased from week 1 to 22 and then fluctuated during summer (week 23-34) and followed a decreasing trend at the end of summer. Overall inter-annual diatom AK has an increasing trend ($R^2 = 0.13$, p = 0.03). These temporal variations in estimated intra-annual and inter-annual AK indicate that phytoplankton K is not constant and changes over time, depending on the environmental conditions. By taking the maximum value of K as a reference (i.e. TMK), we calculated the deviation of AK from this TMK (i.e. ecosystem potential) for both intra-annual and inter-annual cases (Fig. 4). We found that at low deviation the observed diatom densities are higher and at high deviation,

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diatom densities are low for both intra-annual (Fig. 4B; $R^2 = 0.50$, p < 0.0001) and interannual data (Fig. 4D; $R^2 = 0.12$, p = 0.03). Interestingly, inter-annual diatom densities have a significant positive trend ($R^2 = 0.27$, p < 0.001) while deviations have significant negative trend ($R^2 = 0.13$, p = 0.03). This indicates that the ecosystem potentiality for phytoplankton growth has increased on the long-term and thus the diatom densities have also increased.



Fig. 4 Temporal variations of ecosystem potential (i.e. Deviation) and observed diatom densities (A and B), and relationship between ecosystem potential with observed diatom densities (B and D) at the Helgoland Roads Time Series Station. Dashed black horizontal lines in A and C indicate the TMK for intra-annual and inter-annual cases respectively, dashed and solid black lines indicate the temporal variation in AK and observed diatom densities respectively, and grey colored bars (secondary axis) indicate the deviation of AK from the TMK.

Discussion

Carrying capacity is assumed to be constant in population growth models, but the need to treat the K as a function of time has long been recognized in order to model population dynamics in an environment that undergoes change (Dose et al., 2015). In this study we showed that it is possible to estimate the K values also for phytoplankton and, found that as the biotic and abiotic factors in the ecosystem change intra and inter-annual phytoplankton K also changes (Fig. 3). This underpins our expectation that the phytoplankton AK is variable and dependent on environmental conditions.

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We found that estimated diatom K is low during winter season and that is related with the low light availability in the system. During winter light is the limiting factor for phytoplankton rather than nutrients in the shallow North Sea (Wiltshire and Manly, 2004) though during this time nutrients reach at maxima (Hernández-Fariñas et al., 2014). The role of nutrients as determinant of phytoplankton K during winter is less as the system is driven by light during this period. Thus, during winter this light-driven system has low K.

During spring observed diatom densities are high due to spring bloom. At the beginning of spring diatom densities increased and nutrients levels become reduced. At the same time zooplankton grazing on microalgae is less. The spring bloom starts with the increasing light conditions (Richardson, 1989) and ends when conditions of nutrients concentrations in the water column are low (Loebl et al., 2009; Sharples et al., 2006). As spring goes on, nutrients decrease rapidly in the system due to uptake by phytoplankton and winter stock of nutrient is depleted. Even when during spring grazing is low and light is on the increase trend but continuous uptake of nutrients by phytoplankton causes a difference between estimated K and observed diatom densities.

At the beginning of the summer, nutrient levels go up (Hernández-Fariñas et al., 2014; Wiltshire et al., 2015) due to depletion of the water and local remineralization process (Wiltshire et al., 2015). At the same time, less turbulent conditions result higher light penetration depth (Richardson, 1989; Wiltshire et al., 2015) and thus create better conditions for the system to support higher densities of phytoplankton. During autumn, both nutrient levels and light start to decrease and concurrently, diatom K also starts to decrease. During this period observed densities exceed the K and therefore, suffer a crash.

During the early years of this analysis (from 1975 to 1990), diatom K and observed diatom density were concomitant. But since 1990, diatom K and observed diatom cell density have differed from each other significantly. This might be due to the long term changes in nutrient structures. The southern bight of the North Sea has been subject to nutrient enrichment since the 1960s and subsequent nutrient reduction mitigations since the late 1980s (Lenhart et al., 2010). Taking into account these changes in the ecosystem drivers, one key question is how these changes affect the K of the system as mentioned in Wiltshire et al. (2010). In this study we found that AK of the system has increased on the long-term. In addition, the deviation of AK from the TMK which shows a decreasing trend means the potentiality of the system for phytoplankton growth has increased. Years with high potentiality had the high diatom densities.

Here we estimated the K for diatoms and the effect of species composition on K is not evaluated. Therefore, it might be an interesting research question to see how the K is affected by species composition. Moreover, it will be also interesting to see how K varies in other aquatic ecosystems i.e. freshwater and estuary.

Potential application of *K* in relation to fisheries

The production of marine fisheries is limited and influenced by various factors, but phytoplankton is the most important and most fundamental necessity (Cushing, 1995; Hanson and Leggett, 1982; Pauly and Christensen, 1995). We evaluated the relationship between diatom AK and fish (Fig. 5) in the German Bight by using the mean fish trophic level (measure of the position of an organism in food web which starts from 1 which stands for primary producers, trophic level 2 stands for primary consumers that eat primary producers, 3 for secondary consumers, and so on). The pelagic fish catch data for the German Bight came from "The Sea Around Us" project (Pauly and Zeller, 2015). Detailed methods for trophic level calculation have been described in Kleisner et al. (2014). However, this is the first attempt to relate the *K* with fisheries and more detailed data at local level are needed for more insights.



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Fig. 5 Inter-annual variations in pelagic fish catch and mean trophic level (A) in the German Bight (Data source: SAUP, 2015), and relationship of ecosystem potential with pelagic fish catch and mean trophic level (B). Black and grey filled circles (B) represent the pelagic fish catch and mean trophic level of catch in the German Bight.

According to this data (Pauly and Zeller, 2015) the mean trophic level in the North Sea from 1975 to 2006 varied between 3.45 to 3.26 with a mean 3.34 (Fig. 5A). Pelagic fish catch values for the North Sea varied between 14.21×10^5 to 6.29×10^5 tonnes with a mean 8.93×10^3 tonnes for that time period (Fig. 5A). The overall long term mean trophic level (1975-2006) showed a decreasing trend, while an increased trend was observed for both pelagic fish catch and diatom AK. Further comparison of deviation of AK from the TMK with pelagic fish catch data showed a significant positive relationship (Fig. 5B; $R^2 = 0.24$, p = 0.005) while a significant negative relationship was found with mean trophic level data (Fig. 5B; $R^2 = 0.25$, p = 0.004). These indicate that high potentiality for phytoplankton growth in the system supports high pelagic fisheries in the North Sea ecosystem. Thus we conclude that, high AK indicates high potential for growth and therefore higher densities of phytoplankton in the system, which in turn supports high pelagic fisheries. We summarized the relationship between fisheries and deviation of AK from the TMK in Fig. 6.



Fig. 6 Schematic presentation of the relationship of phytoplankton AK (Actual carrying capacity) and deviation from TMK (Theoretical maximum carrying capacity) with the fisheries. Depths of the filled area from the dashed black line indicate the deviation of AK

from the TM*K*. The color gradient from yellow through red to yellow indicates low potentiality through high potential to low potential of the system. Black filled point indicates the point of no deviation (i.e. highly potential) and arrow lines from this point indicate the increase of deviation (i.e. decrease potentiality). Filled grey circles indicate the high deviation point with less potentiality of the ecosystem.

Carrying capacity as management tool

Our study represents the K for past and present time periods. Therefore, it is important to know how one can make K as an active part of future environmental management. Our analyses suggest that ecosystem potential (i.e. deviation of AK form the TMK) and observed phytoplankton in the ecosystem follow a positive linear relationship. Considering this relationship, we considered two scenarios i.e. A and B. Scenario A is a system where ecosystem potential increased at time 2 compared to time 1 and this also caused an increase in observed phytoplankton in the system.

On the other hand, scenario B is a system where ecosystem potential decreased at time 2 from time 1. This low K in current state than previous state indicates the basic requirements those drive the K are in short supply. For example, it might happen if the supply of specific nutrient is low. In addition, unbalanced supply of nutrients (i.e. high nitrogen and low phosphorus supply or vice versa) might change the k of the ecosystem. Decrease in potentiality means the system has differed from its real state and thus supports less phytoplankton. This will lead to a change in the structure of the entire ecosystem (i.e. change the primary production, fisheries production etc.). Therefore, scenario B demands some management practices.

For proper management, first attempt needed to identify the anticipated impact of k change on the ecosystem (i.e. less ecosystem potential will support less fisheries production which results in economical loss). Then it is essential to identify drivers those changed the k (i.e. change in nutrients supply might change the K of the phytoplankton). As next step, proper strategies need to formulate and implement (i.e. how to control suspended particulate matter loads/nutrient inputs). If the supply of a specific nutrient is less but is essential for the growth of phytoplankton then the supply needs to increase. As another option, we can also decide to decrease or stabilize the human population pressure.

In general, management means "able to influence the situation". Therefore, for the open sea, how the concept of K can change the situation? Phytoplankton K is mainly dependent on light, nutrients and temperature and grazing. Among these nutrients are controllable at their input levels. We generally expect a gradient in nutrients distribution from coastal area to open

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sea (i.e. high concentration in the river and low in the open sea). Carrying capacity at the open sea can serve as an indicator of ecosystem health and changes in the nutrients distribution pattern from coast to open sea might change the K. Thus, current state of K can show if reduction of specific nutrients is required at the input level to reach at a balanced nutrients condition. It will then help to develop the guideline to formulate policy toward defining limits of input of ecological drivers from their sources to the ecosystem. Through a better policy formulation and then implementation would help the system to return in its *TMK* state. However, for these we need continuous monitoring.

Apart from management and policy, how this study can put the knowledge in the practice of the oyster and mussel farmers? Farmers can use this study as an indication of ecosystem state. As we did our study based on the one of the world largest and longest quality controlled data set, one can have an indication on long-term change in ecosystem potential in the German Bight. This indication might hold true for the coastal areas also (i.e. long-term trend might be similar). In addition, the seasonal cycle of carrying capacity may offer the information on when to sow and when to harvest the farmed species as both open sea and coastal area supposed to show the same seasonal pattern. However, to estimate the number of farms they can establish and stocking density of the species it is important to estimate the *K* at the local level. Though *K* can be utilized as an excellent management tool, however this approach needs regular monitoring of the ecosystem. This might requires some technical knowledge. As *K* is dependent on the environmental condition, this might be different at different geographical locations.

Conclusion

In conclusion, going back to our title: Is the phytoplankton carrying capacity a viable concept? The answer is "yes". Phytoplankton K is driven by a set of environmental factors which are subjected to both temporal and spatial changes. There is really an AK which is also variable and possible to estimate. The TMK of an ecosystem can be considered an optimum goal and AK in the ecosystem always tends to achieve that goal, and this K concept plays an important role in the fields of population dynamics and resource management. Increase in AK reduces the deviation with TMK, increase the potentiality of the ecosystem and thus increase the phytoplankton densities. Fisheries resources strictly follow the timing and level of this potentiality for success of recruitment, peak of occurrence and decline of stock. As we already showed that high pelagic fish catch in the North Sea is related with the high potentiality of the ecosystem (Fig. 4). Changes in timing of this high potential of the system

will shift the timing of fisheries recruitment and peak occurrence (match and mismatch can occur). Moreover to find a balance between ecosystem and aquaculture farms (i.e. oyster farms), this K can be also served as an important management tool. Thus, monitoring the phytoplankton K serve as an ecosystem based management tool (Box 1) by estimating AK, TMK and potential of the system, and then predicting the timing of fish recruitment, peak occurrence, decline of stock, sowing and harvesting of aquaculture species.

Box 1: Utilization of carrying capacity as fisheries management tool

Step 1: Calculate AK and TMK using environmental data.

Step 2: Calculate the deviation of AK from the TMK.

Step 3: # If deviation is less, the system has high potentiality for growth.

If deviation is high, the system has low potentiality for growth.

Step 4: # Determining the timing of fish recruitments, peak occurrences and stock decline.

Determining the timing of aquaculture species snowing and harvest.

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Supplementary information (S1)

Analytical hierarchy process (AHP): The AHP is a proven, effective means of dealing with complex decision making and can assist with identifying and weighting selection criteria, analyzing the data collected for the criteria, and expediting the decision-making process (Hossain et al., 2007). The AHP is a theory of measurement through pairwise comparisons and relies on mathematics and logics. This approach has following steps:

Pair-wise comparison matrix development: The pair-wise comparison matrix refers to a process of comparing entities in pairs to judge which of each entity is preferred, or which has a greater amount of some quantitative property. The comparison of one attribute with another are systematically scored on a 17 point continuous scale from 1/9 to 9, where a score of 1/9 is the least important and 9 is the most important (Table 1) (Saaty, 1977). If the one attribute is exactly as important as another attribute, this pair receives a score 1. The idea of scale was to rank each criterion as a value <10 and thus, the highest ratio corresponds to 9. Thus, the scale has 17 points (i.e. all integers from 1 to 9) and reciprocal of these integers to represent maximum distinctness among criteria.

Table 1 The relative importance of two criteria (Saaty, 1977)

1/9	1/8	1/7	1/6	1/5	1⁄4	1/3	1⁄2	1	2	3	4	5	6	7	8	9
Extre	Extremely		Very		Strongly		Moderately		Mod	erately	Stro	ongly	Ver	у	Extr	remely
strongly													stro	ngly		
Less important								Mor	e impo	rtant						

A pair-wise comparison matrix $A_{ij} = \left[\frac{W_1}{W_2}\right]$, where $\frac{W_1}{W_2}$ is the comparison of attribute *i* to *j*. The matrix A_{ji} is reciprocal of A_{ij} i.e. $A_{ji} = \frac{1}{A_{ij}}$. All diagonal elements of matrix are equal to 1. Given this reciprocal property, only $\frac{n(n-1)}{2}$ pair-wise comparisons are needed for an $n \times n$ dimensional matrix (Kovacs et al., 2004).

Weighting of criteria: The weights of the individual criteria are calculated in two steps. In first step, the entries in the matrix A are normalized (a_{ij}^*) by Eq. (1). This involves: each value in the matrix (a_{ij}) is divided by the sum of its column $(\sum_{i=1}^{n} a_{ij})$. As the second step, to get the weight of each criteria (W_i) , the mean of each row of normalized matrix (calculated by Eq. (1)) is determined by Eq. 2 and sum of the weights is equal to 1.

$$a_{ij}^* = \frac{a_{ij}}{\sum_{i=1}^n a_{ij}}, \text{ for all } j = 1, 2, ..., n$$
 (1)

$$w_i = \frac{\sum_{j=1}^n a_{ij}^*}{n}$$
, for all $i = 1, 2, ..., n$ (2)

Consistency assessment of the pair-wise comparison matrix: Inconsistency associated with a pair-wise comparison matrix was measured based on the relationship between the vector of weights, W and the matrix A using Eq. (3) as suggested by (Saaty, 1980).

$$A_w = \lambda_{max} W, \tag{3}$$

Where W is the n dimensional eigenvector associated with the largest eigenvalue λ_{max} . The measure of inconsistency is based on the observation that $\lambda_{max} > n$ for positive, reciprocal matrices, and $\lambda_{max} = n$ if and only if A is a consistent matrix (Hossain et al., 2014). Accordingly, $\lambda_{max} - n$ is considered as a measure of the degree of inconsistency. Thus, a consistency index (*CI*) was measured by the Eq. (4) first and then the consistency ratio (*CR*) was computed by the Eq. (5).

$$CI = \frac{\lambda_{max} - n}{n - 1},$$

$$CR = \frac{CI}{RI},$$
(4)
(5)

The random consistency index (Table 2, RI) depends on n (Saaty, 1977). Saaty (1980) suggests that if the CR is smaller than 0.10, the degree of consistency is reasonable. However, if CR is greater than 0.10, indicates the comparison matrix is inconsistent and should be revised.

Table 2 The random consistency index (RI) (Saaty, 1977). RI values corresponds to the order of the matrix n

n	1	2	3	4	5	6	7	8	9	10
RI	0	0	0.525	0.822	1.115	1.252	1.341	1.404	1.452	1.484

Making decisions requires comparing alternatives with respect to a set of criteria. If there are more than two criteria, determining which criteria are more important can itself be a serious problem. One would like to be able to rank the criteria in order of importance, and to assign to the criteria some relative ranking indicating the degree of importance of each criterion with respect to the other criteria.

Finally, to produce a global score/value (Y) for multiple attributes, the AHP method multiply the score/observed value of each attribute (X_i) by the corresponding weight (W_i) calculated using the pair-wise comparison matrix and then these products are summed (Eq. (6)).

$$Y = \sum_{i=1}^{n} (X_i \times W_i), \text{ for all } i = 1, 2, ..., n$$
(6)

Here, it is important to note that the weight of each attribute reflects the relative contribution of that attribute to produce the global score. Therefore, observed score of an attribute is multiplied by its corresponding weight and then all products are summed to get a global score.

CHAPTER III

Does ecosystem variability explain phytoplankton diversity? Solving an ecological puzzle with long-term data sets

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Abstract

Explaining species diversity as a function of ecosystem variability is a long-term discussion in community-ecology research. Here, we aimed to establish a causal relationship between ecosystem variability and phytoplankton diversity in a shallow-sea ecosystem. We used longterm data on biotic and abiotic factors from Helgoland Roads, along with climate data to assess the effect of ecosystem variability on phytoplankton diversity. A point cumulative semi-variogram method was used to estimate the long-term ecosystem variability. A Markov chain model was used to estimate dynamical processes of species i.e. occurrence, absence and outcompete probability. We identified that the 1980s was a period of high ecosystem variability while the last two decades were comparatively less variable. Ecosystem variability was found as an important predictor of phytoplankton diversity at Helgoland Roads. High diversity was related to low ecosystem variability due to non-significant relationship between probability of a species occurrence and absence, significant negative relationship between probability of a species occurrence and probability of a species to be outcompeted by others, and high species occurrence at low ecosystem variability. Using an exceptional marine longterm data set, this study established a causal relationship between ecosystem variability and phytoplankton diversity.

Key words: Plankton, variable environment, Markov chain, Helgoland Roads, North Sea.

Introduction

Phytoplankton is a taxonomically and functionally diverse group of organisms (Bonachela et al., 2015) comprising tens of thousands of species (Mutshinda et al., 2013a). Their ability to utilize solar energy makes them fundamental for ocean productivity and they are responsible for half the global primary production (Field et al., 1998). Phytoplankton are the energy source for larger heterotrophic zooplankton and thus, transfer energy upwards to higher trophic levels (Steele, 1970). They, therefore, play essential roles in food webs and global biogeochemical cycles (Bonachela et al., 2015). Changes in phytoplankton dynamics create an impact on species growth rate and photosynthetic response (Duarte et al., 2006).

Many abiotic factors (e.g. light availability, temperature, salinity, pH and nutrients) and biotic factors (e.g. predators, parasites) are regulators of phytoplankton community structure (Wiltshire and Boersma, 2016b; Wiltshire et al., 2015). In addition, meteorological and climatic factors, such as wind intensity and direction, the North Atlantic Oscillation (NAO), the Atlantic Multidecadal Oscillation (AMO) and El Niño due to their impact on hydrography and ocean stratification are also important for long-term changes in the abundance and diversity of plankton.

The global marine environment is changing rapidly (IPCC, 2007), and significant correlations between changes in marine environment and species abundance and diversity have been reported (Aebischer et al., 1990; Beaugrand and Reid, 2003). Large changes in phytoplankton species distribution in the North Sea over the last decades have been identified (Wiltshire et al., 2015). Phytoplankton colour index seems to have shown a marked increase in this region during the mid to late 1980s (Edwards et al., 2001; Reid et al., 1998). Changes in phenology (Greve et al., 2005; Wiltshire and Manly, 2004) and species composition (Beaugrand, 2003) have also been observed in this area. Although we know that these biotic changes are accompanied by variations in environmental conditions, it remains challenging to establish a causal relationship between environmental variability and community structure change.

The majority of the factors which affect biodiversity show an increasing trend and global diversity shows a decreasing trend (Butchart et al., 2010). Contrastingly an analysis of algal species diversity based on the Helgoland Roads Time Series data set (Wiltshire and Dürselen, 2004) shows that, over the recent years, there is a significant increase in the species diversity (Fig. 1). Therefore, an important question which needs to be addressed is what has caused this phytoplankton diversity increase at Helgoland Roads.



Fig. 1 Long-term weekly mean phytoplankton diversity at Helgoland Roads. Diversity is measured as Shannon diversity index from quality controlled counts data of 26 species from the Helgoland Roads Time Series station.

Several ideas have been developed over the past few decades to explain shifts in species diversity. The intermediate disturbance hypothesis (Connell, 1978) is one of the most overarching concepts of non-equilibrium community theory and explains high species diversity (Craine, 2005; Grime, 2007). The intermediate disturbance hypothesis (IDH) predicts that species diversity peaks at the intermediate levels of disturbance. At low disturbance competitive exclusion reduces diversity. High disturbance produces high stress on species and increases mortality, therefore reduces diversity. Disturbance at intermediate levels prevents competitive exclusion, permits the coexistence of successful competitors and maximizes species diversity (Flöder and Sommer, 1999). This "disturbance" is a result of heterogeneity of the environment in the form of ecosystem drivers, such as nutrient supply, temperature, salinity, light availability and biotic factors (i.e. species interactions, parasites, predation etc.).

We hypothesized that algal diversity at Helgoland Roads are related to disturbance associated with environmental variables. The IDH is able to predict high diversity at the intermediate level of disturbance and therefore, one can assume that this high species diversity at Helgoland Roads might be related to an intermediate level of disturbance. This disturbance is the heterogeneity in the ecosystem drivers which we termed "ecosystem variability" in our study.

Many studies provide analytical methods for the link of ecosystem variability to species diversity (e.g. Flöder and Sommer (1999), D'Odorico et al. (2008), Dornelas (2010) etc.). A number of studies based on field data were reported in Padisák et al. (2013). Here we carry out a study linking ecosystem variability to marine biodiversity based on a marine time series of species abundance at Helgoland Roads in the North Sea. The objectives of this study are:

- (i) the estimation of long-term ecosystem variability as a function of biotic, abiotic and climatic factors,
- (ii) to test if the intermediate disturbance hypothesis (IDH) can explain recent increase (after the 1990s) in algal species diversity at Helgoland Roads, and
- (iii) to explain the observed relationship of phytoplankton diversity ecosystem variability.

Materials and methods

Data source

We used the quality-controlled data of phytoplankton abundance, nutrient concentrations, Secchi depth, temperature and salinity from the Helgoland Roads long-term data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). The Helgoland Roads Time Series station (54°11.3' N, 7°54.0' E) is located between two islands, i.e. Helgoland and Düne, in the North Sea. Long-term monitoring of biological, chemical, and physical parameters has been carried out continuously on a work daily basis since 1962. This data set is one of the longest aquatic data sets in history (Wiltshire and Dürselen, 2004). Water samples are collected from the surface and preserved for further analysis of nutrients, phytoplankton and zooplankton. The nutrients (silicate, phosphate, ammonium, nitrate and nitrite) are measured immediately using the standard colorimetric methods after Grasshoff (1976) on a filtered sub-sample from the daily Helgoland Roads surface water sample (Wiltshire et al., 2010). The phytoplankton sub-sample from the Helgoland Roads sample is preserved in a brown glass bottle with Lugols' solution. The samples are subsequently counted under an inverted microscope using Utermöhl settling chambers and individuals are identified to species level when possible, or otherwise differentiated into defined size classes (Wiltshire and Dürselen, 2004; Wiltshire et al., 2010). Secchi depth and temperature are measured directly on station (Wiltshire et al., 2015). We also used three climatic variables i.e. the NAO (data available from

https://www.ncdc.noaa.gov/teleconnections/nao/), the AMO (data available from https://www.esrl.noaa.gov/psd/data/timeseries/AMO/) and the Tropical Pacific sea surface temperatures in the El Niño 3.4 region (data available from http://www.cpc.ncep.noaa.gov/products/analysis monitoring/ensostuff/ensoyears.shtml) for our study.

Phytoplankton diversity estimation

We used species richness and the Shannon diversity index as a measure of phytoplankton diversity. The Shannon diversity index (Shannon and Weaver, 1949) depends on both species richness and evenness (Pielou, 1966), and is the best measure of their joint influence (Fager, 1972). In addition, this index is not strongly affected by rare species (Stirling and Wilsey, 2001), it is sample size independent (Sanders, 1968), and has been developed as a test statistic that is neutral with respect to physical, functional, and biotic interactions (Caswell, 1976). Therefore, this index is widely used as a measure of biodiversity.

We estimated species richness R as the sum of total number of species present in each sample. The Shannon diversity index (H') was calculated for each sample using the following equations:

$$H' = -\sum_{i=1}^{R} p_i \ln(p_i)$$
(1)
$$p_i = \frac{N_i}{N_{total}}$$
(2)

Where, p_i is the relative abundance of species *i*, N_i is the number of individuals in species *i* and N_{total} is the total number of individuals in the community.

Based on the counts in the Helgoland Roads long-term phytoplankton data set, a taxon list of 261 taxa has been assembled (Kraberg et al., 2015). Numbers for all the species listed at the Helgoland Roads Time Series Station are not continuously available from 1962. Details on the gaps in species abundance data are explained in Wiltshire and Dürselen (2004). However, due to the potential of this data set for examining plankton biodiversity against the backdrop of global change a list of species was made by Wiltshire and Dürselen (2004) to use for comparisons of their long-term occurrence. We used 26 of these species data to estimate the long-term phytoplankton diversity shifts at Helgoland Roads. These 26 species represent different groups and growth types (i.e. fast and slow growing species), and they are merely a sub-community of the overall counts. The reduced community with 26 species means a removal of large number of species from the entire community which is a kind of thinning. This may cause difficulties in comparing trends across different species numbers. Removing

an extremely rare species typically leads to a smaller or similar diversity, while the removal of a dominating species can have the opposite effect of increasing diversity.

Diversity index estimated from the sub-community should be on average equal to the value of diversity index when different species numbers are compared. To examine if our sub-community of 26 species meets these criteria, we performed following analyses:

We took data on observed phytoplankton species abundance from the Helgoland Roads Time Series station for the time period of 1990 to present. For this time period we have continuous observations of species abundance. Ten replicate sub-communities each of sizes N = 30, 50,70, 90, 110 and 130 species were randomly sampled from the phytoplankton species of Helgoland Roads. Then, Shannon index was calculated for each replicate sub-community. Estimated Shannon index from each replicate sub-community were averaged as a ratio to the 26 species sub-community. The ratio < 1 or > 1 indicates that Shannon index of replicate subcommunity is smaller or greater than our 26 species sub-community, respectively. The ratio equal to 1 indicates that our 26 species sub-community has perfect performance to describe the diversity of the replicate sub-community.

Overall, it can be seen that the ratio for most of the replicate sub-communities is close to 1 even when large number of species were considered (Fig. S1). Average ratio across 10 replicates drew for sub-communities each of sizes 30, 50, 70, 90, 110 and 130 species indicate that all of them are located within the $\pm 10\%$ deviation from the ratio 1. This indicates that our 26 species sub-community has nearly perfect performances to describe the diversity of entire community. In addition, we found significant positive correlations of Shannon index of 26 species with the Shannon index estimated from replicates of 30, 50, 70, 90, 110 and 130 species (r = 0.78, 0.82, 0.75, 0.72, 0.71, 0.68 respectively). Therefore, as a representation of long-term shifts in phytoplankton diversity at Helgoland Roads consideration of 26 species is reasonable.

Ecosystem variability estimation

Ecosystem variability was examined by using the annual mean data on biotic, abiotic and climatic factors (i.e. sum of phytoplankton species abundance data, temperature, salinity, Secchi depth, silicate concentrations, nitrate concentrations, phosphate concentrations, NAO, AMO and El Niño index). To reduce the high dimensionality, we first performed a principal component analysis (PCA) of these multivariate data series. The first axis of the PC explained most of the variance (61.44%). Therefore, we took PC1 as a representation of the ecosystem. Then the "local variance" was calculated directly on the first PC to examine the

long-term "ecosystem variability" by following Beaugrand et al. (2008). The "local variance" explains the heterogeneity of a value of an observation with respect to the value of another observation (Beaugrand et al., 2008).

To calculate the "local variance", we borrowed the technique derived from the method of point-cumulative semi-variogram (PCSV) which is developed by Şen (1998). The PCSV function is proposed for identifying the spatial behaviour of any variable around a reference site (Şen and Habib, 1998). This method measures the dissimilarity between a concerned observation with another (Beaugrand and Ibañez, 2002) and therefore, provide valuable information for describing the heterogeneity between observations (Şen and Habib, 1998).

Markov chain model

Markov chain model is the simplest model to analyze multispecies data and the transition matrix of this model summarizes essential parameters related to the community dynamics in a way that few models can achieve. In ecology, Markov chain model is used to estimate the probabilities of species to move from one ecological state to another (Wootton, 2001). The ecological states in the model depend on the major mechanisms that the investigator believes are important (Wootton, 2001). For example, occurrence and absence of a species can represent two different ecological states if the investigator is interested to estimate the probability of a species being present and absent respectively.

Here, we used a Markov chain model to estimate the dynamical processes of species i.e. probability of species occurrence (i.e. probability of a species being present at time t+1 which was absent at time t), probability of species being absent (i.e. probability of a species being absent at time t+1 which was present at time t) and probability of a species to be outcompeted by other species. The Markov chain model used for this study is shown in eqn 3 where C_t denotes a column vector containing proportional abundance of community c_j at time t and C_{t+1} contains proportional abundance of community c_j at time t + 1. The column vector C_t satisfies the conditions $0 \le c_j \le 1$ and $\sum_j c_j = 1$. In transition matrix P at i^{th} row and j^{th} column, the probability (p_{ij}) defines a point in ecological state j at time t, being at state i at the next sampling at the time t + 1. In eqn 3, P is a matrix with S + 1 rows and S + 1 columns where S is the number of species in the model. Columns and rows contain transition probabilities of points which either start from or end in "empty space" (i.e. absence of species), respectively. We considered 26 species (S), thus, we had 27 ecological states (S + 1) in the transitional probability matrix. Twenty-six species represent 26 ecological states (S = 1, 2, ..., 26) and (S + 1)th state or 27th state represents the "empty space".

$$C_{t+1} = PC_t$$
(3)
where $P = \begin{pmatrix} p_{ii} \dots p_{ij} & p_{is} & p_{i(s+1)} \\ p_{si} \dots p_{sj} & p_{ss} & p_{s(s+1)} \\ p_{(s+1)i} \dots p_{(s+1)j} & p_{(s+1)s} & p_{(s+1)(s+1)} \end{pmatrix}$

Probability of species *i* occurrence was estimated according to Wootton (2001) as:

 $p(0ccurance of species i) = p_{i(S+1)}$

Probability of species j being absent was estimated according to Wootton (2001) as:

$$p(Absence of species j) = p_{(S+1)j}$$

Total probability to outcompete species j by other species was estimated according to Wootton (2001) as: $(1 - p_{ij} - p_{(S+1)j} = \sum_{j=1}^{S} p_{ij}; i \neq j)$

The transition matrix P was determined from the observations C through eqn 3 by performing Markov chain Monte Carlo (MCMC) simulations (Gilks et al., 1995) in OpenBUGS software (Thomas et al., 2006). We linked OpenBUGS software with the statistical computing software R (R Development Core Team, 2010) by R2OpenBUGS package (Sturtz et al., 2005) for the MCMC simulations. We ran 20,000 MCMC iterations with three parallel chains. To remove the dependence on the starting values we discarded the first halves from each Markov chain as burn in.

Results

What are the long-term trends in biodiversity and ecosystem variability?

We first estimated the long-term trends in species richness (Fig. 2a), Shannon index (Fig. 2b) and ecosystem variability (Fig. 2c). The polynomial regression analyses of year versus species richness, Shannon index and ecosystem variability explained 87% (p < 0.0001), 49% (p < 0.0001) and 43% (p < 0.001) of variations, respectively. Our trend analyses revealed significant inter-annual variation in all these three variables. Species diversity increased until around mid-1970s before undergoing a decline during the 1980s. From the beginning of the 1990s we observed an increase in species diversity. Overall, the 1980s represented a period of high ecosystem variability with a comparatively less variable period during the 1970s and from the beginning of 1990s to onwards.



Fig. 2 Long-term annual mean of (a) species richness (b) Shannon index and (c) ecosystem variability at the Helgoland Roads Time Series station. Red dots indicate the values of respective variable at different years, grey shade indicates 95% confidence interval and blue solid line indicates the trend estimated as the function of time. The vertical shaded block indicates the decline of species diversity (a, b) and high variability in ecosystem (c) during the 1980s.

Does ecosystem variability explain increase in phytoplankton diversity?

We carried out linear regression analyses of ecosystem variability versus species richness and Shannon index (Fig. 3) data. We found that ecosystem variability is an important predictor of long-term change in phytoplankton diversity. Ecosystem variability explained 47% and 40% of variations in long-term species richness and Shannon index respectively at Helgoland Roads. We also found a significantly negative relationship between ecosystem variability and both the species richness (r = -0.68, p < 0.0001) and the Shannon index (r = -0.63, p < 0.0001).



Fig. 3 Relationship between ecosystem variability and, (a) species richness and (b) Shannon index. Red dots in both plots indicate the values from each year, shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trends.



5.4 What causes high diversity at low ecosystem variability?

Fig. 4 Linear regression to compare the species absence probability and occurrence. Shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trend. Each red dot indicates the average of each species over the study period.

Diversity only peaks at the intermediate level of variability if a negative relationship exists between probability of species absence and occurrence (Petraitis et al., 1989). Our analysis (Fig. 4) indicates non-significant negative relationship (r = -0.095, p = 0.63) between the probability of species absence and occurrence. In addition, species selected for our study differs from each other in-terms of their occurrence probabilities which should be same for all species to support the prediction of the IDH. Thus, species interactions found in the community contradicts the underlying mechanistic assumptions of IDH and therefore, diversity might not peak at the intermediate level of variability.



Fig. 5 Linear regression to compare the species occurrence probability and probability to outcompete. Shaded grey lines indicate 95% confidence interval and blue lines indicate the linear trend. Each red dot indicates the average of each species over the study period (1968-2014).

We found a significant negative relationship between probability of species occurrence and probability to outcompete (Fig. 5; r = -0.81, p = 0.0001). We also found that higher probability of phytoplankton occurrence is related to low ecosystem variability (Fig. 6a; r = -0.58, p < 0.001) while there is a non-significant relationship exists between ecosystem variability and probability of a species to be outcompeted by other species (Fig. 6b; r = 0.13, p = 0.38). Negative relationship between species occurrence and probability of a species to be outcompeted by other species.

reduce species competition at low ecosystem variability and thus, exclusion of species does not occur. Therefore, species diversity increases at low ecosystem variability rather than there being a decrease.



Fig. 6 Relationship between (a) long-term ecosystem variability and species occurrence (each data point indicates the mean of 26 species for a year) probability and (b) long-term ecosystem variability and probability to outcompete by other species (each data point indicates the mean of 26 species for a year).

Discussion

We analyzed long-term quality-controlled Helgoland Roads phytoplankton, temperature, salinity, Secchi depth and nutrient data, and three climate variables (i.e. NAO, AMO and El Niño). First we estimated the long-term ecosystem variability and then explained long-term phytoplankton diversity change as a function of ecosystem variability.

The southern North Sea has undergone considerable change in the last decades, and many examples exist describing changes in the environment (Beaugrand et al., 2008; Beaugrand et al., 2014; Boersma et al., 2015; Edwards et al., 2002; Siegismund and Schrum, 2001). Three temporally persistent shifts were identified in the 1960s, 1980s and during the period 1996 to

CHAPTER III

2003 in the North Sea and the three shifts impacted 40% of the plankton species or taxa considered in a study of Beaugrand (2014). In our study, we identified 1980s as the period of high ecosystem variability at the Helgoland Roads Time Series station while a comparatively less variable period in the ecosystem was identified afterwards (Fig. 2c). Beaugrand et al. (2008) also identified that the 1980s overall were a period of high variability with a low variability in the recent years in the North Atlantic region. Similar change in the late 1980s in long-term records of Mediterranean ecological and hydro-climate variables were also observed (Conversi et al., 2010). The hydrography of the southern North Sea has changed significantly in the last 50 years (Scharfe, 2013), especially around Helgoland, showed a change in phenology of the phytoplankton (Wiltshire et al., 2015). This known shift during the 1980s was also previously described by Wiltshire et al. (2008) for the same data sets in terms of average phytoplankton winter densities and average cell size.

During the 1980s, we observed a decline in phytoplankton diversity while a positive trend is observed from the beginning of 1990s (Fig. 2a & 2b). Reid et al. (2016) have confirmed that the 1980s shift in the ecosystem represented a major change in many of the Earth's biophysical systems. A collapse of global biodiversity occurred during 1980s (Rockström et al., 2015). In a Costa Rican cloud forest, amphibian and reptile populations declined in 1987 (Pounds et al., 1999). From 1984 to 2004, the International Union for Conservation of Nature (IUCN) recorded 27 extinctions of species (Pereira et al., 2012). All these studies mentioned above support our findings of decline in phytoplankton diversity during the 1980s.

From our analyses, we know that phytoplankton diversity at Helgoland Roads has increased significantly over the past years. However, a definite single cause of this increase has yet to be elucidated. Previous studies on this data set found a strong decrease in the densities of calanoid zooplankton (Boersma et al., 2015) and an increase in diatom biomass (Wiltshire et al., 2010). Therefore, lower herbivore densities would release the predation pressure of zooplankton on the algae, and that this may lead to higher algal densities at Helgoland Roads (Wiltshire and Boersma, 2016a). However, in this study we focused on long-term change in the phytoplankton diversity at Helgoland Roads in relation to ecosystem variability. Our study found ecosystem variability as an important predictor of phytoplankton diversity at Helgoland Roads, but due to significantly negative association between these two variables finding of our study contradicts with the prediction of the IDH (Connell, 1978; Grime, 1973). Findings of many experimental studies supported the prediction of the IDH (Flöder and Sommer, 1999; Gaedeke and Sommer, 1986; Robinson and Sandgren, 1984; Sommer, 1995). However, field based studies rarely found the predicted peak in diversity at intermediate

disturbance levels (Fox, 2013). Some studies found completely different patterns i.e. monotonic increases and declines with increasing disturbance intensity (Mackey and Currie, 2001). Collins (1987), Collins and Gibson (1990) and Robinson and Minshall (1986) found diversity decreases with the increase in variability while diversity increases at comparatively less variable ecosystem which are in line with our findings.

Due to contradiction of our finding with most commonly cited prediction of the IDH, we explored the reasons of why diversity peaked at low ecosystem variability. Existing studies suggest that biodiversity only peaks at the intermediate level of variability if there is a negative relationship exists between species absence and occurrence (Petraitis et al., 1989). Our study did not find significant negative relationship between these two parameters (Fig. 4) and thus no peak in biodiversity at the intermediate level of variability might happen. The IDH considered the "equal chance hypothesis" which assumes that the species occurrence probabilities are very similar (Connell, 1978), but in our case species differ in-terms of their occurrence probabilities (Fig. 6). This might be another reason that diversity did not peak at the intermediate level of variability.

Negative relationship between species occurrence and probability of a species to be outcompeted by other species promote biodiversity, and this relationship is also a powerful explanation of species coexistence (Cadotte, 2007). We also found a similar negative relationship (Fig. 5), which indicates that species has higher ability to co-exist. Both diversity and species occurrence probability declined with the increase of ecosystem variability (Fig. 3 and 6, respectively) and these indicate that species are generally inferior to occur at highly variable ecosystem. Moreover, these species are skewed toward the competitive end of probability to outcompete and occurrence probability. This means increasing ecosystem variability should reduce diversity (Cadotte, 2007). In addition, negative relationship between species occurrence and probability to outcompete, and high occurrence probability at low ecosystem variability prevent exclusion of species at low ecosystem variability. Thus, many species can occur in a less variable ecosystem and therefore, increase the diversity. Following the loss of diversity from disturbance or highly variable condition, species increase owing to recruitment and species are able to occur in cleared patches (Hughes et al., 2007). After in the decline of species diversity during the 1980s due to high ecosystem variability, species might had a window for their occurrence in the system afterwards with an ability that was not enough to exclude other species. Therefore, coexisted in a less variable ecosystem and enhanced diversity.

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In conclusion, going back to our title: Does ecosystem variability explain phytoplankton diversity? The answer is "yes". We found that, ecosystem variability is an important predictor of long-term shifts in phytoplankton species diversity at Helgoland Roads. The increasing diversity trend of the last two decades is related to low ecosystem variability. The occurrence of more species at low ecosystem variability without causing the loss of other species indicates the niche differentiation, tend to reduce competition so that exclusion does not occur and directly increases species diversity.

The search for the causal explanation of species diversity and ecosystem variability is one of the key questions in modern community ecology research. In this study we considered annual mean data of biotic, abiotic and climatic factors for ecosystem variability analysis. It would be more interesting to consider seasonality in the analysis. To our knowledge, this is the first report of causal relationship between ecosystem variability and phytoplankton diversity using such a long-term and regularly sampled data set of a marine ecosystem. Our ability to solve this puzzle of phytoplankton diversity increase at Helgoland Roads will help to understand the role of long-term environmental heterogeneity and inherited complexity of community to maintain the biodiversity.

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Supplementary information



Fig. S1 Efficiency of 26 species sub-community to represent the entire community at Helgoland Roads. Each black filled circle represents average across 10 replicate drew from a single data set and vertical bars indicate the standard deviation. The green solid line gives the ratio of replicate to the 26 species sub-community, with 1 representing a perfect match. Upper and lower green dashed lines indicate +10% and -10% deviations of ratio from 1, respectively. Upper and lower yellow dashed lines indicate +25% and -25% deviations of ratio from 1, respectively.

CHAPTER IV

To share or not to share? Phytoplankton species coexistence puzzle in a resource-limited ecosystem

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Abstract

The predictions of the competitive exclusion principle constitute an ecological puzzle for phytoplankton ecosystems. Here we present a synthesizing-unit based competition model taking co-limitation into account. We explore the role of environmental change on species coexistence on a seasonal and a decadal time scale by linking the model forcing to the Helgoland Roads Time Series data sets. Our study confirms that more species than limiting resources can coexist with seasonal variations of environmental conditions. This supersaturation is related to periodic changes in species biomass, variation in interspecific competition and niche configuration, nonlinear functional response, and the resource supply within the convex hull of species resource uptake. Changes in environmental conditions within realistic ranges do not prevent the coexistence of species but rather changes species biomass and turnover time. Our results might be helpful to answer the complex questions on species diversity maintenance in nature.

Key-words: Co-occurrence, nutrients, limitation, plankton, Helgoland Roads.
Introduction

Understanding species coexistence is one of the most important fundamental research objectives in community ecology (Hartig et al., 2014; Laird and Schamp, 2006). The mechanisms of species coexistence have long puzzled ecologists (Segura et al., 2011) and the greatest challenge lies in reconciling of coexistence with the competitive exclusion principle (Laird and Schamp, 2006). The competitive exclusion principle (Hardin, 1960) states that the maximum number of coexisting species cannot exceed the number of limiting resources in equilibrium. This claim however contradicts the observations of species number in plankton communities, which led to the formulation of the paradox of plankton (Hutchinson, 1961). Hutchinson (1961) pointed out that in planktonic systems many phytoplankton species can coexist while it seemed that only a few resources (i.e. light and nutrients) are limiting. Since the formulation of the paradox of plankton, many mechanisms have been proposed to explain phytoplankton coexistence, for example, spatial and temporal effects of various factors, such as the effect of light on plankton growth (Wilson, 1988), seasonal variation of resourcesupply (Armstrong and McGehee, 1980), impact of mesoscale structures such as vortices in hydrodynamic flows (Bastine and Feudel, 2010), resource competition (Segura et al., 2013; Sommer, 1999) and size structures of species (Segura et al., 2011). While all above mentioned mechanisms rely on heterogeneities in the environment, Huisman and Weissing (1999) showed that non-equilibrium coexistence of species is possible in a homogenous environment. However, it is still unclear to which extent and at which scales these mechanisms contribute to the observed coexistence of species (Hartig et al., 2014). For the number of species to exceed that of resources, termed "supersaturated coexistence" (Schippers et al., 2001), species should differ in their resource-use abilities (Dutta et al., 2014). Since the formulation of the competitive exclusion principle a large number of modelling studies have been conducted to explain the species coexistence taking resource limitation into account.

There are two basic concepts to modelling resource limited species dynamics in the presence of several resources: Liebig's law of the minimum (Liebig, 1840) and the multiple resource limitation hypothesis (Gleeson and Tilman, 1992). Liebig's law of the minimum (Liebig, 1840) states that only a single resource limits species' growth at any given time and for many decades it was the dominant theory shaping how scientists viewed phytoplankton ecology (Arrigo, 2005). This idea of limitation of species growth by a single resource has been replaced by the realization that phytoplankton growth can be limited by several resources simultaneously.

Most of the species resource competition models are based on Liebig's law of the minimum (Tilman, 1982). However, supersaturated coexistence of species in a multiple resources limited environment can also be shown based on a product of several Monod functions (Huisman and Weissing, 2002). But the growth rates based on Liebig's law of the minimum and the product of several Monod functions both lack a good fit to data (Sperfeld et al., 2012). Thus, Dutta et al. (2014) developed a new approach allowing "supersaturated coexistence" of species in a multiple resource-limited ecosystem, based on the concept of a synthesizing unit (SU). This SU converts resources into biomass, fulfilling all stoichiometric requirements for the biomass formation (Kooijman, 2010). A SU forms a product according to the rules prescribed by classical enzyme kinetics, with some modifications: the kinetics is specified in terms of arrival fluxes of the substrate molecules to the enzyme, not in terms of substrate complexes. The enzyme-substrate dissociation rate is assumed to be zero and a SU can bind an arbitrarily large number of substrates and transfer them into products. Moreover, recent experimental results on resource co-limitation theory applied to herbivorous consumers have shown that species growth kinetics based on the concept of SU fits the data better than the product law growth rate (Sperfeld et al., 2012). In addition, this approach obeys mass conservation. All the nutrient uptake processes are assumed to be irreversible. Such models produce all known possible outcomes of competition (i.e. competitive exclusion, heteroclinic cycles, and equilibrium).

Due to the prediction of competitive exclusion principle species coexistence in a limited number of resources has been studied widely. However, studies on phytoplankton species coexistence in a multiple resources limited ecosystem based on the concept of a synthesizing unit are rare. Moreover, no previous modelling studies on species coexistence compared the output of species competition with real data sets. Many studies found different behavior in species dynamics in the supersaturated state (e.g. identity of the dominant species change, cycle in species abundance with peaks every couple of years etc.). These findings might hold true for a real data set. For example, long-term phytoplankton data sets from the Helgoland Roads Time Series also show (Fig. 1) that different species might behave differently on the long-term (i.e. few species peaks in species abundance after few years interval and few species peak every year). Therefore, comparison of model outputs with the observed data might offer more realistic and exciting insights on species coexistence from the theoretical studies. Here, for the first time, we test the possibility whether the number of coexisting phytoplankton species can exceed the number of known limiting resources in a shallow-sea ecosystem taking the simultaneous co-limitation based on the concept of a SU into account.

We also test the behaviour of long-term species coexistence by changing environmental forcing based on the Helgoland Roads Time Series data sets (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). In addition, we discuss our species dynamics produced by the model with the real phytoplankton data (Fig. 1) from the Helgoland Roads Time Series Station.



Fig. 1 Long-term monthly abundance of some selected phytoplankton species from the Helgoland Roads Time Series data sets (Wiltshire and Dürselen, 2004)

This study aims to answer the following questions:

- (i) Does the number of coexisting phytoplankton species, exceed the number of limiting resources in a multiple resource limited ecosystem?
- (ii) If yes, then what causes this supersaturated coexistence?
- (iii) What are the consequences of long-term coexistence of species?
- (iv) What happens to species coexistence if environmental forcing is changed?

Materials and methods

Model description

The main goal of our study is to explain the phytoplankton species coexistence in a multiple resource limited ecosystem. More specifically, we aim at understanding how the number of phytoplankton species coexisting can exceed the number of limiting resources. To do so, we based our work on the species competition model developed by Dutta et al. (2014). We extended this model for phytoplankton species in a shallow-sea ecosystem. The model considers interactive effects of three essential nutrients (SiO₂, PO₄ and NO₃), temperature and light on the phytoplankton species dynamics. The model equations for *n* species and *k* nutrients in a shallow-sea system are described as:

$$\frac{dN_i}{dt} = N_i \left(\sum_{j=1}^k G_{ji} - (D + m_i) \right) \qquad i = 1, 2, \dots, n \tag{1}$$

$$\frac{dR_j}{dt} = D \left(S_j - R_j \right) - \sum_{i=1}^n I_{ji} N_i \qquad j = 1, 2, \dots, k \tag{2}$$

where N_i denotes the biomass of species *i* and R_j denotes the concentration of resource *j*. The dynamics of species *i*, $\left(\frac{dN_i}{dt}\right)$, includes growth G_{ji} , mortality m_i , and the dynamics of resource *j*, $\left(\frac{dR_j}{dt}\right)$, includes the nutrient input from a reservoir below the mixed layer S_j with a thermocline exchange rate *D* and the uptake rate I_{ji} by phytoplankton species *i*.

The key part of the model is the formulation of the phytoplankton species' growth G Eq. (3) as a function of nutrients, temperature and light based on a SU approach, as well as, the nutrients uptake rate Eq. (4).

$$G_{ji} = \mu_{ji} f_i(R_1, R_2, R_3) f(T) f(L)$$
(3)
$$I_{ji} = U_{ji} f_i(R_1, R_2, R_3)$$
(4)

where μ_{ji} is the maximum growth rate of species *i* for resource *j* and U_{ji} is the maximum uptake rate of nutrient *j* by species *i*. The term $f_i(R_1, R_2, R_3)$ is the functional response of species *i* to *k* nutrients based on SU (Dutta et al., 2014; Kooi et al., 2004; Muller et al., 2001). The corresponding functional response for species *i* to three nutrients (SiO₂, PO₄ and NO₃) with their half saturation constants (K_{1i} , K_{2i} and K_{3i} respectively) and the concentration of the 3 resources in the water column (R_1 , R_2 and R_3 respectively) can be written as follows according to Dutta et al. (2014).

$$f_i(R_1, R_2, R_3) = \frac{1}{1 + \frac{K_{1i}}{R_1} + \frac{K_{2i}}{R_2} + \frac{K_{3i}}{R_3} - \frac{1}{\frac{R_1}{K_{1i}} + \frac{R_2}{K_{2i}}} - \frac{1}{\frac{R_2}{K_{2i}} + \frac{R_3}{K_{3i}}} - \frac{1}{\frac{R_1}{K_{1i}} + \frac{R_3}{K_{3i}}} + \frac{1}{\frac{R_1}{K_{1i}} + \frac{R_2}{K_{2i}} + \frac{R_3}{K_{3i}}}$$
(5)

In Eq. (3) f(T) and f(L) are factors expressing the impact of temperature and light on the growth rate of the species. The effect of temperature on the species growth rate is described by the Van't Hoff rule and thus the temperature function f(T) is written as:

$$f(T) = (Q_{10})^{(T(t)-10)/10}.$$
 (6)

Equation 6 asserts that a change of the temperature by 10° will multiply the rate at mean temperature by a factor Q_{10} . For phytoplankton species Q_{10} varies between 1.3 and 4 (Freund et al., 2006). The temperature T(t) is the seasonal temperature forcing and described as follows eqn 7 by Freund et al (2006).

$$T(t) = T_m + \Delta T \sin(\Omega t + \varphi)$$
(7)

where mean temperature $T_m = 10.10^{\circ}$ C, $\Delta T = 6^{\circ}$ C, $\Omega = 2\pi/(365 \text{ days})$, and $\varphi/2\pi = 0.59$ were adapted from a fit to the Helgoland Roads time series data sets.

The light function f(L) expresses the effect of light on species' growth and can be written according to Li et al. (2010):

$$f(L) = \left[1 - \exp\left(\frac{-\alpha I_{PAR}(t)}{\delta}\right)\right] \exp\left(\frac{-\beta I_{PAR}(t)}{\delta}\right)$$
(8)

where α and β are the initial slope of the P-I curve and the photo inhibition coefficient respectively, and δ denotes the species' maximum specific growth rate under light saturation. All the simulations were performed using a fixed set of parameters values (Table S1) for the phytoplankton ecosystem. I_{PAR} is calculated as a function of time dependent sunshine hours (*SH*) and Secchi depth (*SD*) as follows using the formula from French et al. (1982).

$$I_{PAR}(t) = 7.5 SH(t) e^{-\frac{1.7}{SD(t)}}$$
(9)

Both sunshine hours SH(t) and Secchi depth SD(t) are seasonal forcing described as Eq. (10) and Eq. (11) respectively.

$$SH(t) = SH_m + \Delta SH \sin \left(\Omega_{SH}t + \varphi_{SH}\right)$$
(10)
$$SD(t) = SD_m + \Delta SD \sin \left(\Omega_{SD}t + \varphi_{SD}\right)$$
(11)

where mean sunshine hour $SH_m = 5.51$, $\Delta SH = 2.98$, $\Omega_{SH} = 2\pi /(365 \text{ days})$, $\varphi_{SH}/2\pi = 0.75$, mean Secchi depth $SD_m = 3.79$, $\Delta SD = 1.59$, $\Omega_{SD} = 2\pi /(365 \text{ days})$, and $\varphi_{SD}/2\pi = 0.75$ were adapted from a fit to the Helgoland Roads time series data sets.

Observed data

We used the Helgoland Roads Time Series data sets for environmental forcing in the model. We also used this data set to discuss the species dynamics produced in our competition model. The Helgoland Roads Time Series Station (54°11.3′ N, 7°54.0′ E) is one of the longterm ocean monitoring sites of Biologische Anstalt Helgoland which was started in 1962. Work daily monitoring of biological, chemical and physical parameters has been carried out continuously at this station since it has started, and is one of the longest aquatic data sets in history (Wiltshire and Dürselen, 2004). Water samples are collected from the surface, and temperature and Secchi depth (as a measure of transparency) are measured *in situ*. Samples are preserved for further analysis of nutrients, phytoplankton and zooplankton. The nutrients (phosphate, ammonium, nitrate and nitrite) are measured using the standard colorimetric methods described by Grasshoff and Almgreen (1976) immediately on a filtered sub-sample from the daily Helgoland Roads surface water sample (Wiltshire et al., 2010).

We ran five models by taking the environmental data from the Helgoland Roads Time Series Station. We split the 1962 to 2010 time period into 5 time blocks i.e. 1962-1970, 1971-1980, 1981-1990, 1991-2000 and 2001-2010, and ran one model for each time block. Later we compared how different environmental forcing affects the species dynamics and coexistence.

Parameter estimations

To estimate a range of each parameter values we performed Markov chain Monte Carlo (MCMC) simulation (Gilks et al., 1995) on observed species data in OpenBUGS software (Thomas et al., 2006). The OpenBUGS software was linked with the statistical computing software R (R Development Core Team, 2010) by R2OpenBUGS package (Sturtz et al., 2005) for the analysis. We used a prior distribution of each parameter of the model in MCMC. With this method extreme values of each parameter were eliminated. Therefore, we had a range of parameter values with which supersaturated communities were found. Later with Monte Carlo search we estimated the best parameter set for this study.

Results

The results of our simulations are summarized under the guise of our overarching questions.

Does the number of species coexists exceed the number of limiting resources?

Our main objective of this paper was to study the possibility of more species coexistence than the number of limiting resources. We studied this question by using the competition model based on SU-based growth rate, considering the multiple resource limitation hypothesis. Our model simulations confirm that more phytoplankton species than resources may coexist. We emphasize that in contrast to previous studies this coexistence persists when taking a seasonal variation of environmental condition into account.

Fig. 2a shows different oscillatory states of four species biomass over time. This suggests that simultaneous co-limitation of multiple resources formulated using the SU concept does not prevent the emergence of a supersaturated coexistence of species.



Fig. 2 Coexistence dynamics of four species competing for three resources. (a) Long-term behavior of four species biomass. (b) Four species dynamics in last 10000 days of the simulation. (c) The corresponding total biomass of four species in last 10000 days.

What causes supersaturated coexistence in a multiple resource limited ecosystem?

We found the following reasons for supersaturated coexistence of species in the model: *Non-equilibrium state*: Competition for resources generates periodic oscillations in species biomass and allows the coexistence of more species than the number of resources. Here, for silicate, species 1 has the lowest half saturation constant (k) and species 4 has maximum growth rate (μ). Therefore, species 1 is a strong competitor for silicate but species 4 is limited by silicate. Similarly, species 2 is a strong competitor for phosphate but species 3 is limited by phosphate. Species 3 is a strong competitor for nitrate but species 1 is limited by nitrate. Species 4 is the intermediate competitor for phosphate and nitrate. This type of competition for three resources by four phytoplankton species (i.e. if a species is a strong competitor for one resource then its' growth is limited by another resource) generates cyclic dynamics in their biomass and leads to a cyclic succession of species. *Resource requirements, competition and niche differentiation*: In our model, if one species has maximum requirements for a particular resource, then it has intermediate and minimum requirements for other resources. These types of resource requirements i.e. differences in feeding traits is one of the important reasons for observed supersaturation.

In addition, differences in resource requirements of species indicate the variation in their interspecific competition ability. This suggests that the four species considered in the model have different niche configuration and thus, competitive exclusion does not occur.

Functional response of species: In our model species exhibit nonlinear functional response. This functional response causes species growth rates to relate to resource abundance in a nonlinear manner. As resources fluctuate over time the species with the more nonlinear functional response is better at exploiting the resource whose abundance is lower and the species with the less nonlinear functional response is better for exploiting the resource when resource abundance is higher. Thus, temporal fluctuations in the resource allow coexistence via resource partitioning.

Nutrient uptake rate and supply: In our model the nutrient supply S_j lies within the convex hull of resource uptake by species. Thus, competitive exclusion does not apply and instead, the species "cooperate" in creating an environment equally favorable for all.

What are the consequences of long-term supersaturated coexistence of species?

To understand the consequences of long-term supersaturated coexistence, we closely observed the species dynamics generated by our model. The model indicates that there is always one dominant species while the other three species have lower biomasses. Therefore, they do coexist. Further, the identity of the dominant species changes over time within the community. The seasonal forcing applied in the model results in a biomass fluctuation periodicity which repeats every one or some years later (Fig. 3). Species with the periodicity of P number of years produce P lines in the phase plane diagram before it returns to its starting point. In the phase plane diagrams (Fig. 3a, b), continuous trajectories of species biomass indicate the characteristic oscillation within the community. This continuous oscillation in each species biomass yields an oscillation of the total biomass with nearly constant amplitude (Fig. 2C). The periodicity in species succession within the community in multiple resource limited ecosystem supports the possibility of supersaturated coexistence.



Fig. 3 Phase plane diagram consisting of three different species for last 10000 days as axes from different angles. (a) Phase plane for species 1, 2 and 3. (b) Phase plane for species 2, 3 and 4.

What happens to species coexistence if environmental forcing is changed?

In order to understand how changes in environmental conditions (i.e. nutrients, temperature and light) affect species coexistence, we changed the model forcing based on the Helgoland Roads Time Series data sets (i.e. environmental forcing of 1970s, 1980s, 1990s, 2000s and 2010s). Our simulations show that, despite changes in environmental forcing, all four species can coexist when competing for three resources (Fig. S1). These changes, however, have a significant impact on species biomass dynamics. With different environmental forcing, species produce different types of limit cycles in phase plane diagram (Fig. 4). The species succession pattern in different simulations remains similar but the dominant species identity changes within the same forcing over time (Fig. 5). We have also shown that in a supersaturated state the turn over time of a species might vary. For example if one species shows a peak at the beginning of the year, that species might not show the peak at the same time of the next year (Fig. 6). In addition when a species enters in its long-term behavior, it might show a major peak after some year's interval, for example one major peak in every fourth year (Fig. 6).



Fig. 4 Phase plane diagram consisting of three different species for last 10000 days as axes from different angles. (a) Phase plane for species 1, 2 and 3. (b) Phase plane for species 2, 3 and 4. Different colors in both phase plane diagram indicate the trajectories of species generated by the model with different environmental forcing.

Discussion

We used and extended the multiple species-multiple resources competition model developed by Dutta et al. (2014) employing an SU-based growth rate to simulate phytoplankton species dynamics in a multiple resource limited system. The primary goal of this study was to test whether the number of coexisting species can exceed the number of known limiting resources in a multiple resource-limited planktonic ecosystem. We considered a system where four species compete for three interactive essential resources in order to examine this hypothesis.



Fig. 5 Dynamics of the four species in different simulations with different environmental forcing. Different colours indicate different species and different line types indicate different environmental forcing.

Our study shows that the number of plankton species coexisting can indeed exceed the number of limiting resources in a multiple resource-limited system. The periodic biomass oscillations resulting from the competition of four species for three resources allow the coexistence of more species than the number of resources in the long-term. Huisman and Weissing (1999), Huisman et al. (2001), Huisman and Weissing (2002) and Baer et al. (2006) found that competition for resources produces periodic as well as chaotic fluctuations in biomass which enable species to coexist. In contrast to their studies, we considered a

planktonic ecosystem in seasonally changing environment and showed this periodic forcing does not prevent supersaturation to occur. The periodic oscillation in species biomass which is observed in nature due to the seasonal forcing and also found in this study is a plausible mechanism for species coexistence. Our finding is compatible with the findings of Dutta et al. (2014) who also found that more species than limiting resources may coexist by producing a periodic oscillation in their biomass but without seasonal forcing. In addition, variation in resource requirements of species causes the variation in interspecific competition and leads to niche differentiation constituting another cause for stable coexistence (Büchi and Vuilleumier, 2014). In our model, species exhibit non-linearity in their functional responses. This non-linearity reduces competition among the species for resources and allows stable coexistence (Armstrong and McGehee, 1980).



Fig. 6 Change in dominance and turnover time of species 1 in different simulations for last 10 years of simulations for the same species. Vertical blue lines indicate the one year interval. Different dots indicate the peak at every 365 days.

We also observed that the long-term species coexistence holds, even if we change the forcing within a realistic range. Dutta et al. (2014), Huisman and Weissing (1999), Huisman et al. (2001), Feng et al. (2011), Schippers et al. (2001) and Kishi and Nakazawa (2013) also

changed the range of environmental forcing with respect to nutrients in the model and found a supersaturated state in species coexistence within a certain range. Environmental forcing exceeding a certain range limited the more species coexistence than the number of limiting resources in their studies.

Comparison of model outputs with empirical data: Our findings show that in the supersaturation state the identity of the dominant species within the community varies over time. This is in line with the findings of Dutta et al. (2014) and Huisman and Weissing (1999). Moreover, we observed cycles in species biomass with peaks every couple of years and changes in the identity of the dominant species. In order to check these model implications we analyzed the long-term real phytoplankton data sets. To infer a relation between model outputs and empirical data we should simply find the similar pattern of peak in species abundance and repetition of peak in empirical data as it was found in our model simulations. To do this, firstly, we plotted the long-term change in species abundance to check their behaviour i.e. change in species dominance and timing of peak abundance. Secondly, we observed the change in species abundance at different environmental conditions. The long-term phytoplankton data (Fig. 1) from Helgoland Roads shows that Asterionellopsis glacialis, Thalassionema nitzschioides, Brockmanniella brockmannii, Odontella aurita and O. regia species show major peaks at several years interval which is similar to our model simulations. A. glacialis shows peak in abundance sometimes after 2 to 3 years interval and sometimes after 5 to 8 years interval. T. nitzschioides generally peaks after 2 to 4 years interval but sometimes 7 to 8 years interval and *B. brockmannii* generally shows the peak in abundance every 4 to 6 years interval. The diatoms Rhizosolenia imbricate and *Guinardia delicatula* show the peak in their abundance during the period from June to August and therefore, are known as summer species. On the other hand, Paralia sulcuta shows the peak in abundance during winter. These species show a major peak in abundance at least once in a year. In the Helgoland Roads data sets there are many other species with similar behaviour which are in accordance with our model implications.

Similar type of repetition of peak in biomass and dominance of species also observed by Dakos et al. (2009) where this type of scenarios were shown due to chaos within the community. Dakos et al. (2009) observed peak abundance of *Asterionella kariana* varies year to year and *G. delicatula* can display several peaks per year at the time series of the Dutch coastal zone. A diatom species, *A. formosa* in Lake Windermere of UK also showed year to year variation in the timing of dominance (Maberly et al., 1994). Another study (Smayda, 1998) on time series data of phytoplankton in Narragansett Bay of USA confirms the

irregular timing of the peak in abundance of species (i.e. *A. glacialis*) and a regular peak at certain time interval (i.e. *Thalassiosira nordenskioeldii* peak at 5-year interval).

These types of scenarios of peaks in species biomass might evolve due to the timing and arrival flux of different resources, and species specific requirements for those resources. Arrival flux of a particular resource might cause the peak of a species that has the highest requirement for that resource. For example, Freund et al. (2006) found that resetting the temperature within the seasonal cycle causes an interchange of bloom and non-bloom modes of phytoplankton which might hold true for nutrients also.

We examined the response of phytoplankton species in different environmental conditions using the Helgoland Roads Time Series data sets. We present results for four taxa: *Chaetoceros spp, A. glacialis, P.sulcata* and *T. nitzschioides* (Fig. S2). All these species change their abundance in different environmental conditions. For example, *C. spp* shows an increase in abundance in recent decades while *T. nitzschioides* shows a decrease. In our model simulations we also found that species change their biomass in different environmental forcing. We admit that the significance of our claimed signature on species peak abundance, repetition of peak and response of species at different environmental conditions needs a more careful statistical evaluation. However, we consider the analyses described in this paper to be a first valuable step towards a better understanding of species coexistence integrating model simulations and empirical data.

In conclusion, what have we learned? More phytoplankton species can coexist than the number of limiting resources even when the system is simultaneously co-limited by resources and species growth is formulated based on SU. This supersaturated state can evolved due to periodic fluctuation in species biomass, variation in interspecific competition and niche configuration, nonlinear functional response of species and resource supply rate. This coexistence of more species than limiting resources occurs considering additionally seasonal variation of environmental condition.

Our study considered a realistic environment of a shallow sea ecosystem. This is the first explanation for phytoplankton species coexistence in a shallow sea system which violates the competitive exclusion principle in a multiple resource-limited system. This study has created new avenues for further research. For example, species coexistence study taking consideration of two diatom species competing for silicate, nitrate and phosphate, and two dinoflagellate species competing for nitrate and phosphate would be interesting. Addition of stochastic terms, and combination generalist and specialist species in the model will be our next goal. Addition of more species with fast and slow growth rates at the beginning and also at different time intervals of the simulations might produce more exciting insights on phytoplankton species coexistence.

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Supplementary information

Fig. S1 Coexistence of four species competing for three limiting resources in a multiple resource limited system with different environmental forcing based on the Helgoland Roads Time Series data set.



Fig. S2 Comparison of phytoplankton species abundance at different time period which are reflecting different environmental conditions at the Helgoland Roads Time Series Station. Displayed as: a) *T. nitzschioides*, b) *A. glacialis*, c) *P. sulcata* and d) *C. sp*

Table S1 Parameters values used for the simulations: D = 0.10, $m_1 = 0.012$, $m_2 = 0.011$, $m_3 = 0.010$ and $m_4 = 0.010$, $S_1 = 8$, $S_2 = 0.50$, $S_3 = 8$, $Q_{10} = 1.5$, $\alpha = 0.3$, $\beta = 0.0002$, and $\delta = 0.025$.

μ				Ι				K			
0.15	0.21	0.21	0.24	0.27	0.3	0.22	0.27	1.33	2.13	2.23	2.25
0.011	0.012	0.014	0.011	0.013	0.017	0.019	0.017	0.14	0.08	0.13	0.09
0.24	0.17	0.19	0.13	0.31	0.22	0.28	0.17	2.1	2.28	1.32	1.7

The other parameters μ_{ji} , I_{ji} , and K_{ji} for each resource *j* and species *i* are given in the three matrices μ , *I*, and *K*, where rows indicate the three different resources (i.e. silicate, phosphate and nitrate, respectively) and columns indicate different species.

Explaining seasonal phytoplankton variability by abiotic and biotic factors in a shallowsea ecosystem

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Abstract

Seasonal variability in phytoplankton abundance is driven by different biotic and abiotic factors. Especially in the context of anthropogenically driven global changes, it is necessary to understand which parameters explain the variability in phytoplankton dynamics. Here, we develop a Bayesian regression model to quantify the relative importance of different biotic and abiotic factors in explaining the seasonal variability of phytoplankton abundance. We applied this model to long-term quality-controlled phytoplankton species abundance and environmental data of the Helgoland Roads Time Series Station (North Sea). Our results show that, during winter, biotic factors are more important than abiotic ones (explaining 9.8% and 7.5% of phytoplankton variance, respectively) and vice versa during the rest of the year (8.2% and 9.6%, respectively). Among different biotic and abiotic factors, diatom bio-volume and nitrate concentration explain most of the variability in phytoplankton abundance throughout the year (6.5% and 2.1%, respectively). Interestingly, the percentage of explained variance is higher under poor growth conditions (31%) than under favorable growth conditions (23%). During poor growth, dinoflagellates bio-volume and nitrate concentration explain most of the variability in phytoplankton abundance (5.7% and 2.8%, respectively), whereas during favorable growth, non-chain-forming diatom bio-volume and nitrate concentration are the major explanatory factors of variability (9% and 2.7%, respectively). Using an exceptionally long-term and comprehensive data set (covering 52 years and 360 recognized phytoplankton species), our analysis explains an unusually high level of variance in total, 18% of variation in phytoplankton abundance through seasonal variation in biotic and abiotic factors.

Key-words: Phytoplankton, biotic forcing, abiotic forcing, MCMC, Helgoland Roads.

Introduction

Phytoplankton is a diverse group of photoautotrophs, comprising tens of thousands of species globally (Mutshinda et al., 2013a) and, despite making up less than 1% of the plant biomass on earth, it accounts for almost 50% of the global primary production (Field et al., 1998). Through diverse strategies of nutrient uptake and storage, phytoplankton affect fluxes of elements in the ecosystem (Falkowski et al., 1998), serve as a major source of trace gases such as dimethyl sulfide that influence climate (Andreae and Crutzen, 1997; Charlson et al., 1987), and play a fundamental role in global biogeochemical cycles maintenance (Follows et al., 2007). Phytoplankton can photosynthetically fix atmospheric carbon dioxide into organic matter (Sunda, 2012) which is sequestered in the deep ocean through the biological pump (Muller-Karger et al., 2005; Tedesco and Thunell, 2003). Thus, considering the ecological importance of phytoplankton, a number of studies focusing on the factors that explain phytoplankton dynamics have arisen over the last decade (Boyd et al., 2010; Wiltshire et al., 2010).

The relative importance of the different factors driving phytoplankton growth in shallow coastal seas depends on the depth, prevailing currents, and riverine inputs to the system (Wiltshire et al., 2015), all of which are subjected to temporal variation (Calijuri et al., 2002). Generally, light availability, temperature, salinity, pH, and the concentration of macronutrients such as nitrate, phosphate, and silicate are important regulators of phytoplankton biomass, productivity, and community structure (Mutshinda et al., 2013b). In addition, zooplankton, the most important secondary producers in oceans, depend on phytoplankton for food and thereby also influence phytoplankton abundance through topdown control (Chassot et al., 2010). However, being able to understand how phytoplankton community dynamics are influenced by environmental conditions remains a major challenge for ecologists (Edwards et al., 2013). Given the large number of biotic and abiotic parameters simultaneously fluctuating, it is often impossible to extricate the few parameters driving a system. For example, large scale changes in phytoplankton species distribution in the North Sea over the last decades have been identified (Wiltshire et al., 2015). Phytoplankton production showed a marked increase across this region during the mid- to late 1980s (Edwards et al., 2001; Reid et al., 1998) and changes in phenology (Greve et al., 2005; Wiltshire and Manly, 2004) and species composition (Boersma et al., 2007) are also observed in this area. Although these biotic changes are accompanied by variations in environmental conditions, it often remains challenging to establish a causal relationship between biotic and abiotic changes.

The practical way to study changes in phytoplankton communities is the analysis of detailed time series of taxonomic and environmental data (Irwin et al., 2012), but very few long-term biological data sets exist for European waters (McQuatters-Gollop et al., 2007). Few pelagic data sets with daily resolution exist, but they often do not include taxonomic identification to the species level and measurements of physico-chemical parameters simultaneously (Wiltshire et al., 2010). Further, the lack of long term quality controlled data on phytoplankton and environmental parameters largely reduces the extent to which the causes of variability in phytoplankton dynamics can be studied. In this context, the Helgoland Roads Time Series (North Sea, Germany) which contains daily measurements since 1962 is unique and one of the richest temporal marine data sets available to study the relationship between phytoplankton variability and environmental condition (Wiltshire et al., 2010).

Statistical modelling of long-term observational data on phytoplankton and environmental parameters can be a valuable tool to address how different environmental factors shape phytoplankton community dynamics. But a straightforward classical regression analysis of the abundance of many phytoplankton species as a function of environmental conditions is unlikely to succeed to achieve the research goal (Mutshinda et al., 2013a). Bayesian regression modelling approach, on the other hand, has the advantage to exploit diverse sources of information to draw inferences on large numbers of latent variables that describe complex relationships (Clark, 2004). Here we performed a multivariate regression model in Bayesian interference to understand how different biotic and abiotic factors explain the seasonal variability in phytoplankton community using the Helgoland Roads Time Series Station data sets.

Materials and methods

Data source

In order to understand the role of biotic and abiotic factors in controlling phytoplankton community dynamics, we used data of phytoplankton and zooplankton abundance, nutrient concentrations, secchi depth, temperature, and salinity from the Helgoland Roads long-term data sets. The Helgoland Roads Time Series Station (54°11.3' N, 7°54.0' E) is located between two islands, i.e. Helgoland and Düne (Fig. 1), in the North Sea. Long-term monitoring of biological, chemical, and physical parameters has been carried out continuously at the Helgoland Roads on a daily basis since 1962, and is one of the longest aquatic data sets in the history (Wiltshire and Dürselen, 2004). Water samples are collected from the surface and preserved for further analysis of nutrients, phytoplankton, and

zooplankton. The nutrients (phosphate, ammonium, nitrate, and nitrite) are measured using the standard colorimetric methods described by (Grasshoff and Almgreen, 1976) immediately on a filtered sub-sample from the daily Helgoland Roads surface water sample (Wiltshire et al., 2010). The phytoplankton sub-sample from the Helgoland Roads sample is preserved in a brown glass bottle with Lugols' solution. The samples are later on counted under an inverted microscope using Utermöhl settling chambers and individuals are identified to species level when possible, or otherwise differentiated into defined size classes (Wiltshire and Dürselen, 2004; Wiltshire et al., 2010) Zooplankton time series started in 1974 and samples are collected twice a week (Greve et al., 2004; Wiltshire et al., 2015). Secchi depth as a measure of water transparency and temperature are measured directly on station (Wiltshire et al., 2015).



Fig. 1 Geographical location of the study area. Left panel shows the map of northern Europe with a black rectangular box indicating the location of the German Bight. Middle panel map shows a close up of the German Bight. Black rectangular box indicates the position of Helgoland. Right panel map shows the location of Helgoland Roads Times Series Station (sampling point marked as filled black circle) located between two islands i.e. Helgoland and Düne.

Preliminary analysis

The Helgoland Roads dataset contains over 360 phytoplankton species (Hoppenrath, 2004). As there are some large gaps in species abundance data (details are explained in Wiltshire and Manly (2004)), instead of doing imputation to fill those gaps, we removed all gaps and zero abundances from the data set. Thus the final data set considered for this study contains only the presence data of species.

After data preparation, we checked the univariate dependence of each species to different explanatory variables using linear regression to test if univariate dependence can explain the variation in phytoplankton abundance. This analysis proved that, single explanatory variable is not enough to explain the variation in species abundance. Thus, a multivariate regression model (i.e. multiple explanatory variables) is required to understand the phytoplankton species response to different explanatory variables.

However, multiple regression analyses can be hindered by the complex nature of ecological data, especially when targeted ecological responses are linked to many explanatory variables that are often correlated among each other i.e. multicollinear (Graham, 2003). To avoid the multicollinearity among explanatory variables in the model, variance inflation factors (VIF) were used to exclude the variables with high VIF (VIF \geq 3).

The addition of many explanatory variables in the model might increase the R^2 value even though some of them have no significant role on the response variable. Considering this fact, to identify a set of suitable explanatory variables, we used Akaike Information Criterion (AIC; Akaike (1974)) which suggests selecting a model with the lowest AIC penalty. We calculated AIC penalties for all possible combinations of explanatory variables by increasing and decreasing the regression dimensionality. This process allowed us to select six abiotic factors i.e. temperature, salinity, Secchi depth, silicate, phosphate, and nitrate, and five biotic factors i.e. chain-forming diatom bio-volume, non-chain-forming diatom bio-volume, *Chaetoceros* bio-volume, dinoflagellates bio-volume, and zooplankton abundance as explanatory variables.

We considered three datatype for the model i.e. full data set, as well as favorable and poor growth condition data sets. The full data set contains data of all 50 years after preprocessing (removing data cells with zero abundance and no data). Favorable and poor growth condition data sets (after splitting the full data set) contain all data for favorable growth condition i.e. years with anomalies of environmental parameters > 0 and poor growth condition i.e. years with anomalies of environmental parameters < 0 respectively. To define favorable and poor growth condition, anomalies of all variables were calculated and then multiplied with their respective weight derived by applying a pair-wise comparison matrix in the context of a decision making process known as the "Analytical Hierarchy Process (AHP)" (Saaty, 1990). The product of anomalies and weight of each variable were added and the year defined as favorable growth condition if the sum was positive and otherwise defined as poor growth condition. Models were run as monthly basis, thus creating a total of 12 months × 3 data types = 36 models.

Statistical analysis

We described the species abundance as a linear function of both biotic and abiotic factors using a Bayesian approach to estimate the effects of the selected explanatory variables on the response variable. Letting $N_{i, t}$ and $X_{i, t}$ denote the species abundance (cells L⁻¹) of species *i* and the value of *j*th explanatory variable at time *t* respectively, the model is:

$$N_{i, t} = \alpha_i + \sum_{j=1}^n \beta_{i, j} X_{j, t} + \epsilon_i \quad (1),$$

where α_i is a species-specific intercept, $\beta_{i, j}$ is the effect of the j^{th} explanatory variable on the abundance of species i and ϵ is the residual term. Species abundance data is a $i \times t$ table $Y = [N_{i, t}]$, which represents abundance of i species (i = 1, 2, ..., K) in column at different time in t rows (t = 1, 2, ..., T). Another $j \times t$ data table $M = [X_{j, t}]$ represents the value of j explanatory variable in columns (j = 1, 2, ..., n) at different time in t rows.

Phytoplankton abundance and explanatory variables data were fitted in equation 1 by performing Markov chain Monte Carlo (MCMC) simulation (Gilks et al., 1995) in OpenBUGS software (Thomas et al., 2006) to generate the posterior of model parameters. The OpenBUGS software was linked with the statistical computing software R (R Development Core Team, 2010) by R2OpenBUGS package (Sturtz et al., 2005) for the analysis. For each month we ran 20,000 MCMC iterations with three parallel chains. To remove the dependence on the starting values we discarded the first halves from each Markov chain as burn-in.

To check the consistency in the model output, we generated some artificial data sets by randomizing the species composition from real data sets. To do this, we first picked one random species in each functional group (diatom and dinoflagellates) and then swapped the picked pair of species across groups. After, 100 such swaps, we obtained a data set of randomized group compositions. We generated 50 data sets for each month and ran the model with 11 explanatory variables. The distribution patterns of variance explained in different data sets by models for each month were tested later.

Results

In order to understand which parameters drive the seasonal variability in phytoplankton abundance, we analyzed phytoplankton abundance data in relation to abiotic and biotic factors. We used long-term quality controlled phytoplankton species abundance and 11 explanatory variables (5 biotic and 6 abiotic) data from the Helgoland Roads Time Series Station data sets for our study.

Biotic factors explain maximum variability in phytoplankton abundance during winter

The proportion of variance explained in phytoplankton abundance by all explanatory variables jointly follow a seasonal cycle characterized by a minimum of 14% in October and a maximum of 24% in May (Fig. 2). The explained variance in species abundance increases from February to May and decreases afterwards. Splitting the total variance explained into biotic and abiotic factors shows that during winter biotic factors explain most of the variability (9.1 - 12.21%) in phytoplankton abundance. On the other hand, abiotic factors explain most of the variability during the rest of the year (6.9 - 11%). The only exception was observed for the month of May during which biotic factors are dominant (15%), probably due to high phytoplankton growth. The variability in phytoplankton abundance explained by biotic and abiotic factors separately follows a similar seasonal pattern with a maximum of 15% in May and minimum of 7.1% in October for abiotic factors.



Fig. 2 Proportions of variance explained by abiotic and biotic factors, both individually and collectively in different months. Total variance explained indicates the sum of variance explained by biotic and abiotic factors. Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

Diatom bio-volume and nitrate concentrations are dominant explanatory factors

Decomposing the variance explained by biotic factors into five components shows that different algal groups bio-volume and zooplankton abundance have different patterns of variance explained throughout the year (Fig. 3). Among the biotic factors, diatom bio-volume is the main explanatory factor of variability (4.3 - 12%) in phytoplankton species abundance. Among the three diatom sub-groups, non-chain-forming, and *Chaetoceros spp* bio-volume explain maximum variation (1.1 - 5.1% and 0.9 - 4.2% respectively) in species abundance. Variability in phytoplankton abundance explained by chain forming and non-chain-forming diatom bio-volume are high around January (4.4 and 5.1% respectively) and May (3.4 and 4.1% respectively). Dinoflagellates bio-volume always shows smaller effect on phytoplankton abundance variability. Zooplankton abundance has a lower explanatory power than diatom abundance.



Fig. 3 Proportion of variance explained by five biotic factors in different months. Total phytoplankton bio-volume indicates the sum of variance explained by chain forming and non-chain-forming diatom bio-volume, *Chaetoceors* bio-volume and dinoflagellates bio-volume. Total diatom bio-volume indicates the sum of variance explained by chain forming and non-chain-forming diatom bio-volume, and *Chaetoceors* bio-volume. Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

Among the abiotic factors, nitrate concentration explains most variability (1.8 - 2.7%) in phytoplankton abundance throughout the year, while silicate concentration is also important during the summer months (1.7 - 2.5%) and light availability (Secchi depth) during early spring (2.6%; Fig. 4a and 4b). The variance explained by silicate, nitrate, and phosphate concentrations increase from January to June. Salinity is however less influential compared to Secchi depth and temperature for explaining variability in species abundance.



Fig. 4 Proportion of variance explained by abiotic factors in different months. Top panel shows the variance explained by three physical factors (Secchi depth, temperature, and salinity) and lower panel shows the variance explained by three nutrients (silicate, nitrate, and phosphate concentration). Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

High explained variance predicted in poor growth conditions

We also divided the influence of different explanatory variables on the variability of phytoplankton abundance (Fig. 5) for favorable growth condition and poor growth condition. Overall, the explained variance was higher under poor growth conditions than under good ones. Explained variances during favorable growth condition and poor growth condition also follow a seasonal pattern. During favorable growth condition the maximum explained variance reaches at 28% in May and the minimum is of 20% in December, whereas during poor growth condition the maximum occurs in May (38%) and the minimum in September (22%). In poor growth conditions, most of the variance is explained by dinoflagellates biovolume and by nitrate concentration from April to July (Fig. 6a and 6b). In the first part of the

year chain forming diatom bio-volume, non-chain-forming diatom bio-volume, salinity, temperature, and phosphate concentrations are also important predictors of variability in species abundance. In favorable growth conditions, chain and non-chain-forming diatom bio-volume are the major explanatory factors of variability in species abundance among all biotic factors (Fig. 7a), and nitrate and silicate concentrations among abiotic factors (Fig. 7b).



Fig. 5 Proportion of variance explained by all 11 explanatory variables in poor and favorable growth conditions in different months. Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

Functional grouping of species

We randomized the species composition between the functional groups to test whether the correct group composition turned out to perform better than the randomized ones i.e. rsulting in a higher proportion of variance explained. We then checked the frequency distribution (Supplymentary information 1-3) of explained variance in randomized data sets. Frequency distributions show a normal distribution pattern for each month. The variance explained in each randomized data set occurred for maximum time does not differ significantly from the variance explained in real data set for the respective month. This satisfies our idea of randomization of species between funcitonal groups as we found variance explained in correct group compositutoin also turned out with maximum frequency in the randomized groups.



Fig. 6 Proportion of variance explained in poor growth condition in different months. Top panel shows the variance explained by five biotic factors and lower panel shows the variance explained by 6 abiotic factors. Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

Discussion

We developed a multivariate regression model within Bayesian interference to investigate the role played by different biotic and abiotic factors in modulating seasonal variability in phytoplankton species abundance. We applied this model to the long-term quality controlled data sets from the Helgoland Roads Time Series Station (Raabe and Wiltshire, 2009; Wiltshire and Dürselen, 2004). Phytoplankton and zooplankton abundances as well as environmental variables at the Helgoland Roads Time Series Station show strong temporal variation. Previous studies based on this data set focused on the drivers of phytoplankton growth (e.g. Wiltshire et al. (2015)), classification and drivers of phytoplankton blooms (e.g. Freund et al. (2006); Mieruch et al. (2010); Wiltshire et al. (2008)), and species realized niche (e.g. Grüner et al. (2011)). Wiltshire et al. (2015) showed that the dominating drivers with

regard to timing and phytoplankton abundance at Helgoland Roads are light availability, temperature and zooplankton. Mieruch et al. (2010) classified the bloom types of 16 phytoplankton species based on their annual maximum cell density and bloom specific growth rate. Wiltshire et al. (2008) compared the changes in environmental factors with the changes in the spring bloom phenology and showed that the spring bloom tends to come later in warmer years but that this is not directly correlated with the overall warming trend. Freund et al. (2006) modelled the bloom dynamics in relation with seasonal temperature change and found that blooms are correlated with rapid upward temperature fluctuations and speculate on their possible role as trigger mechanisms. Grüner et al. (2011) developed a new approach to reconstruct the realized niche of phytoplankton species from biotic and abiotic factors.



Fig. 7 Proportion of variance explained in favorable growth condition. Top panel shows the variance explained by five biotic factors and lower panel shows the variance explained by 6 abiotic factors. Vertical lines through each point represent the 70% (top) and 30% (lower) quantiles (the lines are horizontally staggered to avoid overlap).

Variability in phytoplankton assemblages therefore result from a complex interplay of many biotic and abiotic processes (Jamil et al., 2014; Mutshinda et al., 2016; Mutshinda et al., 2013b). Lindemann and St. John (2014) found that, phytoplankton seasonal dynamics in the North Atlantic can be explained by different biotic and abiotic factors. This concept of variability in phytoplankton abundance explained by abiotic variables is found true for a portion of seasonal cycle in our study and there are other periods of the annual cycle when variability is explained by biotic factors. Similarly, Arhonditsis et al. (2004) found that either biotic or abiotic factors are dominant to explain the phytoplankton dynamics during different time of a season. Our analysis shows that biotic factors explain most of the variability in abundance during winter and May; and during the rest of the year abiotic factors explain most of the variability. During winter, nutrient concentrations are high but low light and temperature limit phytoplankton growth. During May, the amplitude of the bloom is strongly influenced by top-down controls. Thus, during winter and May biotic factors are the best predictors of phytoplankton variability at the Helgoland Roads Time Series Station. For the rest of the year, variability in phytoplankton abundance is largely influenced by the abiotic forcing of the system.

The variation in phytoplankton abundance explained by different biotic and abiotic factors changes continuously throughout the year. After splitting the explanatory biotic factors into different algal bio-volume (i.e. chain forming diatom, non-chain-forming diatom, Chaetoceros spp, and dinoflagellates) and zooplankton abundance, we found that algal biovolume is the major factor responsible of seasonal variability in phytoplankton abundance. Algal bio-volume reflects the trophic state of the ecosystem (Jamil et al., 2014) and is thus considered as an important variable to explain the phytoplankton community dynamics (Recknagel et al., 1997). We show that the bio-volume of different algal types has different levels of variance explained in seasonal phytoplankton abundance, which suggests that one algal group is redundant during one part of the year and may not be redundant at others (Rocha et al., 2012). At the end of the winter, microalgae biomass increases which also depletes inorganic nutrients. Moreover, it also reflects the grazing pressure that zooplankton exert on different phytoplankton groups (Huber and Gaedke, 2006). Zooplankton grazing pressure on phytoplankton is highly seasonal (Griffiths et al., 2015) and zooplankton have low abundances throughout the spring with little ability to reduce phytoplankton abundance during the spring bloom (Wiltshire et al., 2015). Early spring, summer, and autumn are characterized by a non-significant relationship between phytoplankton species abundance and

biotic factors which indicates that different algal bio-volume and zooplankton abundance has little influence to explain the phytoplankton dynamics during this period.

Macronutrient concentrations explained most of the variability in seasonal phytoplankton species abundance among the abiotic factors. Diatom is the dominant micro algal group at the Helgoland Roads Time Series Station (Wiltshire and Dürselen, 2004), and silicate and nitrate concentrations are therefore important to correctly predict the variability of diatoms abundance (Recknagel et al. (1997) and Kim et al. (2007)). We found that nitrate concentrations can be a major predictor of seasonal variability in phytoplankton abundance. This result is consistent with the findings of Mutshinda et al. (2013a) for the CARIACO station at which nitrate concentration is the most important predictor of variability in phytoplankton species abundance among the macronutrients. Lagus et al. (2004) also showed that changes in nitrogen levels explained most of the variation in phytoplankton abundance in northern Baltic Sea. This could be due to the correlation between dinoflagellate growth and nitrogen availability (Dagenais-Bellefeuille and Morse, 2013). Diatom abundance might therefore be rather influenced by competition with dinoflagellate for nutrients and only indirectly influenced by nitrogen. Diatoms also require silicate to grow but the variance explained by silicate concentration was lower than that of nitrate, with the exception of the summer months. The variance explained by silicate and nitrate concentrations follows the same seasonal pattern which indicates that there is no tradeoff for silicate relative to nitrate. Throughout the seasonal cycle, phosphate concentration showed less explained variance in phytoplankton abundance compared to nitrate and silicate concentration. This is probably because variability in phosphate concentration was well represented by different algal biovolumes (Jamil et al., 2014) and thus phosphate concentration explained less variability in phytoplankton seasonal abundance. In our multivariate regression model, temperature, salinity and light availability (Secchi depth) accounted for less variance explained compared to nutrients, with the exception of early spring. Temperature explained less variance than Secchi depth which supports the work of Naselli-Flores (2000). Increasing light availability from the end of winter to the beginning of the spring initiates micro algal growth (Wiltshire et al., 2015) because their increase initiate phytoplankton growth. Therefore light and temperature can be good predictor of phytoplankton variability during this time period. Changes in salinity may be related to advection of new water masses and new communities and prompt species succession which may not necessarily be due to environmental forcing. At the Helgoland Roads Time Series Station, salinity is correlated with the Elbe river discharge and negatively correlated with light availability (for details see Wiltshire et al.,

2015). Salinity showed low variance explained probably because variability of salinity was well represented by Secchi depth.

Here, we focused on the seasonal variability of phytoplankton abundance and we did not discuss the effect of changes in different biotic and abiotic factors on phytoplankton abundance. Our present study is based on a first order regression model and we have not looked into the higher order. Extending our first order regression model to a second order regression model could be an interesting avenue for future research as higher order regression model might explains more variance in seasonal phytoplankton species abundance as increase in parameters in the model increase the proportion of variance explained in the model. It will be also interesting to see how these factors can explain seasonal variability of different functional groups or traits.

Our study establishes the pattern of seasonal phytoplankton dynamics in relation with biotic and abiotic factors by analyzing long-term quality controlled densely sampled phytoplankton, zooplankton and environmental data sets. Our results have wider implications for phytoplankton ecology. First, abiotic factors play a significant role to explain seasonal variability of phytoplankton along with biotic factors. Second, different functional groups have different levels of explained variance. Third, the proportion of explained variance varies in poor and favourable growth conditions. This study enables us to identify the important explanatory variables which are associated with the changes in seasonal the abundance of phytoplankton species at the Helgoland Roads Time Series station. Addition of biotic factors are influencing the community dynamics. Different variance explained by the functional groups is a new insight on how they explain the variability within the community. Our findings strongly indicate that changes in biotic and abiotic factors should be expected to have a consequence on the phytoplankton species abundance.

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Supplementary information





Fig. S2 Frequency distribution (%) of variance explained by using randomized species composition data sets in different month. For each month total N=50 randomized data sets were generated. Solid black curves indicate the density distribution of proportion of variance explained for the respective month. Vertical red line indicates the position of variance explained in real data set.



Fig. S3 Frequency distribution (%) of variance explained by using randomized species composition data sets for poor growth conditions in different month. For each month total N=50 randomized data sets were generated. Solid black curves indicate the density distribution of proportion of variance explained for the respective month. Vertical red line indicates the position of variance explained in real data set.
The primary goal of this PhD thesis is to assess the effect of environmental variables on phytoplankton communities based on the Helgoland Roads long-term dataset. The major objectives are: (i) to estimate the long-term seasonal and annual K, (ii) to evaluate the response of long-term phytoplankton diversity to ecosystem variability, and (iii) to quantify the relative importance of different biotic and abiotic factors in explaining the variability of phytoplankton abundance. In this section, it is shown how the five chapters of this thesis rely on each other as well as how they work together and contribute to the thesis objectives. In addition, the main findings of each chapter are discussed.

Addressing the thesis objectives

MS 1 (Chapter I) is the first compilation of the historical N: P ratio data for the German Bight utilizing all available data sources. This study presents the long-term spatial changes in the N: P ratio in the German Bight and shows that it is becoming P-limited. This change is also evidenced by previous studies on the Helgoland Roads Time Series station. Based on the findings of Chapter I, it is hypothesized that these changes alter the K of the system. MS 2 (Chapter II) addresses the seasonal and annual phytoplankton K by analysing how changes in ecosystem drivers may influence such changes. This is the first estimation of the phytoplankton K for a marine ecosystem by using a long-term quality controlled dataset. This manuscript also establishes a relationship between the phytoplankton K and the higher trophic level. Finally, this study highlights the phytoplankton K as a potential ecosystem management tool. Together, these two manuscripts represent the first objective of the thesis (estimate the long-term seasonal and annual phytoplankton K). MS 1 deals with the changes in the nutrient ratio and MS 2 with the effect of these changes on the K of the system, while MS 3 (Chapter III) deals with changes in ecosystem drivers and how they affect the long-term diversity of phytoplankton. In MS 3, the long-term changes to the ecosystem of the Helgoland Roads Time Series station have been estimated using diverse biotic, abiotic, and climatic factors. This study is the first test of the Intermediate Disturbance Hypothesis (IDH) by using a longterm phytoplankton dataset. Considering the relationship between biodiversity and ecosystem variability, MS 4 (Chapter IV) addresses species coexistence. This represents the first phytoplankton species coexistence model in a multiple resource limited system where the number of co-existing species exceeds that of limiting resources. MS 3 and 4 correspond to the second objective of the thesis (evaluate the response of long-term phytoplankton diversity to ecosystem variability). While MS 1-4 deal with the causal relationship between environmental drivers and the phytoplankton community, MS 5 (Chapter V) explains the

variability in community dynamics through biotic and abiotic factors; it corresponds to the last objective of the thesis (quantify the relative importance of different biotic and abiotic factors to explain the variability of phytoplankton abundance).

Discussion of each chapter

1. Long-term change in the N: P ratio in the German Bight (Chapter I)

In the first chapter of the thesis (MS I), the historical archives (1981–2010) of *in situ* N: P ratio for winter and chlorophyll data for the German Bight are combined. The German Bight of the North Sea has been selected for this study, since this area has historically been subjected to anthropogenic changes in nutrient concentrations and ratios (Hickel et al., 1993). Data is gathered from existing databases and then analysed on a decadal basis, resulting in the analysis of long-term geo-spatial changes in the N: P ratio in the German Bight. In addition, the subsequent impact of the elevated nutrient ratio on the chlorophyll distribution in the German Bight is also discussed.

This study finds that the N: P ratio in the German Bight increases in the long run. This indicates an increase in P-limitation for this area. Contrary to chlorophyll concentrations, the N: P ratio increases gradually from nearshore regions to the offshore ones. After the mid-1980s, P-inputs to the coastal waters of the North Sea decreased, while N inputs decreased at a lesser rate (Lenhart et al., 2010). It can be assumed, therefore, that water with a lower P content entered the North Sea system after the 1980s. In the Dutch coastal zone, P loading reduced at a much higher rate than N loading (de Vries et al., 1998)—this is consistent with similarly observed unbalanced reductions of nutrients in the German Bight. This study, however, finds that chlorophyll concentrations in this area increased over the long term, even though the N: P ratio increased. This was also observed by Cadée and Hegeman (1993), who have reported high primary production at the Dutch coast from the beginning of the 1980s to the 1990s. The results show that the N: P ratio is an important predictor of chlorophyll distribution in the German Bight. The study also finds that a high N: P ratio supports higher chlorophyll concentrations in the coastal zone. Lee et al. (1996) have reported that the growth of phytoplankton in the coast is limited mainly by N indicating that P-limitation might not significantly affect the phytoplankton growth.

This study offers an overall picture of the consequence of unbalanced nutrient reduction on the aquatic ecosystem in the German Bight and suggests that further removal of P from the system would lead the German Bight to a more P-limitation state or a drop in N loading may lead the German Bight to a state near the Redfield Ratio. Either way the positive trend in P deficiency might affect the marine food web.

2. Long-term changes in the phytoplankton-carrying capacity (Chapter II)

In the second chapter (MS II), the phytoplankton K has been estimated using the Helgoland Roads Times Series dataset.

Most theoretical studies consider K as a constant (Safuan et al., 2012). However, carrying capacities in nature are variable and many studies have discussed the importance of time dependency of K (Banks, 1993). The K of a population depends on the physical and biotic environment (Arrow et al., 1995), and phytoplankton K cannot be constant because these are in continuous flux. Therefore, this chapter uses the Helgoland Roads dataset and focuses on estimating K and determining whether it is static or variable. In addition, this MS evaluates the relationship between the phytoplankton K and higher trophic levels. Algorithms are developed to estimate the K based on each controlling factor, and a pair-wise comparison matrix has been used for weighting and integrating these.

This study confirms that K should not be considered a constant. In fact, K has been found to be driven by environmental conditions; thus, when subjected to environmental change, K changes accordingly. Estimated K values are low during winter—this is related to the availability of low light in the system. During winter, light is considered to be the limiting factor for phytoplankton growth rather than nutrients, which, in the shallow North Sea, can reach maximum concentrations during this time (Hernández-Fariñas et al., 2014). In summer, less turbulent conditions allow for higher light penetration depths (Richardson, 1989; Wiltshire et al., 2015) and therefore the system can support higher phytoplankton densities.

The inter-annual *K* displays an overall increasing trend ($R^2 = 0.13$, p = 0.03) possibly due to the long-term changes in nutrient concentrations. The Southern Bight (or southern bight) of the North Sea has been subjected to nutrient enrichment since the 1960s, followed by subsequent nutrient reductions since the late 1980s (Lenhart et al., 2010).

This study highlights that the phytoplankton K is positively correlated with the pelagic fisheries of this area. The overall conclusion is that the phytoplankton K varies over time due to changes in environmental conditions—this variability can be estimated and subsequently used for management strategies.

3. Long-term change in phytoplankton diversity in relation to ecosystem variability (Chapter III)

SYNTHESIS

In the third chapter (MS III), the effects of ecosystem variability on phytoplankton diversity has been assessed by using the data from Helgoland Roads. The ecosystem variability has been defined in terms of the heterogeneity of biotic and abiotic factors; it is measured by using a point cumulative semi-variogram method. A Markov chain model has been used to estimate species interactions.

After the mid-1990s, a significant increase in the species diversity in Helgoland Roads was observed. The Intermediate Disturbance Hypothesis (IDH;(Connell, 1978) is one of the most overarching concepts to explain the increase in species diversity in terrestrial and marine environments. The IDH suggests that species diversity increases at the intermediate level of environmental variability. This study tests if the intermediate level environmental variability can explain the increase in the phytoplankton species diversity at Helgoland Roads after the mid-1990s. It finds that ecosystem variability is an important predictor of species diversity. While the 1980s were identified as a period of high ecosystem variability, the last two decades were relatively stable. This high ecosystem variability during the 1980s has also been identified by Beaugrand et al. (2008) in the North Atlantic region. In this study, a negative relationship has been found between ecosystem variability and species diversity, indicating that IDH did not completely explain the species diversity at Helgoland Roads. This study also discusses the reasons: a negative association between ecosystem variability and species diversity, a non-significant relationship between the species occurrence and absence, a significant negative relationship between the probability of occurrence and the probability to outcompete, and the high species occurrence at low ecosystem variability. Other studies suggest that species diversity only peaks at the intermediate level of variability if there is a negative relationship between species absence and occurrence (Petraitis et al., 1989)—this is something I have not observed in this study. While the IDH is considered as the 'equal chance hypothesis', assuming that probabilities of a species occurrence are very similar (Connell, 1978), this study reveals the fact that species differ in terms of their occurrence probabilities.

This is the first report of the causal relationship between ecosystem variability and phytoplankton diversity by using such a long-term and regularly sampled dataset of a marine ecosystem. The revelations of the increases in the phytoplankton diversity at Helgoland Roads from this study will help us to understand the role of long-term environmental heterogeneity and the inherent complexity of a community to maintain the overall biodiversity.

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4. Phytoplankton species coexistence in a multiple resource-limited ecosystem (Chapter IV)

In the fourth chapter (MS IV), the coexistence of the phytoplankton species in a multiple resource-limited ecosystem has been studied. This study has been motivated by the competitive exclusion principle, which predicts that the number of coexisting species cannot exceed the number of limiting resources. Although many studies have been conducted to solve this ecological puzzle, previous works have not considered simultaneous co-limitation synthesizing units (SUs).

Dutta *et al.* (2014) have developed a species competition model, which, for the first time, included the simulation of co-limitation by resources through formulation of the species growth rate based on this SU. Here this competition model has been extended for phytoplankton with the addition of light and temperature as potential limiting forcers. The parameterization of this model has been novel and derived from observed data. After the model has been run, the results are compared with observations from Helgoland Roads. This has not been carried out in the study of Dutta et al. on species coexistence.

This study confirms that more species than limiting resources can coexist with seasonal variations in temperature and light by using a parameter set estimated from the observed data. This is related to periodic changes in species biomass, variations in interspecific competition and niche configuration, nonlinear functional response, and the resource supply within the convex hull of the species resource uptake. Huisman and Weissing (1999), Huisman et al. (2001), Huisman and Weissing (2002), and Baer et al. (2006) have also found that competition for resources produces periodic as well as chaotic fluctuations in biomass, thus enabling species coexistence. This study observes that the long-term species coexistence holds even if various factors of the model vary within a realistic range. This study shows that the dominant species in the community varies over time in the supersaturation state. In addition, it is observed that the cycles of peaks in species biomass are coupled to changes in the dominant species every two years—these findings match the dataset from the Helgoland Roads Time Series station.

This study, for the first time, explains the coexistence of the phytoplankton species in a shallow sea system that violates the competitive exclusion principle in a multiple resourcelimited system and answers some of the complex questions regarding the maintenance of species diversity in nature.

5. Seasonal variability of phytoplankton in relation to biotic and abiotic factors (Chapter V)

In the fifth chapter (MS V), the seasonal variability of phytoplankton abundance in relation to different biotic and abiotic factors is studied. Phytoplankton abundance is highly dynamic and governed by different biotic and abiotic factors. In the context of anthropogenically-driven global changes, it is essential to understand which parameters explain the observed variability. A Bayesian regression model is used to quantify the relative importance of different biotic and abiotic factors to shed light on the observed seasonal variability of phytoplankton abundance.

The results show that during winter, biotic factors are more important than abiotic ones (explaining 9.8% and 7.5% of phytoplankton variance respectively), a trend that is reversed during the rest of the year (8.2% and 9.6% respectively). Among different biotic and abiotic factors, diatom bio-volume and nitrate concentration explain most of the variability in phytoplankton abundance throughout the year (6.5% and 2.1% respectively). Algal bio-volume reflects the trophic state of the ecosystem (Jamil et al., 2014) and is thus considered as an important variable to explain the phytoplankton community dynamics (Recknagel et al., 1997).

Among the abiotic factors, macronutrient concentrations explain most of the variability in seasonal phytoplankton species abundance. Diatoms, which build silica frustules, are the dominant micro algal group at the Helgoland Roads Time Series station (Wiltshire and Dürselen, 2004), and therefore, silicate and nitrate concentrations are important in predicting their abundance (Recknagel et al. (1997) Kim et al. (2007). In addition, this study finds that nitrate concentrations are a major predictor of seasonal variability in total phytoplankton abundance—this is consistent with the findings of Mutshinda et al. (2013a) and Lagus et al. (2004). This study presents the pattern of seasonal phytoplankton dynamics in relation to biotic and abiotic factors using long-term datasets. Further, the identified important variables (i.e. diatom bio-volume and nitrate concentration) are found to be associated with changes in the seasonal abundance of the phytoplankton species at the Helgoland Roads Time Series station.

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SUMMARY

The work presented in this thesis offers an insight into the role of environmental variables on the dynamics of the phytoplankton community. Long-term changes in nutrient ratios, the effect of these changes on phytoplankton K, the response of species diversity to ecosystem variability, species coexistence mechanisms, and the role of abiotic and abiotic factors in explaining the seasonal variability of phytoplankton abundance have been evaluated by using the long-term dataset of Helgoland Roads. The summary of the thesis is given below:

(1) A spatial gradient in the N: P ratio and chlorophyll concentrations exist from the river mouth to open water. Over the study period, the German Bight became P-limited (i.e. the N: P ratio is increasing) due to the measures taken to control the nutrient loads in the river. A higher chlorophyll concentration is related to the N: P ratio when it is at or near the Redfield ratio.

(2) The phytoplankton K is driven by a set of environmental factors; it changed with changing environmental conditions and can be robustly estimated. Any increase in the phytoplankton K increases the phytoplankton densities. In addition, a higher phytoplankton K is indicative of higher fisheries.

(3) While the 1980s were the most environmentally variable decade that exhibited low phytoplankton diversity, the ecosystem reached a comparatively stable state with high diversity in the last two decades. High phytoplankton diversity may relate to low ecosystem variability due to niche differentiation, which may reduce competition among species so that no exclusion occurs and leads directly to an increase in species richness.

(4) The number of phytoplankton species present can outnumber the number of limiting resources, mainly by producing periodic oscillation in biomass and differentiating resource requirements. In addition, a supersaturation state can evolve with realistic changes in different types of environmental forcing, thereby successfully addressing the 'paradox of the plankton'.

(5) During winter, biotic factors are dominant in determining species diversity. This trend is reversed for the rest of the year when abiotic drivers dominate. Together, they can explain the seasonal variability in the phytoplankton species abundance observed at the HR time-series. In addition, rather than predicting variability under favourable growth conditions, biotic and abiotic factors can predict a higher variability in the phytoplankton abundance under resource-limited conditions.

OUTLOOK

In **MS 1**, long-term changes in the N: P ratio during winter have been analysed for 10-year time blocks. These time blocks could be considered too long; it might be more useful to evaluate five-year time blocks. In particular, spatial seasonal changes in the N: P ratio for shorter time blocks could prove to be valuable. Long-term spatial variation in chlorophyll concentrations has been explained in terms of the N: P ratio. The inclusion of more explanatory variables—i.e. temperature, silicate concentration, and light, among others—would offer more detailed and robust results. The phytoplankton *K* is estimated by considering the resources important for phytoplankton growth in the oceanic ecosystem. Developing a dynamic model to predict the timing of the maximum phytoplankton *K* occurrence in the system would be an interesting research topic in both plankton ecology and fisheries.

Owing to the importance of phytoplankton diversity in marine ecosystems, long-term ecosystem variability has been analysed. Dynamic modelling of phytoplankton diversity might show how diversity can change in different environmental conditions. How biodiversity is maintained can also be explained by the species coexistence model. This thesis only explains how the number of coexisting species exceeds the number of limiting resources in a multiple resource-limited system. The inclusion of more species (i.e. inclusion of more than four species) for limiting resources may give other interesting results. The addition of new species at different time intervals or adding species with fast or slow growth and different mortality rates could also provide new insights into community ecology. Here the seasonal variability of phytoplankton abundance has only been discussed on the basis of a first-order regression model. Extending the first-order regression model to a second-order regression model could be an interesting avenue for future research.

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