Journal of Sea Research 135 (2018) 11–17

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

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

Subrata Sarker[a,*], Peter Lemke[b], Karen H. Wiltshire[a]

[a] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Germany
[b] Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Bremerhaven, Germany

ARTICLE INFO

Keywords:
Plankton
Variable environment
Markov chain
Helgoland Roads
North Sea

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 long-term 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 long-term data set, this study established a causal relationship between ecosystem variability and phytoplankton diversity.

1. Introduction

Phytoplankton is a taxonomically and functionally diverse group of organisms (Bonachela et al., 2015) comprising tens of thousands of species (Mutshinda et al., 2013). 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, 2016; 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

* Corresponding author at: Alfred-Wegener-Institut, Helmholtz-Zentrum für Polar- und Meeresforschung, Biologische Anstalt Helgoland, Helgoland 27498, Germany.
E-mail address: subrata.sarker@awi.de (S. Sarker).

https://doi.org/10.1016/j.seares.2018.02.002
Received 13 July 2017; Received in revised form 16 January 2018; Accepted 10 February 2018
Available online 13 February 2018
1385-1101/

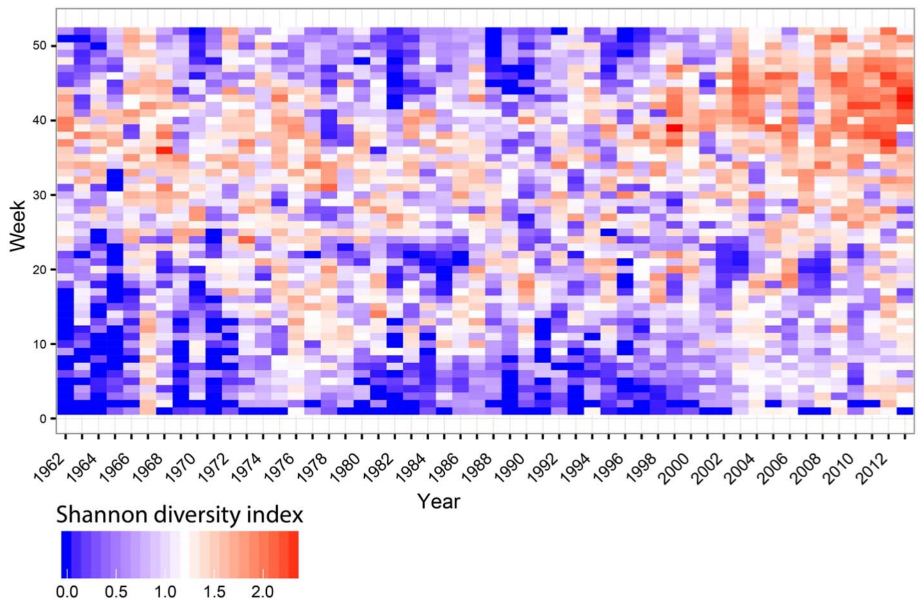

Fig. 1. Long-term weekly mean phytoplankton diversity at Helgoland Roads. Diversity is measured as Shannon diversity index from quality controlled counts data of 26 species from the Helgoland Roads Time Series station.

needs to be addressed is what has caused this phytoplankton diversity increase at Helgoland Roads.

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 is 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.

2. Materials and methods

2.1. 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.

2.2. 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