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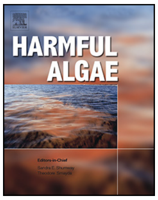

Realized niche analysis of phytoplankton communities involving HAB: *Phaeocystis* spp. as a case study

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ABSTRACT

The link between harmful algal blooms, phytoplankton community dynamics and global environmental change is not well understood. To tackle this challenging question, a new method was used to reveal how phytoplankton communities responded to environmental change with the occurrence of an harmful algae, using the coastal waters of the eastern English Channel as a case study. The great interannual variability in the magnitude and intensity of *Phaeocystis* spp. blooms, along with diatoms, compared to the ongoing gradual decrease in anthropogenic nutrient concentration and rebalancing of nutrient ratios; suggests that other factors, such as competition for resources, may also play an important role. A realized niche approach was used with the Outlying Mean Index analysis and the dynamics of the species' realized subniches were estimated using the Within Outlying Mean Indexes calculations under low (L) and high (H) contrasting *Phaeocystis* spp. abundance. The Within Outlying Mean Indexes allows the decomposition of the realized niche into realized subniches, found within the subset of habitat conditions and constrained by a subset of a biotic factor. The two contrasting scenarios were characterized by significantly different subsets of environmental conditions and diatom species (BV-step analysis), and different seasonality in salinity, turbidity, and nutrients. The subset L environmental conditions were potentially favorable for *Phaeocystis* spp. but it suffered from competitive exclusion by key diatom species such as *Skeletonema* spp., *Thalassiosira gravida*, *Thalassionema nitzschioides* and the *Pseudo-nitzchia seriata* complex. Accordingly, these diatoms species occupied 81% of *Phaeocystis* spp.'s existing fundamental subniche. In contrast, the greater number of diatoms, correlated with the community trend, within subset H exerted a weaker biological constraint and favored *Phaeocystis* spp. realized subniche expansion. In conclusion, the results strongly suggest that both abiotic and biotic interactions should be considered to understand *Phaeocystis* spp. blooms with greater consideration of the preceeding diatoms. HABs needs must therefore be studied as part of the total phytoplankton community.

1. Introduction

The unprecedented rate of global environmental change (Drijfhout et al., 2015), is potentially increasing the spread and impact of harmful algae blooms (HAB) worldwide (Fu et al., 2012; Hallegraeff, 2010; Wells et al., 2015). Attempts to link HABs or undesirable species and anthropogenically-altered environments have often been unclear and contradictory (Anderson, 2009; Davidson et al., 2012; Gowen et al., 2012; Wells et al., 2015). Moreover, the role of biotic interactions in shaping HABs, such as competition for resources, is still poorly studied. Yet, the variability in the magnitude and duration of reported HAB blooms emphasizes the idea that other factors, aside from abiotic variables, play an important role in driving HABs (Bianchi et al., 2000; Borkman et al., 2016; Yin, 2003). Previous research strategies, methods and hypotheses of how environmental pressures mechanistically affect HAB species (Wells et al., 2015) have used modeling (Passy et al., 2016), experiments (Veldhuis et al., 1991), *in situ* measurements (Houliez et al., 2013), and remote sensing imaging (Kurekin et al., 2014) to explore these links. The former studies were based on the hypothesis that HABs could be predicted from environmental variables only.

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Hutchinson's niche concept (1991) allows studying the link between global changes and the phytoplankton community in relation to HABs. Among several multivariate methods available for niche analysis (Braak, 1986; e.g., Calenge et al., 2005; Ter Braak, 1987), Hernández-Fariñas et al. (2015) used the niche through using the Outlying Mean Index (OMI) (Dolédec et al., 2000), assessing the niche of 35 phytoplankton species, including diatoms, along the French coast. Recently, the Within Outlying Mean Indexes calculations (WitOMI; Karasiewicz et al., 2017) was developed as a refinement of the OMI analysis and provides estimations of niche shift and/or conservatism of a community under different subsets of habitat conditions (temporal and/or spatial). The WitOMI calculates the species' realized subniche dynamics (species' niche occupation within subset habitat conditions) within the realized niche resulting from the OMI analysis after selecting subsets. The realized subniches are, therefore, comparable under the same environmental gradients. The decomposition of the niche into subniches, with the WitOMI allows one to observe and measure the part of the existing fundamental subniche that is not used by the species despite being available. The unused part of the existing fundamental subniche is considered as the subset's biological constraints (e.g., competition, predation, mutualism, dispersal and colonization) (Karasiewicz et al., 2017). This last method deciphers the effect of selected environmental factors from unknown biotic factors and is fully adapted to explore the phytoplankton community response to climate change along with HABs.

The study aim was to use the Within Outlying Mean Indexes calculations (Karasiewicz et al., 2017) to understand how the environment influences harmful species realized niches. The method should reveal how the phytoplankton community before and/or during HABs, can influence the harmful algae realized niche. The estimation of the biological constraint should reveal the impact of biological processes on the HAB, providing further insight into the implications on potential competitors. This new method of HAB investigation will be tested with the case study of *Phaeocystis* spp. in the Eastern English Channel. In these waters, the bulk of biomass is represented by the diatom community and *Phaeocystis* spp. (Grattepanche et al., 2011). The genus *Phaeocystis* is one of the most globally distributed marine haptophytes (Lancelot et al., 1994). Although non-toxic (Cadée and Hegeman, 2002), it is classified as undesirable because three species (i.e., *P. globosa*, *P. pouchetii* and *P. antarctica*) are capable of forming large gelatinous colonies, creating impressive foam layers along beaches during bloom collapse (Blauw et al., 2010). This accumulation of excessive organic matter could result in alteration both in the benthic and pelagic compartments. More recently, Breton et al. (2017) suggested with a trait-based approach, that competitive exclusion prevails during *Phaeocystis* spp.'s blooms. The diatoms' taxonomic level, however, was not fine enough to reveal the potential resource competitors of *Phaeocystis* spp. (Breton et al., 2017). To date, no studies have considered the competitive interactions as a possible HAB control.

2. Methods

2.1. Data set

The data were collected as part of the French REPHY-IFREMER (Réseau d'Observation de Surveillance du Phytoplancton et des Phycotoxines) and the Regional Nutrients Monitoring Network (SRN, 2017). Water samples were acquired from a fortnightly to monthly frequency from 1996 to 2012, between 0 and 1 m depth, along with physical measurements, and were completed with chemical analyses. The environmental variables measured included, seawater temperature (°C), salinity (measured using the Practical Salinity Scale), turbidity (NTU), inorganic nutrient concentrations (dissolved inorganic nitrogen, silicate, and phosphate in μmol L^{-1}) and photosynthetically active radiation (PAR, W m^{-2}). Note that PAR is the cumulative sum over the five days preceding phytoplankton sampling. In regards to the quantitative phytoplankton analyses, samples were fixed with Lugol's solution and counted according to the Utermöhl method (Utermöhl, 1958). Organisms were identified to the lowest possible taxonomic level. Taxa that are difficult to discriminate with optical microscopy were grouped (e.g., *Pseudo-nitzschia seriata* complex). In addition, experts identified and counted (cells/L) phytoplankton taxa bigger than 20 mm, and also smaller size species that create chain structures or form a colonies (e.g., *Phaeocystis spp.*). Further details about sampling and processing of phytoplankton and physico-chemical parameters are available in the literature (Lefebvre et al., 2011; Belin and Neaud-Masson, 2012). Unlike Hernández-Fariñas et al. (2015), this study focused on the coastal station 1 of Boulogne-sur-mer because the waters are known for recurrent *Phaeocystis* blooms (Fig. 1).

2.2. Subsets creation

In order to understand the impact of biotic and abiotic factors on the *Phaeocystis* spp. realized niche, two data subsets that gathered years of high and low *Phaeocystis* spp. annual mean abundance events were created (named hereafter subset H and L for high and low respectively). The years of *Phaeocystis* spp. intermediate mean annual abundance were left-out for the rest of the study. This methodology enables deciphering the conditions and the potential resources used by the diatom community and *Phaeocystis* spp. in contrasted events. Each subset has its own environmental habitat conditions and phytoplankton communities ($n = 53$ sampling units for subset L and $n = 71$ for subset H). Additionally, a non-random BV-STEP analysis (Clarke et al., 2001) with 10,000 reiterations was performed to extract the species that correlated most with the entire diatom community during subsets L and H. The diatom species best representing the community under both subsets were used to describe the succession under each subset. Herein, the study does not try to determine the conditions under which the ecosystem is dominated by *Phaeocystis* spp. (e.g., the ratio between diatoms species biomass and *Phaeocystis* spp.) as in Lefebvre et al. (2011), but rather the habitat conditions within which the species can reach high abundances. The environmental habitat conditions are the environmental conditions measured at time *t* of the sampling.

2.3. Niche and subniche analysis

An OMI analysis (Dolédec et al., 2000) was performed including all the sampling dates in order to reflect most of the environmental variability within the OMI axes. Only the significant species identified by the BV step analysis above were used further in the study. The subniche estimations within the subsets H and L (see below) were calculated with the Within Outlying Mean Indexes calculations (WitOMI) (Karasiewicz et al., 2017). Species' subniche dynamics were estimated by comparing the subniche parameters (marginality and tolerance) to the origin G (WitOMIG and Tol), which is the representation of a uniformly distributed theoretical species that would occur at all available habitat conditions (i.e., ubiquitous) (Dolédec et al., 2000). Second, the estimation of the subniche parameters to the subset origin G_K (WitOMIG_K and Tol), which is the representation of the subset mean habitat conditions used by a hypothetical species (Karasiewicz et al., 2017), revealing the species distribution within the subset habitat conditions. The statistical significance of marginality was tested using a Monte