École Doctorale Sciences de la Matière, du Rayonnement et de l'Environnement
Spécialité Géoscience, Ecologie, Paléontologie, Océanographie.

Université de Lille 1

Laboratoire d'Océanologie et de Géosciences
UMR 8187 LOG
Equipe 1 : Diversité, processus et interactions dans les écosystèmes marins

The phytoplankton community response(s) to global changes and their effect(s) on ecosystem functioning with a special focus on *Phaeocystis* spp, a harmful algae.

Thèse de doctorat présentée par
Stéphane KARASIEWICZ

Soutenue publiquement le 22 Décembre 2017 devant le jury composé de :

Directeur de thèse	Sébastien LEFEBVRE, *Professeur*, *Université Lille 1*
Rapporteurs	Valérie DAVID, *Maître de conférences*, *Université de Bordeaux*
	Koen SABBE, *Professeur*, *Université de Gand, Belgique*
Examinateurs	Annie CHAPELLE, *Docteur*, *IFREMER, Brest*
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	Dorothé VINCENT, *Maître de conférences*, ULCO
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Je dédicace cette thèse à mes parents, Diane et Daniel KARASIEWICZ, qui ont su me soutenir et savent que je viens de loin pour en arriver là.

«Science is beautiful when it makes simple explanations
of phenomena or connections between different observations. ».
-Stephen Hawking

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0.1 Résumé

Les écosystèmes côtiers, interfaces entre terre et mer, sont soumis au changement climatique ainsi qu'à de fortes pressions anthropiques. La plupart des eaux côtières sont sujettes à l'eutrophisation, en conséquence de ces activités. Le phytoplancton fait l'objet d'une attention particulière en raison de sa position entant que producteur primaire des écosystèmes marins. Récemment, l'efflorescence des algues nuisibles (HAB) est devenu une préoccupation croissante, dans le monde entier. L'objectif de la thèse a été de décrire et de mesurer les réponses temporelles et les causalités de la structure de communauté phytoplanctonique sous impacts des changements globaux et de l' occurrence d'une algue nuisible. Pour ce faire, le concept de niche écologique et une méthode statistique, ont été adaptés. Les "Within Outlying Mean Indexes" (WitOMI) ont ensuite été proposés pour affiner l'analyse de l' "Outlying Mean Index" en combinant ses propriétés avec la décomposition de la marginalité de l'analyse "K-select". Les dynamics des sous-niches des espèces de la communauté ont été étudiées dans des conditions environnementales contrastées d' abondances basses (L) ou fortes (H) de *Phaeocystis* spp. Le sous-ensemble H était caractérisé par une large niche de *Phaeocystis* spp. ainsi qu'une haute diversité de diatomées. Dans le sous-ensemble L, la sous-niche de *Phaeocystis* spp. a était soumis à une forte contrainte biologique possiblement crée par la compétition pour les ressources par les diatomées. Dans ces conditions environmentales, la relation diversité-productivité du phytoplancton a été étudié à court et long termes. Cette relation s'est avérée plus forte à l'échelle saisonnière. Le déséquilibre des ressources n'a pas eu de lien direct avec la productivité sur le modèle à long terme. Le succès à long terme de l'espèce invasive et de son impact sur la productivité, peut être expliqué par des années froides successives avec des ressources plus élevées mais déséquilibrées, ce qui augmente le nombre de petites espèces de diatomées favorisant son efflorescence. Enfin, je discute des améliorations méthodologiques possibles, du potentiel et de l'intérêt de l'utilisation de l'approches par traits, et d'éventuelles configurations expérimentales afin de renforcer les résultats de la thèse.

0.2 Abstract

Coastal ecosystems, the interfaces between land and sea, are subject to climate change and high anthropogenic pressure. Most coastal waters are prone to eutrophication, as a consequence of the subsequent human activities. The phytoplankton is the subject of special attention because of its position as a primary producer in marine ecosystems. Recently, Harmful Algae Bloom (HAB) outbreaks has become an increasing concern around the world. The aim of the thesis was to describe and to measure the temporal responses and causalities of the phytoplankton community structure, with the occurrence of a harmful algae, under global changes. To do so, the ecological niche concept along with a statistical method were adapted. The Within Outlying Mean Indexes (WitOMI) was then proposed to refine the Outlying Mean Index analysis by using its properties in combination with the K-select analysis species marginality decomposition. The subniche dynamic of the community species was studied under environmental conditions hosting low (L) and high (H) *Phaeocystis* spp. abundance. Subset H was characterized by a large *Phaeocystis* spp. niche and a high diatom diversity. In subset L, *Phaeocystis* spp. subniche was subject to great biological constrain suspected to be caused by diatom competition for resources. In these environmental conditions, the phytoplankton diversity-productivity relationship is expected to vary in the short and long-terms. This relationship was stronger at a seasonal scale. The resource imbalance had no direct link with productivity in the long term model. The long-term invasive species success and its impact on productivity can be explained by successive cold years with higher resource imbalance, which increased the number of small diatom species favoring its bloom. I finally discussed on the possible methodological improvements, the potential interest of using the "trait-based approach", and possible experimental set-ups to reinforce the result of the thesis.

Contents

Chapter 1

General introduction

1.1 Generalities on phytoplankton ecology

Reynolds [2006] defined plankton as "*the collective of organisms that are adapted to spend part or all of their lives in apparent suspension in open water of the sea, of lakes, ponds and rivers.*". The term "*phytoplankton*" comes from the Greek φυτόν(phyton) and πλαγκτόζ(planktons) which can be translated as "plant wanderer" or "drifter". Phytoplankton are defined as "*the collective of photosynthetic microorganisms, adapted to live partly or continuously in open water.*" [Reynolds, 2006]. They are the photoautotrophic components of the plankton community and a key part of oceans, seas and freshwater basin ecosystems [Reynolds, 2006]. Phytoplankton has a primordial place in the biochemical cycles [Pauly and Christensen, 1995; Cloern, 1996] as its dominant communities are responsible for 50 % of the annual primary production on Earth but accounting for only 1% of the global ocean biomass [Field et al., 1998]. Primary production (e.g defined has the quantity of carbon fixed by unit of time [Falkowski et al., 1998]) makes organic carbon (dissolved and particulate) available to the food web and microbial loop [Reynolds, 2006]. Marine ecosystems are then strongly dependent on the phytoplankton [Pauly and Christensen, 1995]. Factors impacting it can ultimately influence ecosystem structure and functioning.

Phytoplankton biomass turns over on the order of 100 times each year as a result of fast growth and equally fast grazing [Calbet and Landry, 2004; Behrenfeld et al., 2006]. Phytoplankton phenology (i.e. defined as the study of periodic variation in the species life cycle in relation with seasonal climatic variability) is a sensitive biological indicator of climate change, its seasonal activity is tightly linked to the annual climate cycle [Winder and Cloern, 2010]. Phytoplankton blooms [Smayda, 1997] are characteristic of the annual phytoplankton growth in pelagic systems. In temperate zones, a well-known pattern in phytoplankton annual cycle is the spring bloom. The event is caused by the seasonal increase in temperature along with light availability while nutrients are available [Cushing, 1959; Sommer et al., 1986] (Figure 1.1). The biomass

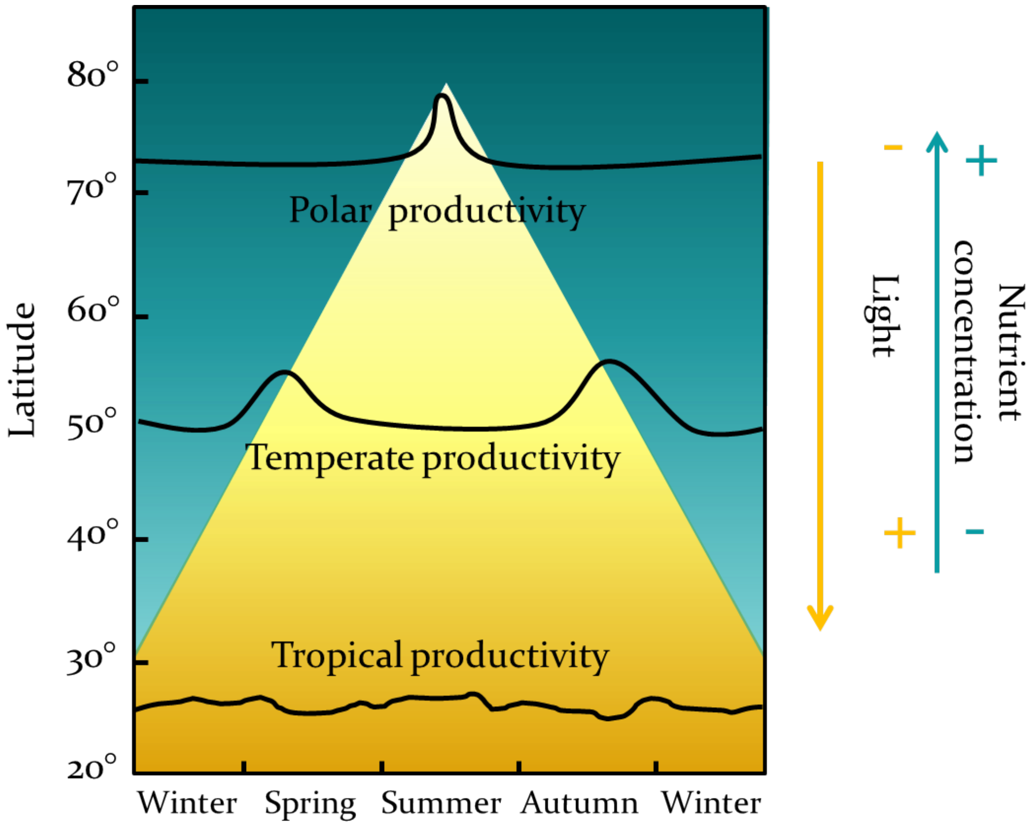

Figure 1.1: Representation of the annual phytoplankton production (in arbitrary vertical scales) cycle at three different latitudes in relation with the light availability (yellow area) and nutrients concentration (green area), illustration from Lalli and Parsons (2006)

Table 1.1: A taxonomic survey of the marine phytoplankton from Reynolds [2006].

Class	Common name	Area(s) of predominance	Common genera
Cyanophyceae (Cyanobacteria)	Blue-green algae (or blue-green bacteria)	Tropical	Oscillatoria Synechococcus
Rhodophyceae	Red algae	Cold temperate	Rhodella
Cryptophyceae	Cryptomonads	Coastal	Cryptomonas
Chrysophyceae	Chrysomonads	Coastal	Aureococcus
	Silicoflagellates	Cold waters	Dictyocha
Bacillariophyceae (Diatomophyceae)	Diatoms	All waters, esp coastal	Coscinodiscus
Raphidophyceae	Chloromonads	Brackish	Heterosigma
Xanthophyceae	Yellow-green algae	-	Very rare
Eustigmatophyceae	-	Estuarine	Very rare
Prymnesiophyceae	Coccolithophorids	Oceanic	Emiliania
	Prymnesiomonads	Coastal	Isochrysis Prymnesium
Euglenophyceae	Euglenoids	Coastal	Eutreptiella
Prasinophyceae	Prasinomonads	All waters	Tetrasalmis Micromonas
Chlorophyceae	Green algae	Coastal	Rare
Pyrrophyceae (Dinophyceae)	Dinoflagellates	All waters, esp warm	Ceratium Gonyaulax Protoperidinium

maximum can persist for weeks or months, until the bloom collapses as the winter nutrient stocks becomes limiting, cells began to sink and grazing pressure increases [Winder and Cloern, 2010]. In temperate zones, a second peak in phytoplankton biomass can flourish, stimulated by excess nutrients leftover in late summer or autumn [Sommer et al., 1986; Longhurst, 1995] (Figure 1.1). The canonical phytoplankton annual cycles are sensitive to climatic changes [Edwards and Richardson, 2004; Winder and Schindler, 2004; Thackeray et al., 2008] with different patterns across ecosystems [Pratt, 1959; Scheffer, 1991; McQuatters-Gollop et al., 2008] and a high year-to-year variability [Cloern and Jassby, 2008; Paerl and Huisman, 2008; Garcia-Soto and Pingree, 2009].

The blooms are characterized by a temporal turnover in phytoplankton composition, or succession, which is, therefore also influenced by the different environmental factors such as temperature and stratification, nutrients and light availability [Barbosa et al., 2010; Pulina et al., 2012; Čalić et al., 2013]. Notable succession patterns involve shifts in dominance from diatom towards green algae, as silica availability relative to other nutrients decreases and while nitrogen to phosphorus ratio is high [Roelke and Spatharis, 2015]. The succession can continue from an assemblage composed of green algae towards nitrogen-fixing cyanobacteria, as nitrogen availability relative to phosphorus decreases [Sommer et al., 1986; Sommer, 1989]. The temporal composition of the phytoplankton community depends on the performance of species [Winder and Sommer, 2012]. Marine phytoplankton species numbers are currently estimated to be between 4000 and 5000 [Sournia et al., 1991; Tett and Walne, 1995], but species are still being discovered. It is estimated that 6800 species exist for the diatoms and dinoflagelate alone [Falkowski and Raven, 2007]. The high number of species reflects the high number of different survival strategies of phytoplankton in an unstable and turbulent environment (Table 4.3).

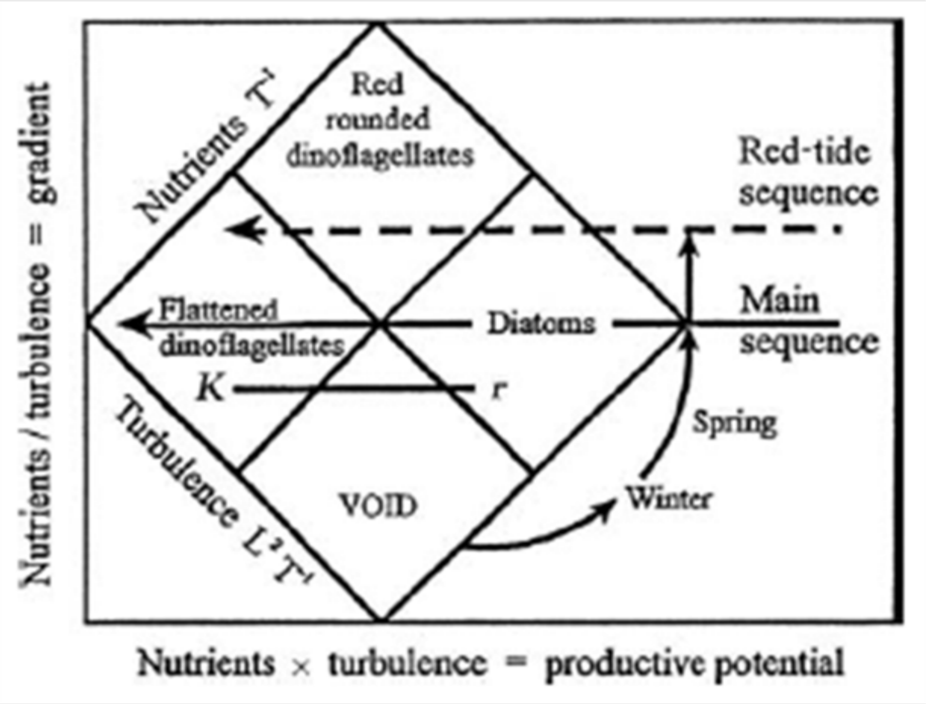

Figure 1.2: Margalef's (1979) diagram representing the seasonal change phytoplankton community composition as a function of turbulence and nutrients. L and T are standard dimensionless units of lenght and time.

Phytoplankton species performance is mostly influenced by the water column thermal stratification's impact on vertical mixing, which alters the position of phytoplankton relative to nutrients and light [Winder and Sommer, 2012]. Margalef [1978] proposed an empirical relationship between turbulence, nutrient supply, and taxonomic composition (Figure 1.2). From the model, Margalef defined specific phylogenetic morphotypes (r versus K growth strategists) which can be positioned along a continuum of habitat mixing and nutrient conditions [Margalef, 1978]. r strategies corresponds to species with rapid reproduction when the conditions are turbulent, nutrient concentration are high, such as the diatoms. *K* strategy are the species with slow reproduction and have a preference for stable habitat conditions, as the dinoflagelates (Figure 1.2). The combination of mixing and nutrient impact the temporal distribution of species during an annual seasonal cycle. Margalef went even further by separating the prediction of species composition under low turbulence conditions: dinoflagellates will dominate under eutrophic conditions (high nutrient concnetrations) and coccolithophore under oligotrophic conditions (low nutrient conditions) (Figure 1.2).

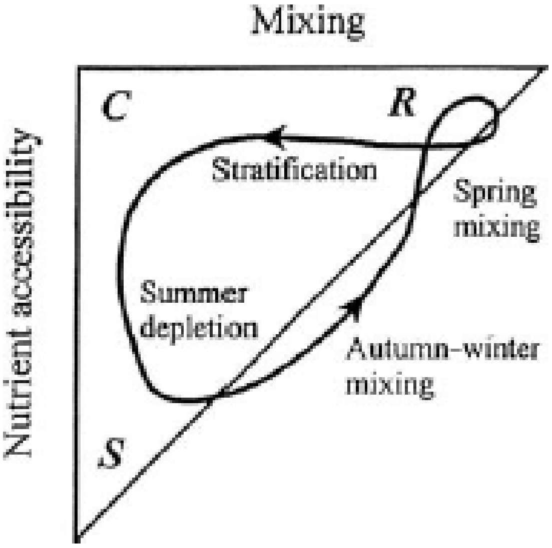

Figure 1.3: Annual selectivity of C, S and R strategy trajectory of the phytoplankton, defined by temperate seasonal variability from Reynolds (2006)

In addition to Margalef's model, Reynolds [2006] developed another model to classify phytoplanktonic species life strategies, based on their respective morphology and physiological traits. The author separated the phytoplankton strategies into three categories: i) colonialist-invasive species (C), ii) stress tolerant species (S) and iii) ruderal species (R) (Figure 1.3). The species using C strategies are characterized by small cell size with a high surface to volume ratio (S/V), low sedimentation rates but highly exposed to predation. The species with S strategies have a low S/V ratio and are flourishing when the water column mixing is weak, and when the vertical gradient of nutrient and light availability is well established. These conditions are well exploited by species capable of using alternative ways of nutrient acquisitions, such as through nitrogen-fixing, predation and vertical migration. Finally, the R species are generally large elongated cell organisms with a large S/V ratio (Figure 1.3).

These species have a preference for turbulent waters with high nutrient concentrations. The CSR scheme was first developed on terrestrial plants and later adapted to phytoplankton for which the spatial and temporal distribution seemed to be highly correlated to the CSR life strategies [Reynolds, 2006] (Figure 1.3).

Despite a well-known seasonal pattern of phytoplankton, the temporal response of the phytoplankton community to the ever changing climatic system is highly variable. The climate system affects phytoplankton fluctuations through many processes, at many time scales in addition to the annual cycle. Therefore understanding the response of the phytoplanktonic community to the changing climate is crucial as it can potentially have severe repercussions on the ecosystem functioning and food-web.

1.2 Global change

The growth of human population goes in line with the increasing production of food which had altered biogeochemical cycles of nitrogen (N), phosphorus (P), carbon (C) and silica [Seitzinger et al., 2010]. The rate of biologically available nitrogen entering the terrestrial biosphere has doubled in the past decades because human activities via fertilizer production and use, fossil fuel combustion, and cultivation of leguminous crops [Galloway et al., 2004]. The increasing P inputs into the environment has also doubled due to increasing waste water from plant treatments, mining, use of rock phosphate as fertilizer, detergent additives, animal feed supplement and other technical uses [Bouwman et al., 2005; Bennett et al., 2001; Mackenzie et al., 1998]. The major part of N and P is recycled through the terrestrial biosphere but still a significant fraction enter groundwater and surface water, transported by rivers to coastal marine systems [Galloway and Cowling, 2002; Seitzinger et al., 2010]. In combination with the anthropogenic impacts on ecosystems, the Earth's climate has warmed, during the last century, by approximately 0.6 °C, which was unprecedented compared to the past millennia [McKibben, 2007]. More alarming the rate of warming is expected to increase in centuries to come. Additionally, it has been recognized that the large temporal and spatial variability in the Earth's climate was due to the atmosphere-ocean system [Stenseth et al., 2003]. Local climatic conditions are greatly influenced by the interannual, subdecadal fluctuations within large-scale climate oscillations [Mantua and Hare, 2002; Stenseth et al., 2003]. Long-term climate change and large-scale climate fluctuations are a crucial attribute of global change, and a wide range of studies have shown links between fluctuations in climate and ecological processes that affect phytoplankton dynamics [Behrenfeld et al., 2006; Paerl and Huisman, 2008]. Phytoplankton dynamics are linked to the annual fluctuations of temperature, water column stratification, light availability [Sommer et al., 1986; Cloern, 1996]. Climatic change affect these environmental factors and alter phytoplankton community structure and composition. Phytoplankton response can be physiological and/or mediated through effects on environmental factors limiting primary production, most notably light and nutrients [Winder and Sommer, 2012].

1.2.1 Temperature effects on phytoplankton

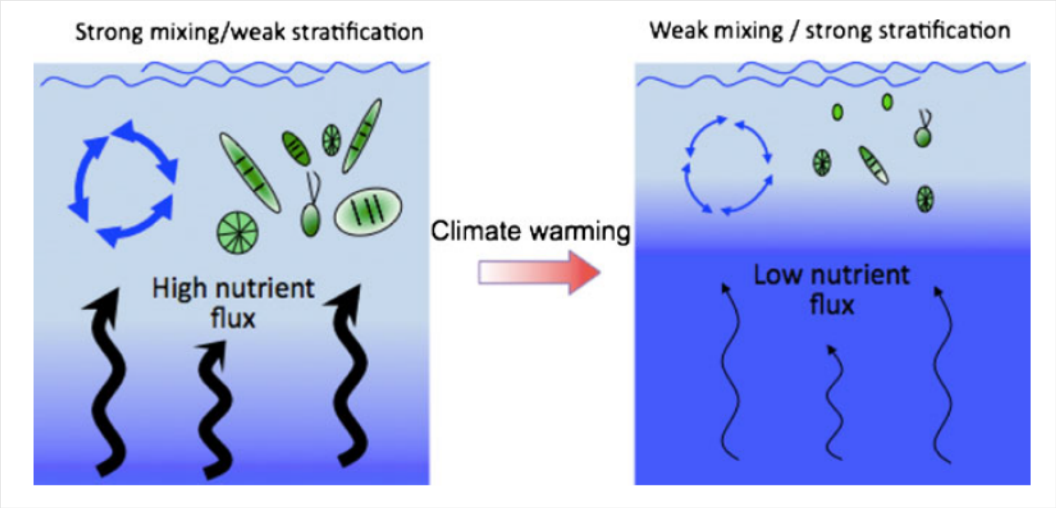

Figure 1.4: Warming effect on the water stratification (blue arrows), in association with nutrient mixing (black arrows), phytoplankton production and cell size Winder et al. (2012).

Plant metabolism, photosynthesis and respiration, are directly affected by temperature but primary producers metabolic rates are mostly limited by the former rather than the latter [Dewar et al., 1999]. Phytoplankton can bloom on sea ice margins [Smith and Nelson, 1985] and under clear ice in lakes [Vehmaa and Salonen, 2009] revealing tolerance of some species which still flourish under conditions of low temperature. Light-limited photosynthetic rates are therefore less sensitive to temperature. Oppositely, light saturation can potentially occur as light-saturated rates increase with temperature and light availability [Tilzer et al., 1986]. With global warming, an increasing production of light-saturated rates photoautotrohic will go along with a decline of the light-limited ones [Winder and Sommer, 2012]. Warming should lead to rising plant growth rates and increase biomass with sufficient resource supply [Padilla-Gamino and Carpenter, 2007]. However, the heterotrophic organisms' respiratory metabolism is more sensitive to temperature [Allen et al., 2005; López-Urrutia et al., 2006]. Therefore global warming should increase herbivory more strongly than primary production and potentially should increase the top-down control with rising grazing rates [O'Connor et al., 2009; Sommer et al., 2011]. The increase grazing pressure should affect phytoplankton's production and taxonomic composition [Winder and Sommer, 2012]. Phytoplankton community composition would most likely be affected by the thermal stratification of the water column which can extend the growing season and vertical mixing processes [Schindler et al., 1996; Rodriguez et al., 2001; Diehl et al., 2002; Smol et al., 2005] (Figure 1.4). As previously mentioned, mixing is a key factor for phytoplankton growth as it affects resource acquisition, nutrient and light of individual species [Diehl et al., 2002; Salmaso, 2005]. Heat exchange stratifies the water column and inhibit mixing, while wind action creates turbulent kinetic energy enhancing the mixing [Wetzel, 2001] (Figure 1.4). The two opposite factors structure the seasonal cycle: summer stratification versus winter mixing. The balance between these two states of stratification will also be affected by global warming [King et al., 1997; Boyd and Doney, 2002; Livingstone, 2003]. The variability in thermal stratification magnitude will directly affect turbulence along with the sinking velocity of phytoplankton community [Livingstone, 2003; Huisman et al., 2006]. It will favor smaller, buoyant species which willl have a competitive advantage over the larger sinking species which will not have as many opportunities to resuspend [Findlay et al., 2001; Huisman et al., 2004; Strecker et al., 2004]. Water column mixing affects nutrient available for phytoplankton. Nutrient-depleted conditions in surface waters is enhanced by stratification which decreases the upward flux of nutrients from deep-water [Livingstone, 2003; O'Reilly et al., 2003; Schmittner, 2005]. Altering mixing regimes affects the competitive advantage of specific phytoplankton morphology, that are better competitors for nutrients [Falkowski and Raven, 2007] and more buoyant at the surface water, such as cyanobacteria [Huisman et al., 2004]. In association with climate change, the increasing nutrient concentration can be related to anoxic conditions [Wilhelm and Adrian, 2008], resulting to similar condition than the processes eutrophication. Moreover, the frequency of extreme rainfall and severe drought has increased since 1970s [McKibben, 2007; Stocker, 2014], increasing terrestrial nutrient runoff [Briceño and Boyer, 2010].

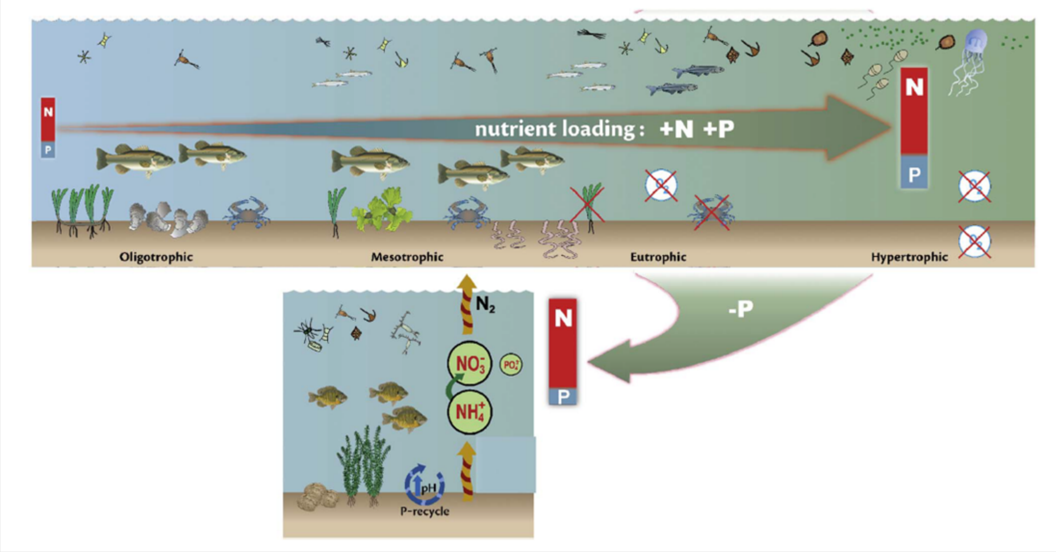

Figure 1.5: Glibert et al. 2017 scheme showing the effect of eutrophication with increasing N and P loading on biodiversity and biogeochemistry. The lower panel illustrates the effect of increasing imbalance between N and P.

1.2.2 Eutrophication

The increasing runoff modifies the resource ratio of the ecosystems, depending on the catchment geochemistry modifying the competitive advantage of phytoplankton species [Winder and Sommer, 2012] (Figure 1.5). The impact of increasing N export of rivers into estuarine, coastal, and marine ecosystems depends on phosphorous (P) and silicon (Si) availability. N and P limit phytoplankton growth, in general, and Si limits diatoms' growth in particular [Rabalais, 2002] (Figure 1.5). The eutrophication process is a biogeochemical enrichment response of plants to nutrients, often to nitrogen (N), and phosphorous (P) increase [Bouwman et al., 2005]. In aquatic systems, the consequences of eutrophication is correlated with an increasing primary production and respiration [Bouwman et al., 2005] (Figure 1.5). Eutrophication has advanced, worldwide, in all densely populated countries, and it is affecting lakes, reservoirs, estuaries, and coastal seas [Vollenweider, 1992]. During the past decades, whilst the flux N and P are increasing [Smith et al., 2003], the loads of Si remained constant and even decreased in rivers where dams were built [Conley, 2002]. Consequently, it altered the stoichiometric balance of N, P, and Si [Rabalais, 2002], consequently impacting the primary production in coastal marine systems, quantitatively and qualitatively. Species, other than diatoms become competitively superior and become dominant, such as flagellated algae which including noxious bloom-forming communities [Turner et al., 2003]. Therefore the food web dynamics leading to fisheries harvests are affected by shifts in the relative availability of N, P, and Si [Bouwman et al., 2005]. For coastal regions, enhanced upwelling with increasing temperature are expected to increase the availability of nutrients and stimulate phytoplankton production [Rabalais, 2002] but changes in the amount, form (dissolved inorganic, organic, particulate), and ratios will contribute to numerous negative human health and environmental impacts [Seitzinger et al., 2010]. Along with eutrophication, a loss of habitat and biodiversity, hypoxia and fish kills are expected with increasing harmful algae bloom (HAB) [Billen et al., 2007; Diaz and Rosenberg, 2008; Howarth et al., 1996; Rabalais, 2002; Turner et al., 2003; Davidson et al., 2012; Heisler et al., 2008].

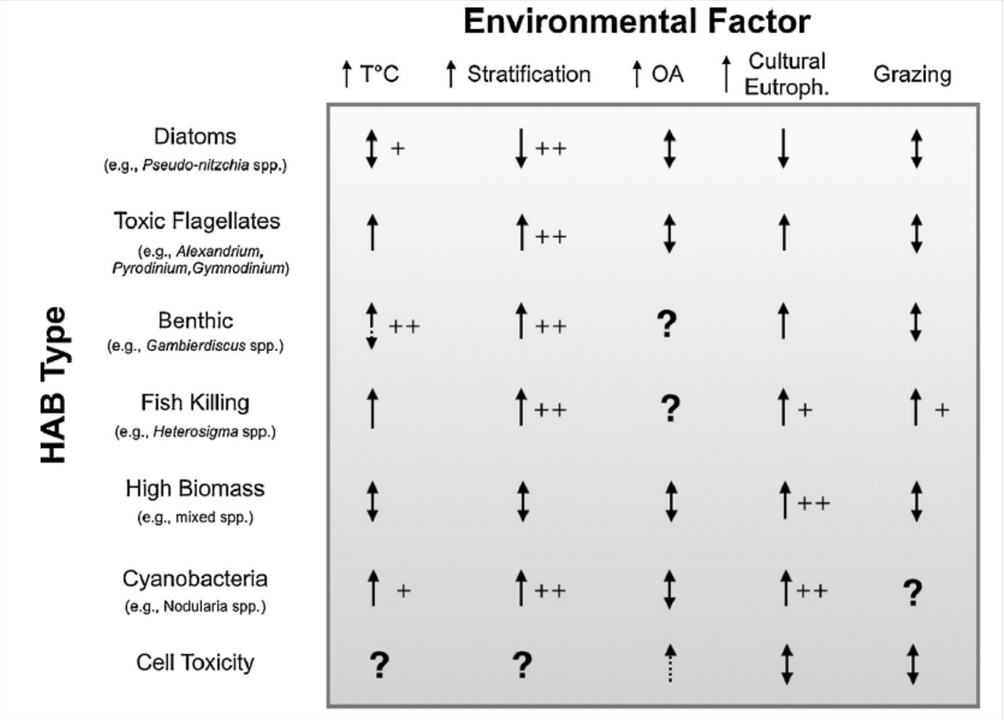

Figure 1.6: Wells et al. 2015 literature overview of the climate change effet on the different types of HAB. Arrows indicating the trend of the changes and the + indicate the confidence level: (+) reasonably likely and (++) more likely. OA: Oceanic acidification.

1.3 Harmful Algae

1.3.1 Generalities

A subset of phytoplankton species may be harmful to human health (e.g. through the production of natural biotoxins), or to the ecosystem service used by humans (e.g. causing mortality of farmed fish and restricting the harvesting of shellfish). They are widely referred to as "Harmful Algae" and the term "Harmful Algal Bloom" (HAB) refers to their occurrence and effect [Davidson et al., 2012]. The phenomena occurs throughout the world's oceans leading to increasing concerns for human health and environmental preservation [McPartlin et al., 2017]. Additionally, the economic loss associated with HABs was estimated at tens of billions of US dollars annually [Sanseverino et al., 2016]. Two different types of harmful algae exist (Figure 1.6). The first group produces toxins or harmful metabolites, such as toxins linked to wildlife death or human seafood poisonings. The toxins of some phytoplankton species are so potent, even at very low concentrations, it makes their bloom very dangerous. The second group of species are nontoxic but causes harm by being highly productive, creating foams or scums, depleting oxygen as bloom collapses, or the destruction of habitat for fish or shellfish by shading of submerged vegetation [Davidson et al., 2012] (Figure 1.6). Nutrient ratios have been suggested to influence biotoxin producing HAB species magnitude [Fehling et al., 2004; Granéli and Flynn, 2006]. The nutrient ratio hypotheses [Officer and Ryther, 1980; Tilman, 1977] stipulated that perturbation in the nutrient supply ratio will result in the environmental selection of potentially harmful species [Smayda, 1990; Heisler et al., 2008]. The perturbation in the nutrient ratio is thought to be anthropogenically induced [Falkowski, 2000; Conley et al., 2009], and the changes in N:P ratio seemed as a possible mechanism for HABs. The nutrient form may also be important. Phytoplankton has a preference, for uptake of a more reduced form of N, such NH_4^+ [Dortch, 1990; Flynn et al., 1993; Rees et al., 1995] which can be produced by the food web [Davidson et al., 2005], or have natural and anthropogenic origins [Eppley et al., 1979]. The availability of the natural and anthropogenic dissolved organic nutrients (i.e . runoff of nitrogenous nutrient urea and fertilizer), has also been suggested to have a significant impact on HABs [Antia et al., 1991; Carlsson et al., 1993; Bronk, 2002; Lønborg et al., 2009]. But in reality the response of HAB to the climate change and eutrophication are highly speculative [Wells et al., 2015] (Figure 1.6). Fundamental changes in HAB research strategies is necessary to meet the complex ecological and multi-environmental stresses that shape phytoplankton communities [Wells et al., 2015]. Two key challenges are needed to move forward in HAB research. First, to obtain evidence that global change can cause alterations in HAB distribution, prevalence or character (Figure 1.6). And second, to develop a scenario with empirical evidences on the causal effect of the environmental and ecological factors which can impact the range of expansion or contraction, and emergence of new patterns for HAB.

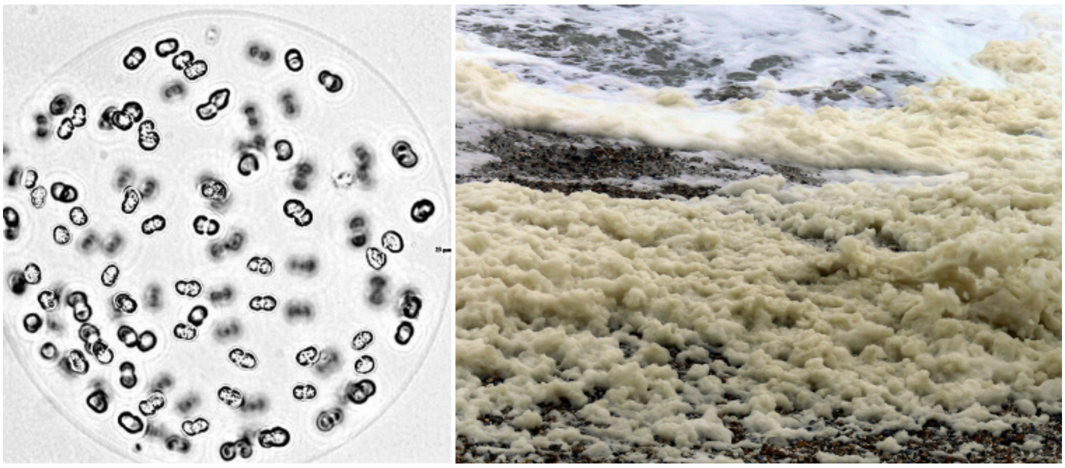

Figure 1.7: Left: a microscopic view of Phaeocystis globosa colony. Right: Foam accumulation produced by the degradation of the colonies

1.3.2 An invasive species: *Phaeocystis* spp.

The marine prymnesiophyte *Phaeocystis* genus is a common species of the winter-spring phytoplankton community in north-temperate coastal seas [Cadée and Hegeman, 2002; Schoemann et al., 2005]. *Phaeocystis*' is capable of forming high monospecific blooms of gelatinous colonies (>10 mg.C.L^{-1}; up to 200×10^{6} cells.L^{-1}) [Schoemann et al., 2005] which endorses a substantial amount of resources from the ecosystem, altering trophic pathways [Tang et al., 2001] (Figure 1.7). Consequently *Phaeocystis* is considered to be one of the few "keystone" phytoplankton species whose blooms can significantly alter the functioning of an ecosystem [Lancelot et al., 1994; Verity and Smetacek, 1996; Verity et al., 2007] by modifying the biogeochemical cycling [Smith Jr et al., 1991; Stefels et al., 1995] and the food web structure [Rousseau et al., 2000]. The variability of *Phaeocystis* high abundance occurrence from year to year is still not well understood. The "silicate-Phaeocystis hypothesis", suggesting that diatoms outgrow *Phaeocystis* until silicate becomes limiting was first proposed as an explanations for *Phaeocystis* bloom variability [Lancelot et al., 1987; Reid et al., 1990]. Since, other researches had shown that low silicate concentration is not the only condition. Peperzak et al. [1998] and Peperzak [2002] showed that diatoms can be out-competed by *Phaeocystis globosa* under high light availability. *Phaeocystis* annual bloom regulation seemed to be multifactorial involving variation in both long-term climate trends [Cadée and Hegeman, 1986, 2002] and the influence of anthropogenic activity on nutrient concentration [Riegman and Noordeloos, 1992; Cadée and Hegeman, 2002; Tungaraza et al., 2003; Gypens et al., 2007; Lancelot et al., 2007; Breton et al., 2006] and nutrient ratios [Lancelot et al., 1987]. Ecosystems which are dominated by *Phaeocystis* are often related with commercially important stocks of crustaceans, mollusks, fishes and mammals. *Phaeocystis* potential impact on higher-trophic levels makes it a threat to human activities, such as fisheries, aquaculture, and tourism via odorous foams on beaches during the bloom's wane [Lancelot et al., 1987] (Figure 1.7). During period of high abundance, the blooms have been reported to cause net-clogging [Savage, 1930], fish mortality [Savage [1930]; Hurley [1982]; Rogers and Lockwood [1990]; Huang1999] and altering fish taste along with a decrease in shell fish growth and reproduction [Levasseur et al., 1994; Pieters et al., 1980; Davidson and Marchant, 1992; Prins et al., 1994; Smaal and Twisk, 1997]. Additionally, toxins have been collected from *Phaeocystis* [He et al., 1999; Stabell et al., 1999; Hansen et al., 2003]. Obtaining evidence of *Phaeocystis* response to global change and its impact on the local biodiversity and ecosystem functioning is crucial due to its high HAB potential. Furthermore, understanding the causal link between, the HAB, biodiversity and the global change will shed light on its capacity range expansion or contraction, and emergence of new phytoplankton communities.

1.4 Link between diversity and productivity

One of the oldest questions in biology is how resource, species diversity and productivity are related. Historically, it was long thought that productivity drives diversity, creating the common relationship where diversity is highest at intermediate levels of productivity [Currie, 1991, Rosenzweig and Abramsky [1993]]. Theories explaining the causalities between resources and communities' diversity include the Species-Energy Theory (SET) [Wright, 1983] and the Resource-Ratio Theory (RRT) [Tilman, 1982]. SET hypothesis that the variation in species richness can be explained by the available energy which also controls, population sizes and stochastic extinction's probability [Wright, 1983] (Figure 1.8). The quantity of available energy is measurable in units of energy per time (e.g. joules per year). RRT stipulates that species richness is determined by the resources supply imbalance which increases the

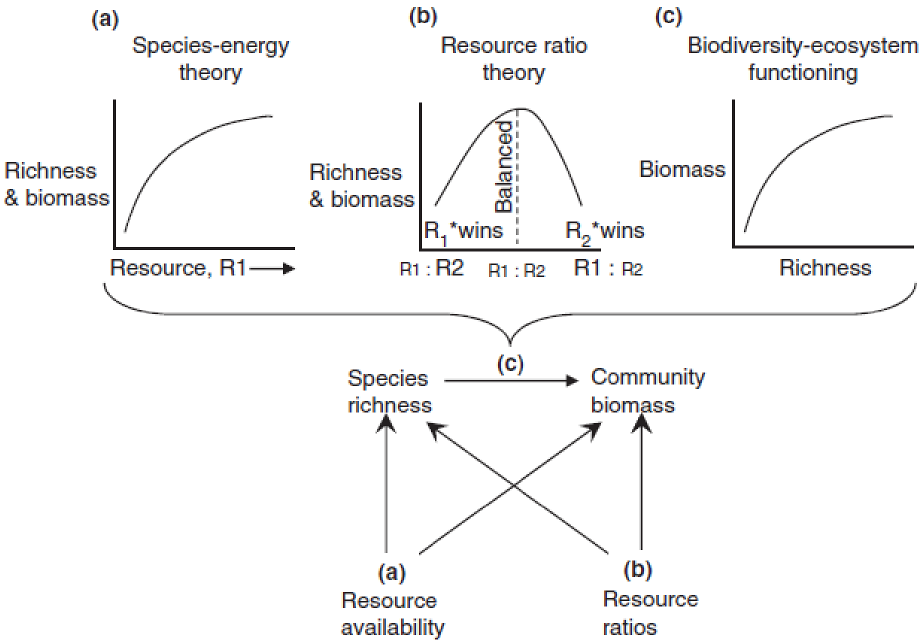

Figure 1.8: Cardinale et al. 2009 Multivariate Productivity-Diversity (MPD) model regrouping three theories, (a) Species-energy theory, (b) Resource ratio theory and (c) Biodiversity-ecosystem functioning

competitive possibilities for replacements [Tilman, 1982] (Figure 1.8). More recently, researchers have tackled the problem from a different angle, viewing species diversity as a driver of productivity [Chapin et al., 2000; Tilman, 2000; Fridley, 2001; Loreau et al., 2002; Naeem, 2002; Hooper et al., 2005] the "biodiversity-ecosystem functioning" (BEF) theory [Naeem et al., 1994; Gross and Cardinale, 2007; Hillebrand and Matthiessen, 2009] (Figure 1.8). The paradigm elaborates connections between our distinct variables: (1) the amount of available resources, (2) the resources' stoichiometric ratios, (3) the produced biomass by the studied community, and (4) the diversity of co-occurring species in the community [Cardinale et al., 2009b] (Figure 1.8). The biodiversity-productivity relationship is constrained by the resource supply rates and ratios making ecosystem stoichiometry (ES) an essential component in the biodiversity and productivity relationship [Hillebrand and Lehmpfuhl, 2011]. This contemporary view on productivity-diversity relationships has often been studied in the anthropological context when biodiversity decreases due to human impact on natural systems, such as eutrophication, causing an imbalance resource ratio and a reduction of productivity [Cardinale et al., 2009b; Hillebrand and Lehmpfuhl, 2011; Gross and Cardinale, 2007]. Since, the theory had been mostly applied on terrestrial ecosystem and on freshwater ecosystems. Marine diversity-productivity relationship still remains to be studied. Only recently, meta-analyses and experiments have shown the effect of the resources availability and ratios onto the diversity-productivity within the phytoplankton community [Lewandowska et al., 2016; Lehtinen et al., 2017; Hodapp et al., 2015]. Small-scale experimentation with artificially assembled microbial communities have been increasingly applied to diversity-productivity studies, especially in aquatic environments [Striebel et al., 2009; Gamfeldt and Hillebrand, 2011]. Under the current global changes the phytoplankton community will be impacted by the changing climatic conditions, affecting the annual, and the long-term diversity-productivity relationship. Furthermore, the possible increasing HAB occurrence could have an additional effect on the diversity-productivity relationship. Phytoplankton having such an pivotal role in the marine ecosystem and ecosystem functioning, the understanding of the response in diversity-productivity relationship is of crucial importance.

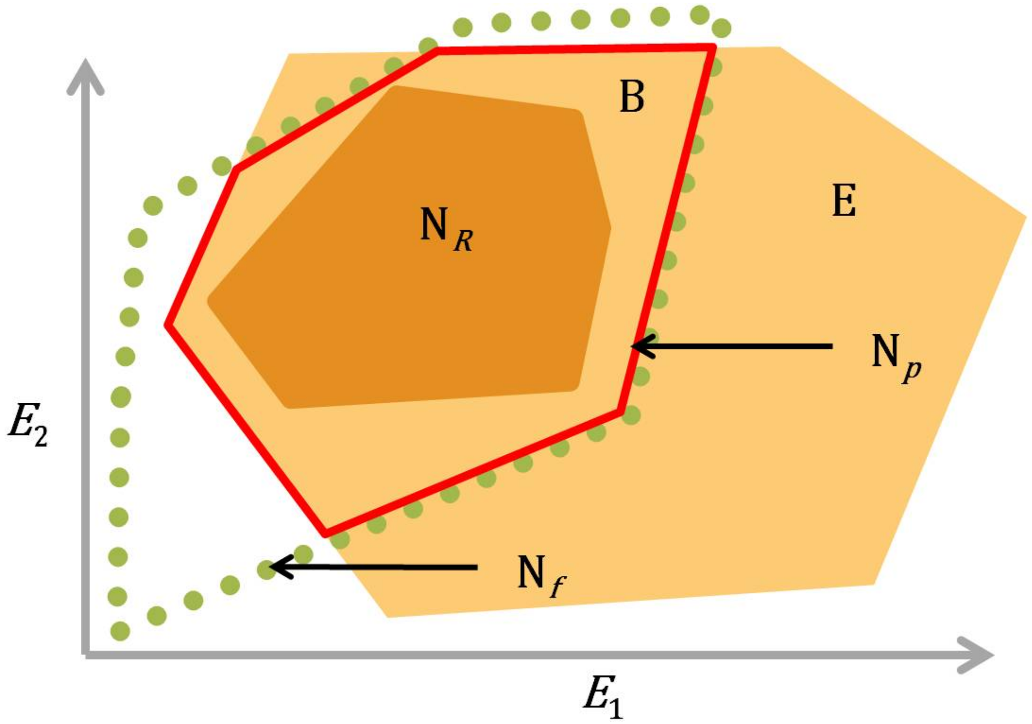

Figure 1.9: Figure inspired from Jackson S, Overpeck JT. (2000). The environmental gradients, E_1 and E_2, define the realized environmental space **E**. The fundamental niche, $\mathbf{N_f}$, intersect **E**, creating the existing fundamental niche, $\mathbf{N_p}$. The realized niche, $\mathbf{N_R}$ is therefore included into $\mathbf{N_p}$ but it further restricted by the biotic interaction, **B**.

1.5 Niche concept

Ecological niche is a pivotal theory to understand how the changing environment affects species abundance patterns. J. Grinnell and C. Elton first developed the idea in the early 20th century, an idea which was latter brought back by G. E. Hutchinson and R. MacArthur during the 1950s' and 60s'. Under ongoing global changes, the niche concept has regained interest as it has the potential to predict the future of living species [Peterson et al., 1999; Chase and Leibold, 2003; Wiens et al., 2009]. There are three different niche perspectives focusing on different aspects of the niche concept. First, the Grinnellian niche concept in which, the niche is considered to be included in the environmental space that a species can occupy and is defined by abiotic factors [Wiens et al., 2009]. The Eltonian niche focuses on the species or group of species' functional role in the ecosystem [Polechová and Storch, 2008; Wiens et al., 2009]. Finally, Hutchinson [1957] niche concept is a n-dimensional conceptual space, defined by environmental factors that influences fitness of individuals of a species. Two types of niches were defined. The fundamental niche is described as the n-dimensional hypervolume, restricted by multiple resources and environmental factors, where a species can live indefinitely, in the absence of biotic interactions [Hutchinson, 1957]. The realized niche is described as a subset of the fundamental niche that is constrained by additional biotic interactions (e.g., competition, predation, mutualism, dispersal, and colonization). Despite being an attractive concept, the applicability of the concept onto the real world is questionable. As Griesemer [1992] reported, Hutchinson's niche concept is static and does not consider temporal environmental changes and the variability of the species response. Environmental change creates different combinations of niche variables and could be challenging to identify the relevant factors leading to the species persistence through time [Jackson and Overpeck, 2000]. Therefore, the finite combinations of n-environmental factors relevant to a species exist at any given time and the environmental conditions which actually occurs at a time t is called the realized environmental space, $\mathbf{E}$ (Figure 1.9). The intersection between the realized environmental space and the fundamental niche, $\mathbf{N_f}$, is named the existing fundamental niche, $\mathbf{N_p}$ (Figure 1.9) [Soberón and Nakamura, 2009; Peterson, 2011a]. The realized environmental space should change with global changes and the realized niche, $\mathbf{N_R}$, of any given species of a community should also vary. Therefore the biotic interaction, $\mathbf{B}$, between species will also be subjected to change (Figure 1.9). The omission of biotic interactions in niche research is a major setback for measuring accurate niches [Davis et al., 1998; Soberón and Nakamura, 2009] and its temporal variability and affect onto the species community is essential for understanding the fate of phytoplankton along with HAB.

1.6 Problematic

Phytoplankton annual cycle will most likely be affected by global warming. For the most pessimistic scenario, the climatic model predict an increase of 4°C for the sea surface temperature. Human activity is expected to rise along with their respective nutrient input, especially N and P, disturbing the N:P ratio within the aquatic ecosystem. The concomitant changes will affect the phytoplanktonic community composition, diversity, and consequently, the primary production impacting the rest of the food web like some other ecological functions. The study of the modification caused by these disturbances on the phytoplanktonic composition is a necessity due to their key role in the ecosystem functioning. A relative small number of studies have investigated the simultaneous effect of several environmental variables on the phytoplankton response and effect on productivity. Despite this limitation, it was revealed that the phytoplankton growth and life strategies would be modified and this will have as a consequence the appearance of harmful algae species. It was reported that the diversity and productivity is expected to increase and to decrease respectively during the bloom of an invasive species [Sax and Gaines, 2003; Byrnes et al., 2007]. The harmful algae blooms are suggested to be increasing with further anthropogenic eutrophication and warming. In reality, the hypothesis remain highly speculative as environmental multifactorial studies on HAB are still lacking. The development of a new method is required to prevent and predict the occurrence of HAB. In combination with global change, the response of phytoplankton community, composition and succession, under conditions of HAB and non-HAB remains to be revealed. The diversity-productivity relationship in phytoplankton community has already been reported, but mostly in small time scale experimental condition and more rarely *in situ*. Furthermore, its study in marine ecosystem is still in its infancy and awaits to be developed. The marine phytoplankton diversity-productivity relationship, in association with global change and the invasive species, is still unknown but it is expected to differ on an annual, and from a year-to-year basis. The Hutchinson's niche concept has regained interest to study species' response to global changes and invasive species studies. Researchers on species' niche acknowledge the biotic interaction as a limitation, and its potential dynamic effect on realized niche under changing climatic conditions, but it persists to be neglected. The actual theory suggests that the fundamental niche is needed to estimate the biotic interaction effect onto the species' realized niche. Unlike the realized niche which can be measured, the fundamental niche cannot be observed in nature, and requires extensive calculation and modelling. The actual niche concept could be revised for greater application to investigate the species niche response under temporal, spatial and/or episodical scale and with biological interaction taken into account explicitly. This is of special importance for phytoplankton to study to so-called Hutchinson's "plankton paradox".

The thesis aim was to describe and to measure the temporal responses and causalities of the phytoplankton community structure, with the occurrence of a harmful algae, under global changes. The investigation will be divided into three sections and related questions:

1. Can a niche concept and a statistical method be developed to allow the observation and quantification of the species' niche response to global changes? Can the biotic interaction affecting the species' niche be observed and quantified?

2. What is the response of the phytoplankton community structure under HAB or no HAB conditions? What environmental conditions explain the occurrence of a harmful algae?

3. How global change and the invasive species affect the diversity-productivity relationship in a short-term and long-term scales?

Chapter 2

Materials and Methods

2.1 Data

Since 1984, IFREMER (Institut Français de Recherche et d'Exploitation de la Mer) have established an observation and monitoring network for marine phytoplankton, the REPHY (Réseau d'Observation et de Surveillance du Phytoplancton Marin). The network was created to answer two complementary objectives:

- An environmental heritage objective for the sake of acknowledging the biomass, abundance and the composition of marine phytoplankton in coastal and lagoonal waters, in order to describe the spatial-temporal dynamic of the different phytoplanktonic species. Through this objective, the REPHY also aims to establish an inventory of exceptional blooms, as such as the colored waters.
- A health monitoring objective, in order to detect and follow the development of toxin producing species, which accumulates in sea product destined for human consumption and represents a potential health issue. It is completed by toxin research in bivalve mollusk present in production area or in natural stocks.

Within the REPHY framework, three phytoplankton observation strategies are in place. They are mentioned in the REPHY's Protocole Chart 2012-2013 [Belin and Neaud-Masson, 2012]. Only the "*Total Phytoplankton*" strategy, from which the data were used for the analysis, are briefly reported bellow: "*Total Phytoplankton*" strategy is concerned by regularly covering locations to report and count all recognizable phytoplankton species present in a sample,under an optical microscope. It provides the essential time series required for phytoplanktonic community studies. The acquisition frequency of the data, so called "*Total Flora*" is monthly to bimonthly basis depending on the location. For all monitoring locations, the REPHY applies a standardize protocol for sampling, observation, counting of the phytoplankton along with environmental parameter measurements.

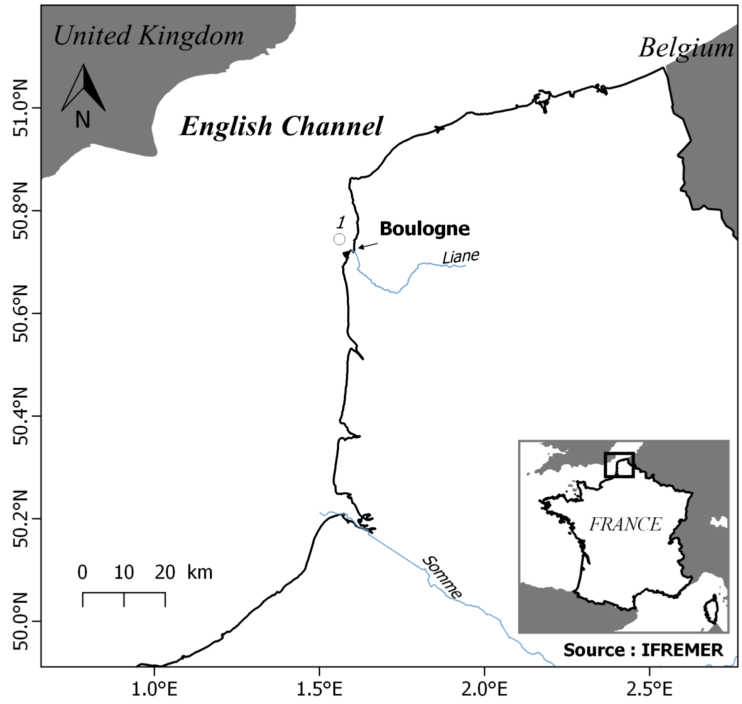

Figure 2.10: Location of station where data is collected along the coast of France.

The species biovolume were collected from the Olenina et al. [2006] study, and if the species' biovolume was not reported in the the article, the biovolume was searched on `http://eol.org/traitbank` by using the R packages "Reol" and "traits" [Banbury and O'Meara, 2014; Chamberlain et al., 2016].

2.2 Community analysis

The phytoplankton species do not equally contribute to the community abundance. A set of species combination which contribute the most into the community abundance pattern is required to reveal the most important species. The search for the best combination of species possible was done with the BV-step analysis [Clarke and Warwick, 2001]. The analysis requires two matrices, the faunal matrix (fixed matrix) and its transposed version, from which the similarity matrix (Bray-Curtis distance) are calculated [Clarke and Warwick, 2001]. The idea is to find the smallest possible species combination, from the transposed matrix, that matches as near as possible the full species set from the fixed matrix. The Bray-Curtis similarity matrix for the smallest species subset has to be at least correlated at $\rho = 0.95$ with the fixed matrix. The analysis uses the step-wise procedure, which subsequently operates and includes the both forward and backward-stepping phases. The procedure starts with a null set, choosing the species which best maximizes ρ, then adds a second and a third species to improve ρ. The backward elimination now starts and checks if the first selected species can be dropped. In other words, if the second and third species alone have a greater ρ than with the three species together. The algorithm continues, with each step selecting the best species to add (forward phase) or to drop (backward phase) from the existing combination. The procedure goes on until no further improvements are possible by the addition of a species to the existing combination of species [Clarke and Warwick, 2001].

2.3 Niche analysis

Since Hutchinson [1957] niche concept, authors promoted different measurements for niche separation and niche breadth [Hurlbert, 1978; Colwell and Futuyma, 1971; Feinsinger et al., 1981]. In community studies, the term niche refers the preferential habitat for species [Braak and Verdonschot, 1995]. The selection of the appropriate ordination technique in terms of species response models and weighting options depends mainly on the objectives. Herein, the aim is to understand how species respond to environmental gradients. Among other method, the Outlying Mean Index (OMI) is a multivariate statistical analysis which separates community species niches and measures the distance between the mean habitat conditions used by each species and the mean habitat conditions of the study area [Dolédec et al., 2000; Thuiller et al., 2004]. Unlike other methods, the OMI makes no assumption about the shape of species response curves to the environment (e.g. unimodal or linear). Furthermore, OMI analysis gives equal weight to species-rich and species-poor sites, which is not the case for the canonical correspondence analysis (CCA) and redundancy analysis (RDA). The OMI analysis gives the mean position of the species in the environmental space (along each environmental axis), which represents a measure of the distance between the mean habitat conditions used by the species and the mean habitat conditions of the study area. It measures the species susceptibility to select a specialized environment. The OMI analysis calculates the species niche of the community over the entire data set, meaning that it comprises all sampling dates (or sites). Therefore, in order to extract events or specific time scale, the analysis needs to be divided into subsets. The OMI analysis, being a two table ordination method (species table $\mathbf{Y}$ responding to the environmental table $\mathbf{Z}$), both tables have to be decomposed. In addition, the species' mean position, at a time t, should be calculated from the mean environmental habitat condition and, from the mean environmental habitat condition at time t.

2.3.1 Species frequency table

Here and elsewhere, we follow the mathematical notations used by [Dolédec et al., 2000]. Let us extract $\mathbf{Y}_K(k\ samples \times t\ species)$, from the faunistic table $\mathbf{Y}(n\ samples \times t\ species)$ with $1 \leq k \leq n$. Let us transform subset $\mathbf{Y}_K$ into a species profile table (noted $\mathbf{Fr}_K$) that contains the frequency of species for each SUs, $f_{K_{i_s/j}}$ as follows:

$$f_{K_{i_s/j}} = \frac{y_{K_{i_sj}}}{y_{K_{.j}}} \qquad 1 \leq i_s \leq k,\ 1 \leq j \leq t \tag{2.1}$$

where $y_{K_{i_sj}}$ is the abundance of species j in SU i_s and $y_{K_{.j}}$ the column total of species j equal to

$$y_{K_{.j}} = \sum_{i_s=1}^{k} y_{K_{i_sj}} \tag{2.2}$$

Then the species profile table $\mathbf{Fr}*$ concatenates $\mathbf{Fr}_K$ as follows:

$$\mathbf{Fr}* = \begin{bmatrix} \mathbf{Fr}_1 \\ \vdots \\ \mathbf{Fr}_K \\ \vdots \\ \mathbf{Fr}_N \end{bmatrix} \quad 1 \leq K \leq N \tag{2.3}$$

with N the number of subsets.

Inspired by the OMI analysis [Dolédec et al., 2000] and the decom position of marginalities used in K-select analysis [Calenge et al., 2005], we propose to calculate two additional marginalities. First, the Within Outlying Mean Index to G (WitOMIG) is the species marginality (i.e., the weighted average of sampling units of a given subset used by the species) to the average habitat conditions of the sampling domain (G; see Eq. 2.7 in the followed section). Second, the Within Outlying Mean Index to G_K (WitOMIG_K) is the species marginality compared to the average habitat condition used by the community in a K subset habitat conditions (G_K; see Eq. 2.16 in the followed section)

2.3.2 Subniche parameters calculated from the origin G

The center of gravity (G) of SUs is at the origin of the axes of the OMI analysis and corresponds to the overall mean habitat conditions used by the taxa in the assemblage [Dolédec et al., 2000]. Let us consider N subsets habitat conditions of the environmental table $\mathbf{Z}_0$ equals to:

$$\mathbf{Z}_0 = \begin{bmatrix} \mathbf{Z}_1 \\ \vdots \\ \mathbf{Z}_K \\ \vdots \\ \mathbf{Z}_N \end{bmatrix} \quad 1 \leq K \leq N \tag{2.4}$$

Let us extract $\mathbf{Z}_K(k \times p)$, a matrix of $\mathbf{Z}_0(n \times p)$, having k rows, with $1 \leq i_s \leq k$ and p variables (Figure 3).

Let the faunistic frequency table, $\mathbf{Fr}_K(k \times t)$ contains the frequency of t species in the k SUs. M_i represents SU i of table $\mathbf{Z}_0$ in the multidimensional space R^p. Let consider $M_{K_{i_s}}$, representing SU i_s of table $\mathbf{Z}_K$ in the same multidimensional space R^p. The total inertia of table $\mathbf{Z}_K$ equals:

$$I_{T_K}(j) = \sum_{i_s=1}^{k} f_{K_{i_s/j}} \parallel M_{K_{i_s}} \parallel^2_{\mathbf{I}_p} \tag{2.5}$$

The inertia $I_{T_K}(j)$ represents the total inertia of $\mathbf{Z}_K$ weighted by the species j profile. Similarly to the proposal of Dolédec et al. [2000], the SUs i_s that do not have species j do not add to the species j inertia. Let consider a $\mathbf{I}_p$-normed vector $\mathbf{u}_K$ ($\parallel \mathbf{u}_K \parallel^2_{\mathbf{I}_p}= 1$). The projection of the k rows of the matrix $\mathbf{Z}_K$ onto the vector $\mathbf{u}_K$ results in a vector of coordinates $\mathbf{Z}_K\mathbf{u}_K$. Therefore, the average position of species j on $\mathbf{u}_K$, equivalent to the center of gravity of species j, is defined as:

$$T_{K_j} = \mathbf{f}_K^\top \mathbf{Z}_K \mathbf{u}_K \qquad \mathbf{f}_K^\top = (f_{K_{1/j}}, \ldots, f_{K_{i_s/j}}, \ldots, f_{K_{k/j}}). \tag{2.6}$$

With Eq. S8, marginality within a subset of habitat conditions, or within-subset outlying mean index (WitOMIG) of species j {[}noted $m_{a_K}(j)${]} along $\mathbf{u}_K$ equals:

$$m_{a_K}(j) = T^2_{K_j} = (\mathbf{f}_K \mid \mathbf{Z}_K \mathbf{u}_K)^2_{\mathbf{I}_p} = (\mathbf{Z}_K^\top \mathbf{u}_K \mid \mathbf{f})^2_{\mathbf{I}_p} \tag{2.7}$$

This marginality represents the deviation between the average position of species j within subset K from the origin (G). Also equivalent to the distance between the subset average habitat conditions used by species (j) and the overall average habitat conditions found in the area (G).

From Eq. 2.7, the maximization of $m_{a_K}(j)$ has for solution $\mathbf{u}_K$ equal to:

$$\mathbf{u}_{K_j} = \frac{\mathbf{Z}_K^\top \mathbf{f}_K}{\parallel \mathbf{Z}_K^\top \mathbf{f}_K \parallel_{\mathbf{I}_p}}. \tag{2.8}$$

Vector $\mathbf{u}_{Kj}$, defined the direction of the species j, within the subsets (marginality axis of species j within subset K), for which the average position of species j within subset K is as far as possible from the overall average habitat conditions (G).

In addition, the dispersion or tolerance [noted $T_{m_K}(j)$]of SUs i_s which contains species j, can be calculated. Let $m_{K_{i_s}}$ be the projection of $M_{K_{i_s}}$, onto the marginality axis, as follows:

$$T_{m_K}(j) = \sum_{i_s=1}^{k} f_{K_{i_s/j}} \parallel G_{K_j} - m_{K_{i_s}} \parallel_{\mathbf{I}_p}^2 \tag{2.9}$$

$T_{m_K}(j)$ represents the subniche breadth of species j under the habitat conditions defined by $\mathbf{Z}_K$. Finally, similarly to the proposal of Dolédec et al. [2000], the projection of the SUs of subset K onto the plane orthogonal to the marginality axis returns a residual tolerance {[}noted $T_{r_K}(j)${]} and the decomposition of the species j total inertia under the subset habitat conditions can be written as follows:

$$I_{T_K}(j) = m_{a_K}(j) + T_{m_K}(j) + T_{r_K}(j) \tag{2.10}$$

The niche variability of the species j thus comprises of the three components advocated by Dolédec et al. [2000]: (1) an index of marginality or WitOMIG, *i.e.*, the average distance of species j within subsets to the uniform distribution found in the sampling domain (G); (2) an index of tolerance or subniche breadth and (3) a residual tolerance, *i.e.*, an index that helps to determine the reliability of the subset habitat conditions for the definition of the subniche of species j.

Furthermore the total species inertia $I_T(j)$ calculated in Dolédec et al. [2000], can be recalculated using the inertia of species $I_{T_K}(j)$ as follows:

$$I_T(j) = \sqrt{\sum_{K=1}^{N} (I_{T_K}(j) \times \frac{y_{K.j}}{y_{.j}})^2} \tag{2.11}$$

where $y_{.j}$ corresponds to the total species j abundance in the faunistic table $\mathbf{Y}$.

2.3.3 Subniche parameters calculated from a sub-origin G_K

In the previous section, the subniche parameters are estimated considering the average habitat conditions (G) used by the all species in the assemblage. The subniche parameters can also use the average subset habitat conditions (G_K) and the corresponding subsets of species.

Let us consider again the matrices $\mathbf{Z}_K$, which are centered using their respective mean to yield $\mathbf{Z}_{K^*}$, thus making the global table $\mathbf{Z}^*$:

$$\mathbf{Z}^* = \begin{bmatrix} \mathbf{Z}_{1^*} \\ \vdots \\ \mathbf{Z}_{K^*} \\ \vdots \\ \mathbf{Z}_{N^*} \end{bmatrix} \tag{2.12}$$

Let us consider again the faunistic table, $\mathbf{Fr}_K(k \times t)$ that contains the species frequency (Figure 3). The equations are the same as previously but considering the N centered subset habitat conditions $\mathbf{Z}_{K^*}$ (Details in the Appendix S1). We obtain similarly the total inertia of $\mathbf{Z}_{K^*}$, $I_{T_{K^*}}$, and the inertia of species j, $I_{T_{K^*}}(j)$, can be decomposed into its marginality or WitOMIG_K, $m_{a_{K^*}}(j)$, its tolerance $T_{m_{K^*}}(j)$ and its residual tolerance $T_{r_{K^*}}(j)$.

Let us extract $\mathbf{Z}_{K^*}(k \times p)$, a matrix of $\mathbf{Z}^*(n \times p)$ with k rows. Let the faunistic table, $\mathbf{Fr}_K(k \times t)$ contain the frequency of t species in the k SUs. Let M_{i_s} represent SU i_s of table $\mathbf{Z}_{K^*}(k \times p)$ in the multidimensional space R^p. Let $M_{K^*_{i_s}}$ represent the SU i_s subset habitat conditions of table $\mathbf{Z}_{K^*}$ in the same multidimensional space R^p. The total inertia of the matrix $\mathbf{Z}_{K^*}$, equals:

$$I_{T_{K^*}} = \sum_{i_s=1}^{k} p_{K^*_{i_s}} \parallel M_{K^*_{i_s}} \parallel^2_{\mathbf{I}_p} \tag{2.13}$$

with $p_{K^*_{i_s}}$ being the weight of SU i_s. The inertia of species j considering the matrix $\mathbf{Z}_{K^*}$ equals:

$$I_{T_{K^*}}(j) = \sum_{i_s=1}^{k} f_{K_{i_s/j}} \parallel M_{K^*_{i_s}} \parallel^2_{\mathbf{I}_p} \tag{2.14}$$

The inertia $I_{T_{K^*}}(j)$ represents the inertia weighted by the species profile j. The SUs i_s that do not have species j do not add to the species j inertia. Let us consider a $\mathbf{I}_p$ normed vector $\mathbf{u}_{K^*}$ ($\parallel \mathbf{u}_{K^*} \parallel^2_{\mathbf{I}_p} = 1$). The projection of the k rows of the matrix $\mathbf{Z}_{K^*}$ onto the vector $\mathbf{u}_{K^*}$ results in a vector of coordinates $\mathbf{Z}_{K^*}\mathbf{u}_{K^*}$. Therefore, the average position of species j on $\mathbf{u}_{K^*}$, equivalent to the center of gravity of species j within a subset of habitat conditions is defined as:

$$T_{K^*_j} = \mathbf{f}_K^\top \mathbf{Z}_{K^*}\mathbf{u}_{K^*} \qquad \mathbf{f}_K^\top = (f_{K_{1/j}}, \ldots, f_{K_{i_s/j}}, \ldots, f_{K_{k/j}}). \tag{2.15}$$

With the Eq. S19, marginality within a subset of habitat conditions, or within subset outlying mean index to G_K (WitOMIG_K) of species j [noted $m_{a_{K^*}}(j)$] along $\mathbf{u}_{K^*}$ equals:

$$m_{a_{K^*}}(j) = T^2_{K^*_j} = (\mathbf{f}_K \mid \mathbf{Z}_{K^*}\mathbf{u}_{K^*})^2_{\mathbf{I}_p} = (\mathbf{Z}_{K^*}^\top \mathbf{u}_{K^*} \mid \mathbf{f}_K)^2_{\mathbf{I}_p} \tag{2.16}$$

This marginality represents the deviation between the average position of species j within subsets from the subset habitat origin (G_K). Also equivalent to the distance between the average subset habitat conditions used by species j and the average subset habitat conditions of the subset area.

From Eq. 2.16, the maximization of $m_{a_{K^*}}(j)$ as for solution $\mathbf{u}_{K^*}$:

$$\mathbf{u}_{K^*_j} = \frac{\mathbf{Z}_{K^*}^\top \mathbf{f}_K}{\parallel \mathbf{Z}_{K^*}^\top \mathbf{f}_K \parallel_{\mathbf{I}_p}}. \tag{2.17}$$

Vector $\mathbf{u}_{K^*j}$, defined the direction of the species j, within the subsets (marginality axis of species j within the subsets), for which the average position of species

j within subsets is as far as possible from the subset habitat conditions found in the area G_K.

In addition, the dispersion or tolerance [noted $T_{m_{K^*}}(j)$] of SUs i_s that contains species j can be calculated. Let $m_{K^*_{i_s}}$ be the projection of $M_{K^*_{i_s}}$, onto the marginality axis as follows:

$$T_{m_{K^*}}(j) = \sum_{i_s=1}^{k} f_{K_{i_s/j}} \parallel G_{Kj} - m_{K^*_{i_s}} \parallel^2_{\mathbf{I}_p} \tag{2.18}$$

$T_{m_{K^*}}(j)$ represents the subniche breadth of species j under the subset habitat conditions defined by $\mathbf{Z}_{K^*}$. Similarly to the proposal of [Dolédec et al., 2000], the projection of the k SUs of subset K onto the plane orthogonal to the marginality axis returns a residual tolerance [noted $T_{r_{K^*}}(j)$] and the decomposition of the species j total inertia under the subset habitat conditions equals:

$$I_{T_{K^*}}(j) = m_{a_{K^*}}(j) + T_{m_{K^*}}(j) + T_{r_{K^*}}(j) \tag{2.19}$$

2.4 Structural Equation Modelling

2.4.1 Description and approaches

The Structural Equation Modelling (SEM), or pathways analysis, are multivariate statistical calculations which allow to concurrently analyse a network of variable relationships and considering direct and indirect relationships with error measurements. It is a well adapted method to analyse ecological processes due to their hierarchical structure and patterns [Grace, 2006; Arhonditsis et al., 2006]. For instance, the SEM gives the opportunity to create relationship models between ecological concepts, such as biodiversity and ecosystem productivity, which are often not measured but represented by indices. The ecological concept are included in the model by using the latent variable and considering the error associated with the measurements of their indicators. The SEM is composed of two components:

1. The measurements model, includes the relationship between the latent variable and their respective in indicator.

2. The structural model, comprising the direct and indirect relationships between the latent variables.

Furthermore, the latent variable which predict other latent variables are named exogenous variable. The latent variables which requires at least one causal relationship from another latent variable are the endogenous variables. The indicator can be divided into two groups:

1. Reflective indicators are supposed to be consequence of the latent variable.
2. Formative indicators, which can be multidimensional, are the cause and affect the state of the latent variable.

In the study, we only used the reflective model type, as it seemed to be the most logical within an ecological context due to the association of the correlated indicators [Haenlein and Kaplan, 2004]. Two different approaches are used in the SEM analysis:

1. Covariance-based (CB) SEM [Jöreskog, 1973], aims to reproduce, as near as possible, the covariance matrix from the original data which is supposed to represent the mechanism of the relationships between the measured variables.
2. Partial Least Square (PLS) SEM [Lohmöller, 1989], is used to minimize the difference between the observed and the modeled covariances. The PLS, or maximum likelihood estimation has already been previously thoroughly described by authors [Grace, 2006]. The PLS SEM includes the characteristics of a multivariate statistical method, as the principle components analysis with multiple regression [Haenlein and Kaplan, 2004; Abdi, 2007]. Along with iterative regression processes, or even bootstrapping, it helps to overcome the limitations (i.e. model complexity and the ignore measurement error in predictor variables) in order to maximize the variances of the endogenous latent variables. Greater details of the development and use of the PLS SEM can be found in the following literature [Vinzi et al., 2010; Hair et al., 2011; Hair Jr et al., 2014].

The CB-SEM is mostly used as a confirmatory analysis for confirming previously established hypothesis regarding the theoretical relationship between concepts. In contrast, PLS SEM as a greater exploratory aim by focusing on maximizing the explained variance in the observed data [Hair Jr et al., 2014]. These conceptual differences made the PLS SEM better suited for the aim of the study. Moreover the PLS SEM is less strict regarding the data distribution, sample size and on the required number of indicators defining the latent variables [Hair et al., 2011]. More details on the differences and application of the CB-based and PLS SEM approaches are described in Chin [2010] and Hair et al. [2011]. Further reading on the differences and adequate application of the two approaches can be found in the literature (Chin 2010, Hair et al. 2011).

2.4.2 Model evaluation

PLS SEM approaches were chosen has no data distributional assumptions are required. Therefore the performance of the model is quantified with non-parametric measurements to explain the load of variance and the model power of prediction. Bootstrapping procedures were used to analyse the model uncertainties [Chin, 2010; Götz et al., 2010].

The model evaluation is a two step procedure:

1. The reliability and validity of the measured indicators representing the latent variables are assessed. The factor loading correspond to the correlation of each indicator to the latent variable [Hodapp et al., 2015].They indicate how much of the indicator's variance can be explained by the latent |latent variable. Values of > 0.7 imply a proportion of explained variance of more than 50%, which is regarded as acceptable.

2. The model 's structural pathways are evaluated. They are two satisfactory conditions which revealed if the indicators, associated with the latent variables, are adequately representing the convergent and discriminant validity. The Average variance extracted (AVE), Composite reliability [Fornell and Larcker, 1981] and CronBach's Alpha [Hodapp et al., 2015] are criteria for *convergent validity.* They are measure of models that theoretically *should* be related to each other are, in fact, observed to be related to each other (that is, you should be able to show a correspondence or *convergence* between similar latent variables). And the Heterotrait-Monotrait Ratio (HTMT) [Henseler et al., 2015] is a criteria for *Discriminant Validity.* It is a measure of models that theoretically *should not* be related to each other are, in fact, observed to not be related to each other (that is, you should be able to *discriminate* between dissimilar latent variables.).

The model should only be validated if, and only if, all the validity criteria are met. Then a bootstrapping procedures, over 1000 permutations, was used to reveal the significance of the relationship between latent variables.

Table 2.2: The evaluation measure and the threshold used for the model

Evaluation Measure	Accepted threshold
Factor Loading	> 0.7
Average Variance Extracted (AVE)	> 0.5
Composite Reliability	> 0.6
Cronbach's Alpha	> 0.6
Heterotrait-monotrait (HTMT) ratio of correlations	< 0.9

Chapter 3

Within Outlying Mean Indexes: refining the OMI analysis for the realized niche decomposition.

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3.1 Introduction

The ecological niche concept has been reactivated due to increasing concern over global environmental change, making the niche shift and the conservatism between different areas and time periods important fields of study [Peterson, 2011a]. The ecological niche of a species can be decomposed into two related components [Hutchinson, 1957]. First, the fundamental niche is the n-dimensional hypervolume within which the population of a species can persist, survive and reproduce indefinitely, and it is not constrained by any biological interactions. Secondly, the realized niche is the proportion of the fundamental niche within which the species actually persist, *i.e.*, taking into account the effect of abiotic and biological interactions. The fundamental niche cannot be measured by observation, but rather by broad examination of speciesâ physi-

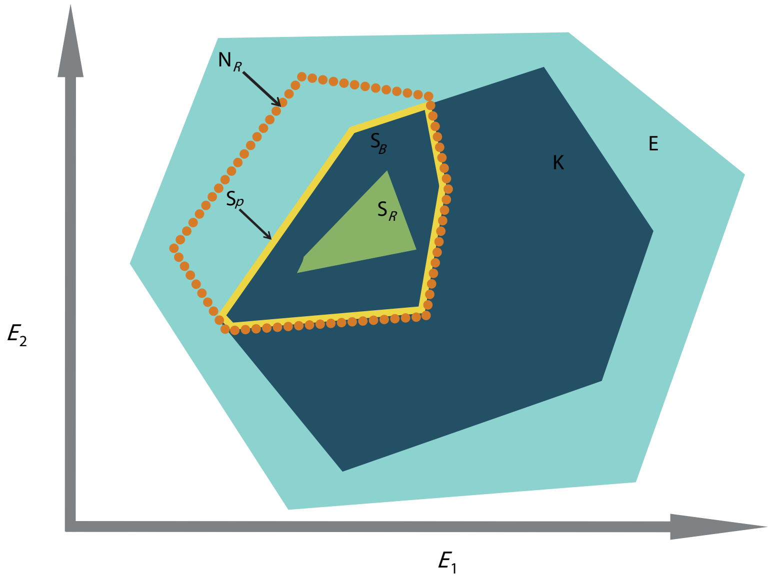

Figure 3.11: The concept of the existing fundamental niche and biotic interactions of Jackson and Overpeck [2000] adapted to the calculation of the realized subniche $\mathbf{S}_R$. $\mathbf{E}_1$ and $\mathbf{E}_2$ are the environmental gradients calculated after an ordination technique. $\mathbf{E}$ is the realized environmental space (filled light blue minimum convex polygon). $\mathbf{N}_R$ is the species realized niche (dotted orange contour). $\mathbf{K}$ is the subset realized environmental space (dark blue minimum convex polygon). $\mathbf{S}_P$ is the existing fundamental subniche (the yellow contour)- a union of $\mathbf{S}_B$ and $\mathbf{S}_R$. $\mathbf{S}_B$ is the subset biotic reducing factor (the part of $\mathbf{K}$ found within the orange contour), or biological constraint, and $\mathbf{S}_R$ is the realized subniche (the green minimum convex polygon).

ological requirements using mechanistic approaches [Peterson, 2011b]. On the contrary, the realized niche, in a community context, is the âdifferential habitat preferences of speciesâ [Braak and Verdonschot, 1995] and can be estimated by correlative approaches [Peterson, 2011a].

However, the lack of study on the role of biotic interactions (*e.g.*, competition, predation, mutualism, dispersal and colonization) is a major limitation for defining species' niches appropriately [Davis et al., 1998; Soberón and Nakamura, 2009]. Studies have shown that incorporating biotic factors can lead to better predictions of speciesâ distributions [Heikkinen et al., 2007], yet, despite this evidence, biotic factors are still underused and greater assessment is required to fully understand speciesâ niche dynamics [Soberón and Nakamura, 2009]. According to Jackson and Overpeck [2000], the constraints exerted on the realized niche by biotic process are the differences between the potential niche (*i.e.*, the intersection between the fundamental niche and the realized environmental space [Soberón and Nakamura, 2009]) and the realized niche; the realized environmental space being "the portion of the total n-dimensional environmental space that is actually represented [. . .] within a specified region at a given time" [Jackson and Overpeck, 2000]. Later on, the potential niche was renamed "the existing fundamental niche" by Peterson [2011b]. Therefore, the biotic interactions are the differences between the existing fundamental niche and the realized niche. The role of biotic interactions is not directly measurable by observation, as it requires an estimation of the fundamental niche. However, in order to estimate biological interactions, adaptation of the concept of the existing fundamental niche concept can be applied to the decomposed realized niche, which can be measured by observation. This concept requires the decomposition of the realized environmental space, $\mathbf{E}$, into subsets of the realized environmental space, $\mathbf{K}$, so that $\mathbf{K}$ is a subset of $\mathbf{E}$ (Figure 3.11). $\mathbf{K}$ represents the available conditions found within $\mathbf{E}$, at a smaller time and/or spatial scale than in $\mathbf{E}$. Now considering $\mathbf{N}_R$, the realized niche, found within $\mathbf{E}$, as the best estimation of the “fundamental niche” of the species under $\mathbf{K}$, the intersection between $\mathbf{K}$ and $\mathbf{N}_R$ represents the existing fundamental subniche, $\mathbf{S}_P$ (Figure 3.11). The existing fundamental subniche corresponds to the abiotically reduced part of $\mathbf{N}_R$ by $\mathbf{K}$. Therefore, $\mathbf{S}_P$ includes the subset biotic factor, $\mathbf{S}_B$, reducing $\mathbf{S}_P$ into the realized subniche, $\mathbf{S}_R$ (Figure 3.11). In summary:

$$\mathbf{S}_R \bigcup \mathbf{S}_B = \mathbf{S}_P = \mathrm{K} \bigcap \mathbf{N}_R$$

$\mathbf{S}_B$ can be caused by negative biological interactions (*e.g.* predation, competition, parasitism, etc.) but also can be due to dispersal limitation from the species itself (*i.e.*, lack of time for migration) or occupancy by another species [Peterson, 2011b] (Figure 3.11).

The realized niche can be measured directly from the n-dimensional hypervolume [*e.g.* Blonder et al., 2014] but ordination techniques are also well suited to investigate species and environmental relationships. The Outlying Mean Index (OMI) analysis is an ordination technique designed to explicitly take into account the ecological niche of each species within a community [Dolédec et al., 2000]. The OMI analysis seeks combinations of environmental variables that maximize average species marginality, *i.e.*, the squared Euclidean distance between the mean habitat conditions used by a species and the mean habitat conditions of the sampling domain (the sampling domain can be defined on a temporal and/or spatial scale). Ecologically, as Hernández-Fariñas et al. [2015] stipulated “species with high values have marginal niches (occur in less

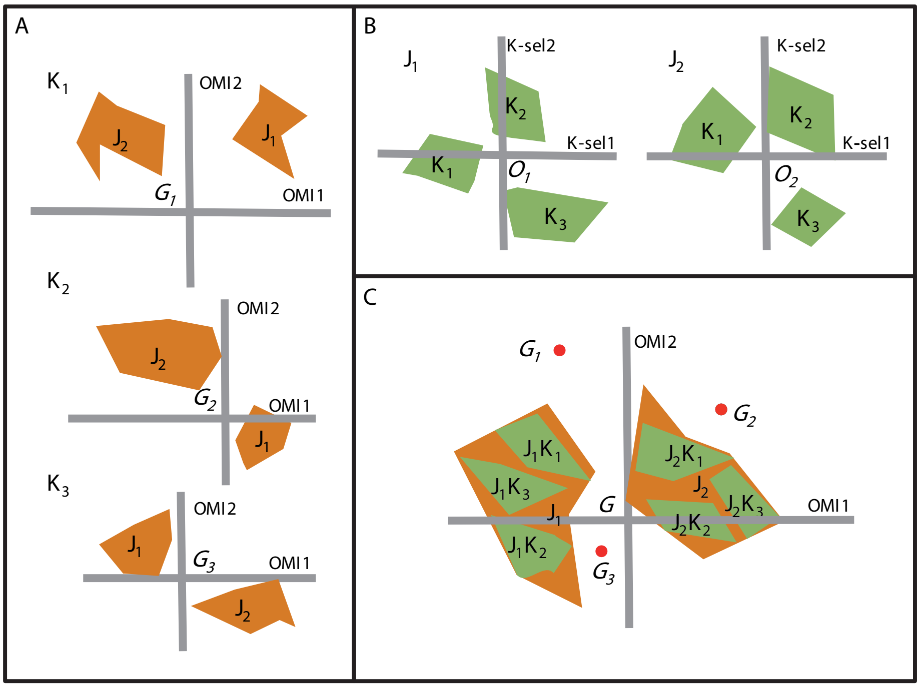

Figure 3.12: A) OMI analyses performed on three hypothetical subsets (K_1, K_2 and K_3) and two species (j_1, j_2). The three positions of the two species niches with their corresponding minimum convex polygon (*i.e.*, niche breadth) are not comparable across subsets (K_1, K_2 and K_3) because ordination is performed for each subset, creating new origins, G_1, G_2 and G_3 (*i.e.*, equivalent to the average habitat conditions used by the community). B) Separate K-select analyses performed for each species, j_1 and j_2, in the three subsets, K_1, K_2 and K_3. The resulting niches for each subset of the two species are not comparable because the origins O_1 and O_2 represent the average habitat used by the species j_1 and j_2 respectively. C) Species' niche position and breadth analyzed with the OMI analysis. WitOMI, further decompose the species niche into subniches (j_1 K_1, j_1 K_2, j_1 K_3 and j_2 K_1, j_2 K_2, j_2 K_3 for j_1 and j_2 respectively) and indexes can be calculated from G, WitOMIG. The black dots (G_1, G_2 and G_3), representing the average subset used by one assemblage, are used to calculate subniche indexes, WitOMIG_K.

common habitats in the studied region), and those with low values have non-marginal niches (occur in typical habitats in the region)". In other terms, in OMI analysis, the position of each species in the multidimensional space depends on its niche deviation from a uniformly distributed theoretical species, which would occur under all available habitat conditions (*i.e.*, ubiquitous). In addition, the technique provides information on species' niche breadth or tolerance where "high tolerance values are associated with taxa occurring in a wide range of environmental conditions (generalist taxa) while low values of tolerance imply that the taxa are distributed across a limited range of environmental conditions (specialist taxa)" [Hernández-Fariñas et al., 2015].

Beside OMI analysis, the K-select analysis is another ordination technique which is also based on marginality [Calenge et al., 2005]. The K-select analysis consists of a non-centered principal component analysis calculated on a table containing the marginality vector coordinates of a species population for the habitat variables [Calenge et al., 2005]. The output of the K-select analysis is a multicollinearity of habitat variables for which the marginality is the greatest; in other words, a synthesis of the variables which contribute most to habitat selection. The main difference between the two techniques concerns the weighting of the sampling units (SUs), *i.e.*, one unit of the sampling domain. The OMI analysis assumes the equal availability of SUs (*i.e.*, colonizable) to all monitored species regardless of time and/or space, whereas the K-select analysis considers an equal availability of SUs within each subset (*i.e.*, group of SUs) of the sampling domain (*e.g.*, seasons within a year or sites within a region for one species) [Thomas and Taylor, 1990]. Let us consider an assemblage of two species (j_1 and j_2) collected within a sampling domain divided into three subsets (K_1, K_2 and K_3). To study species' niche dynamics within the community over the three subsets, one can perform three separate OMI analyses, *i.e.*, one for each subset (Figure 3.12A) or two K-select analyses, *i.e.*, one for each species (Figure reffig:Figure2bB). However, whichever of the two analyses used, a new environmental gradient is created for each analysis performed.

To study niche dynamics, some researchers have used several distinct OMI analyses on habitat condition subsets. For example, Grüner et al. [2011] performed 40 OMI analyses (one per year) on a time series of three phytoplankton species to depict their temporal niche trajectories. Hof et al. [2010] performed 14 OMI analyses (one per region and per family) to assess the phylogenetic relatedness between different amphibian families and genera within each geographical region. Mérigoux and Dolédec [2004] performed two OMI analyses on freshwater invertebrates (one per season, spring and autumn) to address seasonal shifts in the hydraulic niche of taxa. One drawback of these approaches lies in the available habitat conditions [as defined by Dolédec et al. [2000]], which may greatly vary between each subset, impacting the calculations of indexes such as marginalities and tolerances (Figure 3.12A). As a result, the observed changes in marginalities can be partly attributed to temporal [annual for Grüner et al. [2011] and seasonal for Mérigoux and Dolédec [2004]] or spatial changes [Hof et al., 2010] in average habitat conditions used by taxa in the assemblage. Hence, performing separate OMI analyses on different habitat condition subsets, using the same domain of habitat conditions, does not make the species' niches comparable across subsets, because average habitat conditions most likely vary from one subset to another. To our best knowledge, K-select analyses have not yet been performed on species assemblages, but rather on several populations of one species (reindeer) [Pape and Loffler, 2015]. In this case study, the authors performed 9 K-select analyses (one population per season), creating 9 different habitat gradients [Pape and Loffler, 2015]. However, the average habitat conditions used changed for each ordination, giving different meanings to the marginality values for each analysis, making comparisons between seasons inaccurate.

Here, our main goal is to provide a method to estimate the dynamics of the realized subniches, $\mathbf{S}_R$, of each species of an assemblage, compared to G, representing the overall average habitat condition found in $\mathbf{E}$. Furthermore, the subniche can also be compared to G_K, which represents the average subset habitat conditions found in **K.** We therefore, propose to combine the properties of the OMI analysis (maximizing the average species marginality within a community) and the K-select marginality decomposition within a species (maximizing the species marginality within subsets, *i.e.*, the subniche). Our proposal allows comparing the ecological niche and ecological subniches of species in the n-dimensional environmental space, by fixing the ecological conditions using the OMI analysis (Figure 3.12C) and then decomposing the occupation of the realized niche in the same manner as the preliminary calculations of K-select analysis. In addition, it describes the possible subniche shift and/or conservatism of species within an assemblage across temporal an/or spatial subsets within the habitat conditions of the sampling domain. Finally, the difference between the existing fundamental subniche, $\mathbf{S}_P$, and the realized subniche, $\mathbf{S}_R$, would therefore correspond to the observed biological constraint, $\mathbf{S}_{B.}$ We illustrate the potential of this method using published studies including both a temporal case [seasonality; see Mérigoux and Dolédec [2004]] and a spatial case [longitudinal stream gradient; see Dolédec et al. [2000]].

3.2 The Within Outlying Mean Indexes (WitOMI) concept

The Outlying Mean Index measures the marginality of a species (*i.e.*, the weighted average of sampling units used by the species) from the average condition of the sampling domain, G [Dolédec et al., 2000]. OMI originates from the combinations of $\mathbf{Z}_0$, the standardized environmental variable table, and Fr, the species frequency table. Here, we aim to estimate the niche occupation dynamics of each species within the community, at different subsets of habitat conditions within the sampling domain. In other words, we aim to scrutinize the subniches of species within a community in the same reference plane, made by the resulting factorial axes from the OMI analysis. The subniche is defined hereafter, as a subset of habitat conditions used by a species.

Inspired by the OMI analysis [Dolédec et al., 2000] and the decomposition of marginalities used in K-select analysis [Calenge et al., 2005], we propose to calculate two additional marginalities. First, the Within Outlying Mean Index to G (WitOMIG) is the species marginality (*i.e.*, the weighted average of sampling units of a given subset used by the species) to the average habitat conditions of the sampling domain (G; see Eq. 2.7 in materials and methods). Second, the Within Outlying Mean Index to G_K (WitOMIG_K) is the species marginality compared to the average habitat condition used by the community in a K subset habitat conditions (G_K; see Eq. 2.16 in materials and methods).

To obtain WitOMIG, we first calculate the species frequency relative to each $\mathbf{K}$ subset (with $1 \leq \mathbf{K} \leq N$). Second, the N Fr_K matrices are concatenated to yield the overall species frequency table (Fr^*). Third, the standardized environmental table $\mathbf{Z}_0$ is used in combination with (Fr^*) to calculate WitOMIG following the Eq. 2.7 in materials and methods.

The calculation of WitOMIG_K first requires centering each of the k subsets of the standardized environmental table $\mathbf{Z}_0(n \times p)$, independently yielding several matrices $\mathbf{Z}_{K^*}$. The N $\mathbf{Z}_{K^*}$ are then concatenated to yield another environmental table $\mathbf{Z}^*$. Finally, $\mathbf{Z}^*$ is used in combination with (Fr^*) to calculate WitOMIG_K following the Eq. 2.16 in materials and methods.

OMI analysis is then used as the reference ordination technique. The subniche coordinates in the n-dimensional space, R^p, are projected onto the OMI factorial plane by multiplying their values by the corresponding eigen-vectors. As a result, the niche and the subniche parameters (marginality and tolerance) of the species are all in the same reference factorial plane.

WitOMIG and the WitOMIG_K calculations are shown in materials and methods, and do not include the OMI calculations and the OMI analysis, which are fully described in Dolédec et al. [2000]. The WitOMI calculation, as well as other computational tools, is available in the “subniche” package for R software [R Core Team, 2013] and can be downloaded for free at the `http://cran.r-project.org`. The "subniche" tutorial, is available at `https://github.com/KarasiewiczStephane/WitOMI`.

3.2.1 Statistical significance

The statistical test for significance of the species marginality in the K subsets, which is inspired from Dolédec et al. [2000], uses a Monte Carlo test [Manly, 1991]. First, the significance of the subset habitat conditions K was calculated by considering the equiprobability of $n!$ permutations of the habitat conditions table $\mathbf{Z}_0$. We compared the observed average of subset habitat conditions, G_K, to the distribution of the 1000 permutations values following the null hypothesis that G_K is not different from overall average habitat conditions, represented by G.

The significance of the species marginalities from the average habitat condition G, WitOMIG, and from the average subset habitat conditions G_K, WitOMIG_K, were calculated by considering the equiprobability of $k!$ permutations of the species profile $\mathbf{Fr}_K$. Second, a comparison of the observed WitOMIG (Eq. 2.7, materials and methods), and WitOMIG_K (Eq. 2.16, materials and methods) with the distribution of the 1000 permutations values, found under K subsets, following the null hypothesis that the species within a subset is uninfluenced by its overall average habitat conditions (ubiquitous), for WitOMIG and by subset habitat conditions for WitOMIG_K respectively. Third, the means of the observed WitOMIG and WitOMIG_K across the K subsets were compared to their respective simulated mean.

3.2.2 Graphical display

The graphical display of the species’ realized niche and subniche can be obtained by projecting the available SUs of matrix $\mathbf{Z}_0$ on the first two factorial axes of the OMI analysis (OMI1 and OMI2 in Figure 3.13 and 3.14),

$$\mathbf{Z}_0^{\mathbf{u}} = \mathbf{Z}_0 \times \mathbf{u}$$

with $\mathbf{u}$ being the eigenvectors chosen after the OMI analysis and $\mathbf{Z}_0^{\mathbf{u}}$ corresponding to the matrix of coordinates of all available SUs projected onto the OMI analysis plane.

The graph origin is the center of gravity of all available SUs, G, which represents mean overall habitat conditions. Similarly, the subset origin, G_K, is the barycenter of available k SUs within the K subset, since $\mathbf{Z}_{K^*}$ is centered. The species niche and subniche positions correspond to the weighted mean of coordinates, whose weight is equal to the species frequency (See materials and methods). Finally, the minimum convex polygon's contour of available SUs (black in Figure 3.13 and 3.14) and of used SUs (blue and the purple dotted and dashed in Figure 3.13 and 3.14) complete the realized niche and subniche breadth representation of species. The the minimum convex polygons were drawn with the package "ade4“ for R software [Dray and Dufour, 2007]. The species niche and subniche positions and their respective minimum convex polygons, relative to the origins, give us an idea about the habitat conditions used by species within the constraining habitat highlighted by the OMI analysis.

3.3 Ecological application

To illustrate the potential of combining the OMI analysis with the WitOMI we used two data sets that address the question of subniche dynamics according to temporal or spatial characteristics of the habitat.

3.3.1 Temporal subniche dynamics

The first data set investigated the hydraulic requirement of 57 invertebrate taxa [Mérigoux and Dolédec, 2004]. Herein, instead of performing an OMI analysis for each season (*i.e.*, spring and autumn as done by authors) we performed one for the entire year. 35 out of 57 taxa had significant outlying mean indexes (Appendix 1; Table S3). We selected the first two OMI axes, which represented 89% of the explained variability (Figure 3.13A), in order to represent the subniches. As depicted by Mérigoux and Dolédec [2004], the first axis shows that FST hemisphere number and Froude number are the most influential hydraulic parameters on the species' realized niche (Figure 3.13B and 3.14C). WitOMI were then calculated for spring and autumn for each of the 35 significant species. All WitOMI (WitOMIG and WitOMIG_K) were significant (Appendix 1; Table S3).

As an example, *Caenis* sp. used an uncommon habitat (OMI =2.09) compared to the rest of the community (Appendix 1; Table S3). *Caenis* sp. has a preference for high bed roughness compared to most species (Figure 3.13B and C). A similar pattern can be found with its realized subniches (WitOMIG =

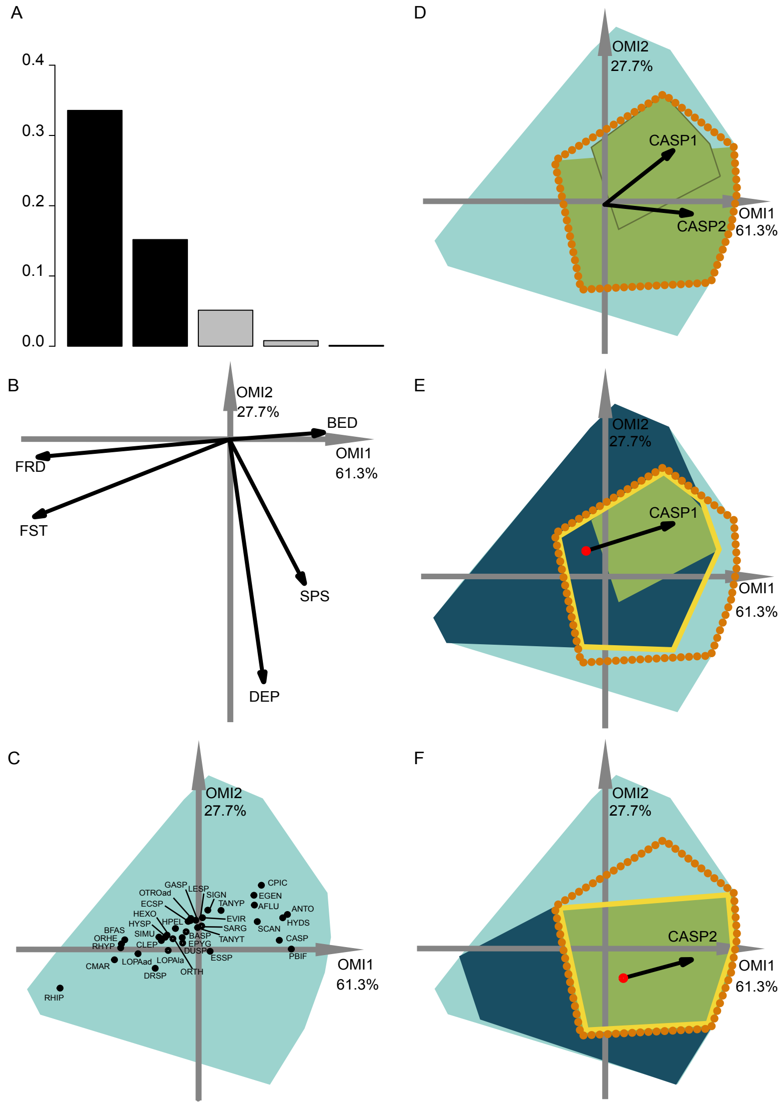

Figure 3.13: OMI analysis of the invertebrate community and the WitOMI. A) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axes. The black bars are the chosen factorial axis, OMI1 and OMI2. B) Canonical weights of environmental variables (FRD = froude, FST = hemisphere number, BED = bed roughness, SPS = substratum particle size and DEP = Depth). C) Representation of the statistically significant species' realized niche positions on the first two factorial axes (Appendix 1; Table S1) (see codes in Appendix 1; Table S3). The light blue minimum convex polygons represent the habitat conditions constraint of all SUs domain. D) The realized subniches dynamism of *Caenis* sp. (CASP) is the green minimum convex polygon, subsetting the realized niche, the orange dotted polygon. The arrows represent the WitOMIG. E and F represent the *Caenis* sp. realized subniches under the subset habitat conditions K, the dark blue polygon, subsetting the existing fundamental subniche (the yellow contour), encountered in spring and autumn for E and F respectively. The red dots represent the suborigin, G_K and the arrows represent the WitOMIG_K.

2.28 and 2.24 for spring and autumn respectively) (Appendix 1; Table S3). The realized subniche positions demonstrate a shift, seemingly caused by the increasing depth in autumn (Figure 3.13D). *Caenis* sp. tolerance also showed an increase from spring to autumn (Tol = 0.45 and 0.75 respectively) (Appendix 1; Table S3). Now considering each season separately, *Caenis* sp occupied different parts of its realized niche (Figure 3.13E and F). *Caenis* sp. thus used a more atypical habitat compared to the one used by the assemblage in spring and autumn (WitOMIG_k = 2.44 and 2.46) (Appendix 1; Table S3). Despite the seasonal habitat change, the marginality of the habitat used by the species stayed similar. The tolerance also increased when considering the two habitat conditions separately (Tol =0.46 and 0.75). *Caenis* sp. occupied a greater part of its existing fundamental subniche in autumn than in spring, which suggests more appropriate abiotic conditions or less constraint by biotic interactions.

In spring, the *Caenis* sp. realized subniche (the green minimum convex polygon, Figure 3.13E) did not fully occupy the intersection between the niche (orange dotted contour) and the subset habitat condition (dark blue minimum convex polygon) (*i.e*, existing fundamental subniche). Herein, the empty part of the existing fundamental subniche therefore corresponds to the biological constraint exerted on the species realized subniche. The decreasing biological constraint exerted on the *Caenis* sp. realized subniche from spring to autumn seems to be correlated with the decreasing number of species having a significant marginality (35 to 23 from spring to autumn).

3.3.2 Spatial subniche dynamics

The second data set investigated the fish assemblages used by Dolédec et al. [2000]. We selected the first two OMI axes, which represented 97.9% of the explained variability, in order to represent the realized subniches (Figure 3.14A). We divided the data along the first axis, which is mostly defined by altitude and slope, considering distinct upstream and downstream habitat conditions. All of the WitOMI (WitOMIG and WitOMIG_k) were significant (Appendix 1; Table S4).

As an example, minnow (*Phoxinus phoxinus*), was distributed over the entire longitudinal gradient and used common habitat (OMI=0.45). However, the used habitat was more marginal downstream than upstream (WitOMIG = 0.33 and 4.61 for upstream and downstream respectively) (Figure 3.14D) (Appendix 1; Table S4). In addition, we observed a shift in the species' marginality and tolerance within its realized niche (Figure 3.14D). The reason for the realized subniche change in marginality and tolerance can be explained by the difference between upstream and downstream subset average habitat conditions (red dot, Figure 3.14E and F) and subset habitat condition constraints (dark blue minimum convex polygon, Figure 3.14E and F), impacting the species' realized niche. Focusing on the upstream and downstream habitat conditions separately, minnow's marginality upstream was higher than downstream (WitOMI$G_K = 0.3$ and 0.04 for upstream and downstream respectively) (Appendix 1; Table S4). In both conditions, the species used a similar habitat to the one used by the assemblage. Furthermore, upstream conditions seemed to have greater constraint on the species realized niche occupation, contracting the minnow realized subniche breadth (Figure 3.14E), whereas downstream conditions allowed the species to occupy a greater part of its existing fundamental subniche (Figure 3.14F).

In addition, both young and adult trout were found along the entire longitudinal gradient with a preference for upstream conditions (WitOMIG_K= 0 for old and young trout respectively) (Appendix 1; Table S2). Minnow, stone loach and chub were mostly found downstream while the nase, southwestern nase and streambleak species were exclusive to downstream average habitat conditions (Appendix 1; Table S2). These results were coherent with those of Dolédec et al. [2000] on the same data set (Figure 3.14C). In addition, WitOMI showed that the conditions found downstream offered greater habitat variability because other environmental variables, aside from altitude and slope, influenced speciesâ subniches. The greater variability of habitat downstream permitted hosting more species than upstream, where trout appeared to use most of the habitat conditions.

3.4 Discussion

The WitOMI offer new interpretations to niche dynamics by considering subsets of habitat conditions within which the species' realized subniches are developed. WitOMI complement the OMI approach by shifting how realized niches are perceived along fluctuating habitat conditions. WitOMI make all realized subniches comparable along the same environmental gradient as they all refer to the same OMI analysis. The realized subniche parameters can be explained by the average habitat conditions used by the assemblage over the entire sampling domain, WitOMIG, and by the average habitat conditions used within a subset of SUs WitOMIG_K. The advantage of decomposing the realized niche into realized subniches is that the WitOMI are simple measures, which integrate the species realized subniche specialization from the habitat studied (WitOMIG) and from the decomposed habitat (WitOMIG_K), giving

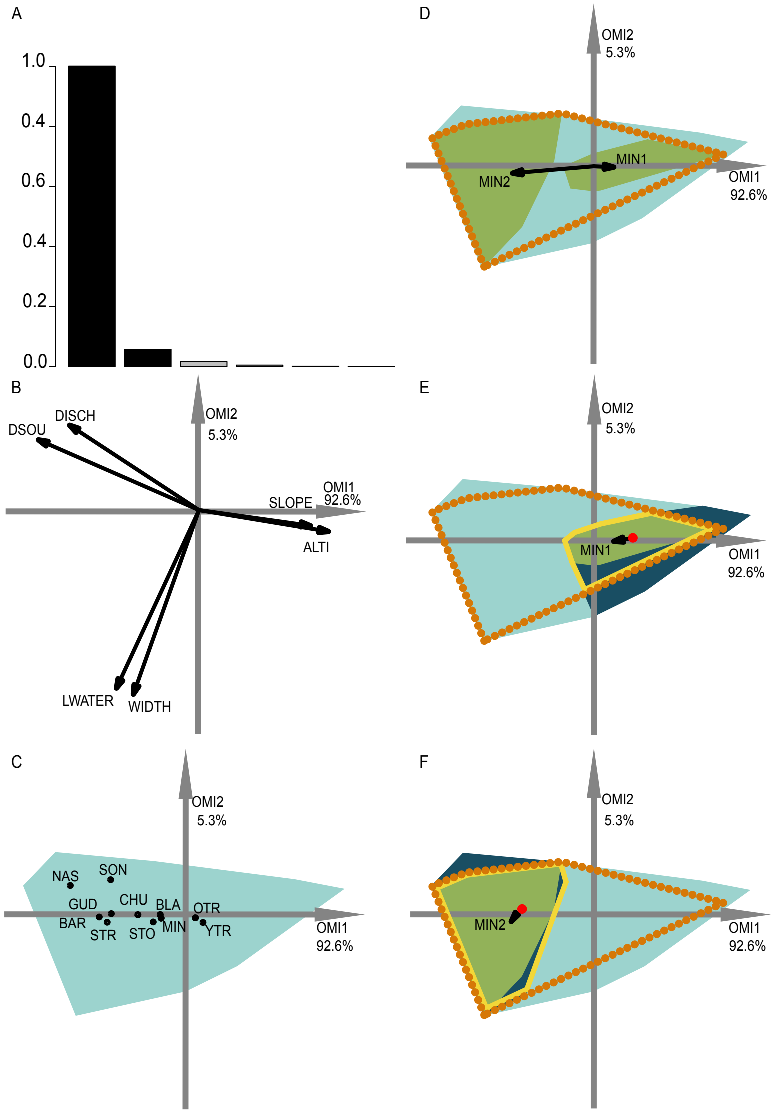

Figure 3.14: OMI analysis of the streamfish and the WitOMI. A) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axes. The black bars are the chosen factorial axis OMI1 and OMI2. B) Canonical weights of environmental variables (DSOU = distance to the source, DISCH = mean annual discharge, LWATER = lowest monthly discharge occurring every five years, WIDTH = mean stream width, SLOPE = slope, and ALTI = altitude). C) The realized niche position on the first two factorial axes of the significant species (Appendix 1; Table S4) (see codes in Appendix 1; Table S4). The light blue minimum convex polygons represent the habitat conditions constraint of all SUs domain. D) The realized subniche dynamics of Minnow (*Phoxinus phoxinus*) are the green minimum convex polygons, subsetting the realized niche, the orange dotted minimum convex polygon. The arrows represent the WitOMIG. E and F represent the Minnow (*Phoxinus phoxinus*) realized subniches under the habitat conditions constraint, the dark blue minimum convex polygon, subsetting the existing fundamental subniche (the yellow contour), encountered upstream and downstream for E and F respectively. The red dots represent the suborigin G_K and the arrows the WitOMIG_K.

additional hints on the role played by different environmental variables. However, our approach has the same experimental limitation as the OMI analysis. The environmental variables used may not be sufficient to define the realized niche parameters, making the decomposition of the realized niche into realized subniches irrelevant.

The reference species, which represents a theoretical ubiquitous species using the overall average habitat conditions of a sampling domain, helped quantify the shift in realized subniches. The utilization of G as a reference smoothens the atypical conditions, avoiding an over-interpretation of habitat condition effects on the species' niches. Reconsidering the results of Mérigoux and Dolédec [2004], who performed a separate OMI analysis on each season, we found less species common to both seasons with a significant marginality (23 herein and 35 in Mérigoux and Dolédec [2004]). Nonetheless, the pattern found in Figure 3.15 was similar to the one found in Figure 3.12 of the authors, *i.e.*, with more species in autumn having significant marginality than in spring, thus underlying the fluctuating effect of hydraulic constraints advocated by the authors (Appendix 1, Table S1). The WitOMI thus provide more relevant comparable values. In addition, the use of G_K, which can be representative of more variable conditions, can provide additional information about the environmental variables driving the species niche and community composition.

However, the method is limited by the number of SUs defining the sampling domain. This limitation underlines the inapplicability of the WitOMI to an unsignificant realized niche of the OMI analysis. WitOMI are also limited by the number of subsets used to decompose the sampling domain. In the ecological application, we used two subsets of habitat conditions to decompose the realized niche into two realized subniches. The K SUs defining a subset have an impact on the subniche parameters' significance. Even if it was not the case in our study, a low number of SUs within subsets can cause the test of significance to give a low probability of estimating subset habitat conditions (G_K).

Realized subniches can be compared to their respective subset origins, the subset theoretical ubiquitous species using the most general subset of habitat conditions, in how they differ from G. This comparison provides a more detailed interpretation in the realized niche shift. For instance, similar to Dolédec et al. [2000], there was a negative relationship between species richness and realized niche breadth (Figure 3.16). The negative relationship was greater upstream ($R^2 = 0.68$ and 0.21 for upstream and downstream respectively)(Figure 3.16). In other words, there was increasing competition upstream because the

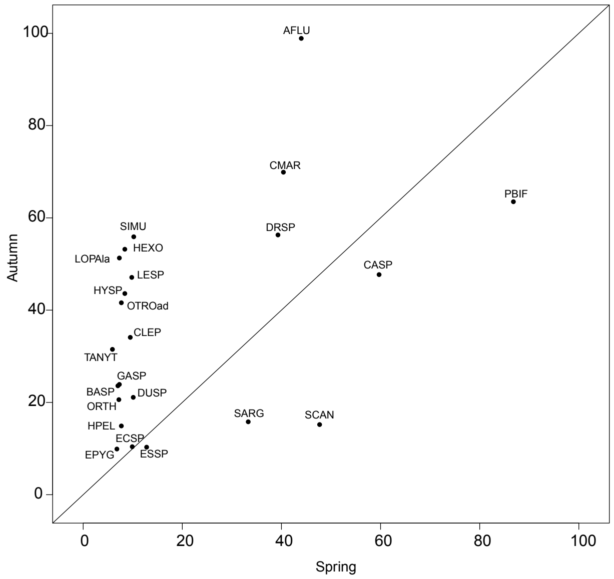

Figure 3.15: Within Outlying Mean Index to G values (as percentage of the total variability, Appendix 1; Table S1) of the 23 significant taxa common to both seasons. Names are abbreviated using codes given Appendix 1: Table S4.

most common species (with the lowest WitOMIG_k) found upstream, the trout (WitOMI$G_k = 0$ for upstream), has a broad realized subniche upstream (Tol = 1.62 and 1.09 for upstream and downstream respectively), which decreases species diversity (8 and 11 species for up and downstream respectively). In this spatial example, the WitOMIG_k allows assessing which species were common upstream, giving a more accurate description of the fish distribution pattern Dolédec et al. [2000], and community structure.

The subsets of habitat conditions and the two WitOMI can be tested with random permutations to assess whether subset habitat conditions and the species marginality are significantly different from what would be expected by chance. They follow the null hypothesis that the subset habitat conditions G_K are not different from the overall habitat conditions G, and that a species is not influenced by habitat conditions for WitOMIG, or by the subset of habitat conditions for WitOMIG_K. Lack of significance in the permutation test can be explained by the defined subset conditions, which might not be appropriate enough, making G_K weakly relevant and the WitOMI unsignificant. This emphasizes the need for a reference habitat condition and a significant realized niche $\mathbf{N}_R$ (*e.g.* OMI analysis), which can be further decomposed to study realized subniche dynamics. The total inertia of the species (see Eq. 13, in

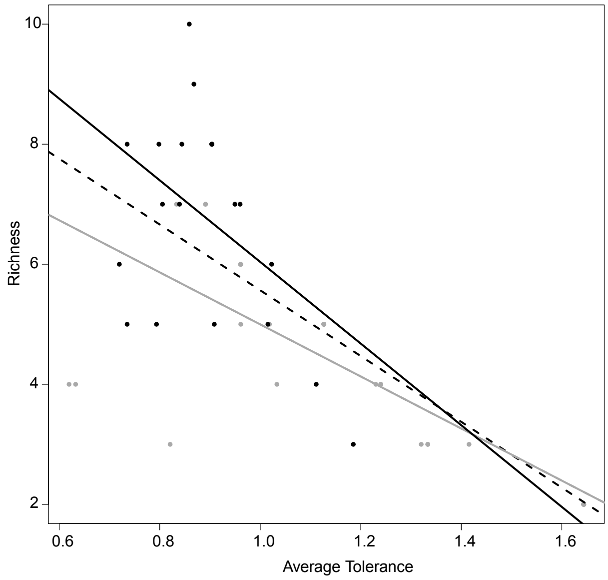

Figure 3.16: Relation between the average tolerance values of sites upstream and downstream, and their fish species richness. Overall, dashed black line, $R^2 = 0.64$ with $P<0.001$; Upstream, grey line, $R^2 = 0.68$ with $P<0.001$; Downstream, plain black line $R^2 = 0.21$ with $P = 0.034$.

materials and methods) characterizes the decomposition of the realized niche, $\mathbf{N}_R$, calculated with the OMI analysis, into the species realized subniches, $\mathbf{S}_R$, within the subset habitat conditions, G_K.

The decomposition of the realized niche allows estimating the biological constraints, $\mathbf{S}_B$, exerted on a species (*e.g. Caenis* sp) in our temporal example. The comparison between the subniche, $\mathbf{S}_R$, and the existing fundamental subniche, $\mathbf{S}_P$,revealed an unused part of $\mathbf{S}_P$ which can be attributed to biological constraints. The quantification of biological constraints is dependent on the envelope chosen to represent the niches and subniches. Quoting Guisan et al. [2014] the niche envelope is "the envelope of conditions in multivariate environmental space defining a species niche. The boundary of the envelope can be defined in many different ways *e.g.*, percentiles; Broennimann et al. [2012]." In this study we used the minimum convex polygon. Therefore our quantification of the biological constraints, $\mathbf{S}_B$, consisted of measuring the difference between the area of $\mathbf{S}_P$ and $\mathbf{S}_R$. The biological constraints can be given in percentage of the $\mathbf{S}_P$ area but is the minimum convex polygon truly the best envelope? For example, (Blonder et al. 2014) developed a method to calculate the n-dimensional hypervolume which can be used to quantify the hypervolume of $\mathbf{N}_R$, $\mathbf{S}_R$, $\mathbf{S}_P$ and the biological constraints. As suggested by [Blonder et al., 2014], hypervolume might have holes, which may be the equivalent of the biological constraints of a species niche estimated, within the n-dimensional hypervolume. This perspective could bring further insight into the invasive species strategy as explained in Blonder [2016]. $\mathbf{S}_B$, which is now quantifiable under subset habitat conditions, can be of a different nature. It can either be due to negative biological interactions, or dispersal limitation [Peterson, 2011b]. As a result, caution should be taken while interpreting the nature of $\mathbf{S}_B$.

The description of the subset conditions of the different variables can reveal how the community responds to changing habitat conditions. We can imagine the case where the shifted speciesâ realized subniches do not shift in the same direction as the sub-origins. What mechanisms would be involved in species realizing their niches? Would the community be threatened by a changing environment? These questions emphasize the need for using the WitOMI that enables comparing different speciesâ realized niches in a community under changing habitat conditions. Our proposed refinement of the OMI analysis allows us to make hypotheses on the mechanisms involved in a species realizing its niche. The ecophysiological requirements of species should vary with changing habitat conditions, since species must respond to the environmental variation in order to survive. Kleyer et al. [2012] recently developed this idea using the Outlying Mean Index followed by Generalized Additive Modelling (OMI-GAM). First, the method consists of using the OMI analysis to determine the speciesâ responses to habitat conditions and their realized niche positions and breadths. Second, traits are used as explanatory variables in a generalized additive model (GAM) to explain the above species responses. The OMI-GAM thus answers the question "How do trait expressions of species respond to environmental gradients?" Similarly, the WitOMI could be used as a first step of OMI-GAM to study trait expressions within different habitat conditions and to reveal shifts in species life-strategies via a change in the functional trait hierarchy.

The main strength of Within Outlying Mean Indexes is that they can be applied to any species, population, community, or ecosystem. Regarding the previous example, reanalyzing the data with the WitOMI, should improve the accurary and details of the results [Hof et al., 2010; Grüner et al., 2011; Pape and Loffler, 2015]. This proposal can be used in various aspects of ecology, such as the structure and dynamics of populations and interactions among individuals of the same or different species. In the context of global change, the methods can reveal the response of individuals and groups of organisms, and the organization of biological communities [Hof et al., 2010; Grüner et al., 2011]. The WitOMI can be used as a statistical basis for future ecological niche models such as modelling the potential of an invasive species to establish itself in a new ecosystem [Broennimann et al., 2012; Guisan et al., 2014]. As a perspective, the WitOMI can be applied to study community responses to environmental change, including the impacts of possible community resource-competition.

3.5 Acknowledgements

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Chapter 4

Environmental response of *Phaeocystis* spp. realized niche

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4.1 Introduction

The predicted global environmental change at a unprecedented rate [Drijfhout et al., 2015], increases With regard to the potential linkage with the spread and impact of harmful algae blooms (HAB) worldwide [Fu et al., 2012; Hallegraeff, 2010; Wells et al., 2015]. Attempts to make the link between HABs or undesirable species and anthropogenically-altered environment have been often 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 HABs bloom emphasize the idea that other factor, than abiotic variables, play an important role in driving HABs [Bianchi et al., 2000; Borkman et al., 2016; Yin, 2003].

The genus *Phaeocystis* is one of the most worldwide spread marine haptophytes [Lancelot et al., 1994]. Although not 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]. During these periods, *Phaeocystis* spp. can potentially alter the structure and functioning of ecosystems. Besides biodiversity loss [Christaki et al., 2014], the considerable input of organic matter into coastal ecosystems disrupts the mesozooplankton trophic relationships (*e.g.* [Daro et al., 2006; Gasparini et al., 2000; Rousseau et al., 2000]. The *Phaeocystis* colonies resist against grazing and viral infection [Schoemann et al., 2005], and further provoke various adverse effects on fish [Levasseur et al., 1994; Rogers and Lockwood, 1990] and shellfish stocks [Davidson and Marchant, 1992; Pieters et al., 1980; Prins et al., 1994; Smaal and Twisk, 1997].

Current research strategies, methods and hypotheses of how environmental pressures mechanistically affect HAB species [Wells et al., 2015], including *Phaeocystis* spp. Modellisation [Lacroix et al., 2007; Lancelot et al., 2014; Passy et al., 2016], experiments [Veldhuis et al., 1991], *in situ* measurements [Bonato et al., 2016, 2015; Houliez et al., 2013], and remote sensing imaging [Kurekin et al., 2014] were previously used to explore these links. The former studies were based on the hypothesis that *Phaeocystis* spp. blooms could be predicted from environmental variables only. The proliferation of *Phaeocystis* seemed to be favored by the excess of nitrate and limiting silicate [Bradley et al., 2010; Breton et al., 2006; Egge and Aksnes, 1992; Lancelot et al., 1987; Lundgren and Granéli, 2010; Reid et al., 1990], and sufficient underwater light intensity [Breton et al., 2017; Jahnke, 1989; Peperzak et al., 1998]. Furthermore, the appearance of *Phaeocystis* was correlated with high N:Si [Tett et al., 1993; Tett and Walne, 1995] and/or high N:P ratio [Riegman and Noordeloos, 1992] and also frequently with elevated salinity [Borkman et al., 2016]. More recently, Breton et al. [2017] had demonstrated with a trait-based approach, that competitive exclusion prevails during the bloom of *Phaeocystis*, in the coastal waters of the eastern English Channel. In these waters, the bulk of biomass is represented by diatoms [Breton et al., 2000; Cadée and Hegeman, 1974; Grattepanche et al., 2011; Uitz et al., 2010]. However, the use of diatoms at a coarse taxonomic level in the study of [Breton et al., 2017], was not fine enough to reveal the potential competitors for resources of *Phaeocystis* spp.

Hutchinson's niche concept (1991) allows studying the link between global changes, and the diatom community in relation with *Phaeocystis* spp.. Among the several multivariate analysis available for niche analysis [Braak, 1986; Calenge et al., 2005; Ter Braak, 1987].Hernández-Fariñas et al. [2015] used the niche approach 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 (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 which is not used by the species despite being available to it. 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 following aim. Herein, we intend to understand how the environment influences *Phaeocystis* spp. realized niche by determining the effects of N, P and Si concentration (and their ratios), photosynthetically active radiation, salinity and turbidity. Moreover, in the context of HAB, we intend to reveal how the diatoms, which are present before and/or during *Phaeocystis* spp. blooms, can influence its realized niche. The estimation of the biological constraint should reveal the impact of biological processes on the blooming of *Phaeocystis* spp. and further implications on potential competitors will be discussed.

4.2 Methods

4.2.1 Data set

The data was retrieved from the study of Hernández-Fariñas et al. [2015] who used the 1998-2012 period of the French REPHY-IFREMER network (Réseau d'Observation de Surveillance du Phytoplancton et des Phycotoxines) collecting information on the species composition and abundance of the phytoplankton communities along the coasts of France since 1987, on a fortnightly to a monthly basis. In parallel, seawater temperature (°C), salinity (measured using the Practical Salinity Scale), turbidity (NTU), inorganic nutrient concentrations (dissolved inorganic nitrogen, silicates, and phosphates in μmol. L^{-1}) and photosynthetically active radiation (PAR, $W.m^{-2}$) were measured. Note that

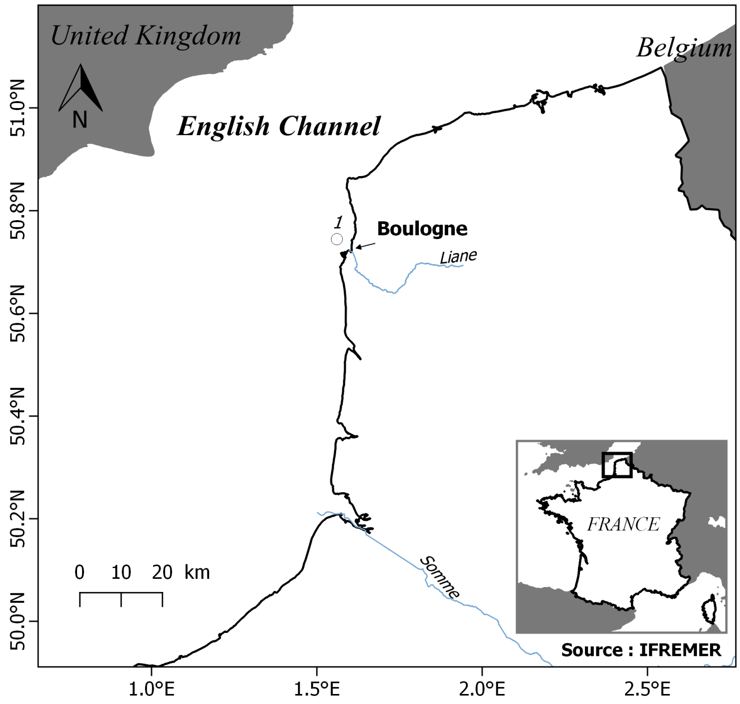

Figure 4.17: Map of North of France with the main station location the French REPHY-IFREMER network

PAR is the cumulative sum over the five days preceding phytoplankton sampling. Unlike Hernández-Fariñas et al. [2015], we focused on the coastal station 1 of Boulogne-sur-mer because the waters which are known for recurent *Phaeocystis* blooms (Figure 4.17).

4.2.2 Subsets creation

In order to understand the impact of biotic and abiotic factors on *Phaeocystis* realized niche, we created two data subsets that gathered years of high and low *Phaeocystis* spp. annual mean abundance events (named thereafter 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 to decipher 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 and Warwick, 2001] with 10000 reiterations was performed to extract the species which correlated the most with the entire diatom community during subsets L and H. The diatom species representing at best the community, under both subsets, were used to describe the succession under each subsets. 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.

4.2.3 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 in regard to 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 (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, which would occur at all the 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], revealed the species distribution within the subset habitat conditions. The statistical significance of marginality was tested using Monte Carlo permutation procedure [Manly, 1966] with 10000 permutations.

4.2.4 Biological constraint

The existing fundamental subniche, $\mathbf{S}_P$, corresponds to the realized niche, $\mathbf{N}_R$, which is reduced abiotically by the subset habitat conditions, $\mathbf{K}$. Therefore, $\mathbf{S}_P$ includes the subset biotic factor, $\mathbf{S}_B$, reducing $\mathbf{S}_P$ into the realized subniche, $\mathbf{S}_R$ (Figure 4.18). In summary:

$$\mathbf{S}_R \bigcup \mathbf{S}_B = \mathbf{S}_P = \mathrm{K} \bigcap \mathbf{N}_R$$

$\mathbf{S}_B$ represents the negative biological interactions (e.g. predation, competition, parasitism, etc.) and the species dispersal limitation (*i.e.*, lack of time for migration) or occupancy by another species [Peterson, 2011a] (Figure 4.18). $\mathbf{S}_B$ unit is in percentage of $\mathbf{S}_P$, and represents the biological constraint exerted

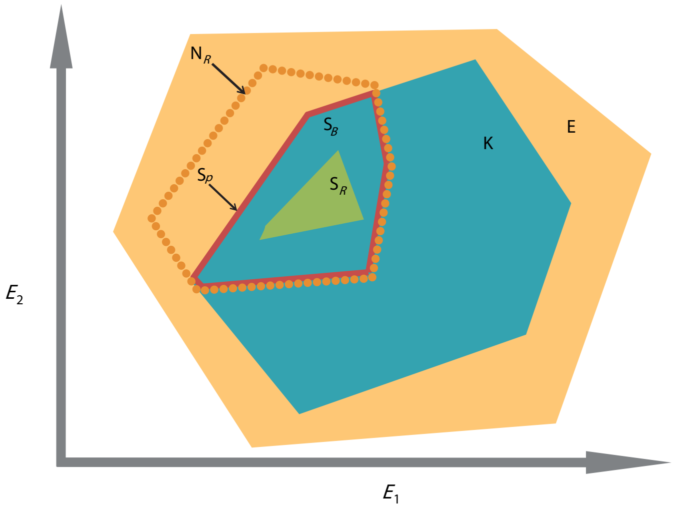

Figure 4.18: The subniche concept from (Karasiewicz et al, 2017). $\mathbf{E}_1$ and $\mathbf{E}_2$ are the environmental gradients calculated after an ordination technique. **E** is the realized environmental space (filled light orange minimum convex polygon). $\mathbf{N}_R$ is the species realized niche (dotted dark orange contour). **K** is the subset realized environmental space (blue minimum convex polygon). $\mathbf{S}_P$ is the existing fundamental subniche (the red contour)-a union of $\mathbf{S}_B$ and $\mathbf{S}_R$. $\mathbf{S}_B$ is the subset biotic reducing factor (the part of **K** found within the orange contour), or biological constraint, and $\mathbf{S}_R$ is the realized subniche (the green minimum convex polygon).

on the subniche. Under the subset habitat conditions H or L, the biological constraint which is exerted on *Phaeocystis* spp. subniches and the effect of some other unselected abiotic variables, can be discussed.

All analyses and graphical representations were performed with R software [R Core Team, 2013] with the package "ade4" [Dray and Dufour, 2007] and "subniche" available for free on the CRAN repository `www.cran.r-project.org` and on GitHub `www.github.com/KarasiewiczStephane/WitOMI`.

4.3 Results

4.3.1 Subset habitat conditions

Low (<50 cell.L^{-1}) and high (>160 cell.L^{-1}) mean annual *Phaeocystis* spp. abundance events (named thereafter subset L and H, respectively) occurred on four and five occasions, respectively (L: 1996, 1997, 2000, and 2005, H: 2001, 2004, and 2010-2012; Figure 4.19). The non-random BV-step analysis

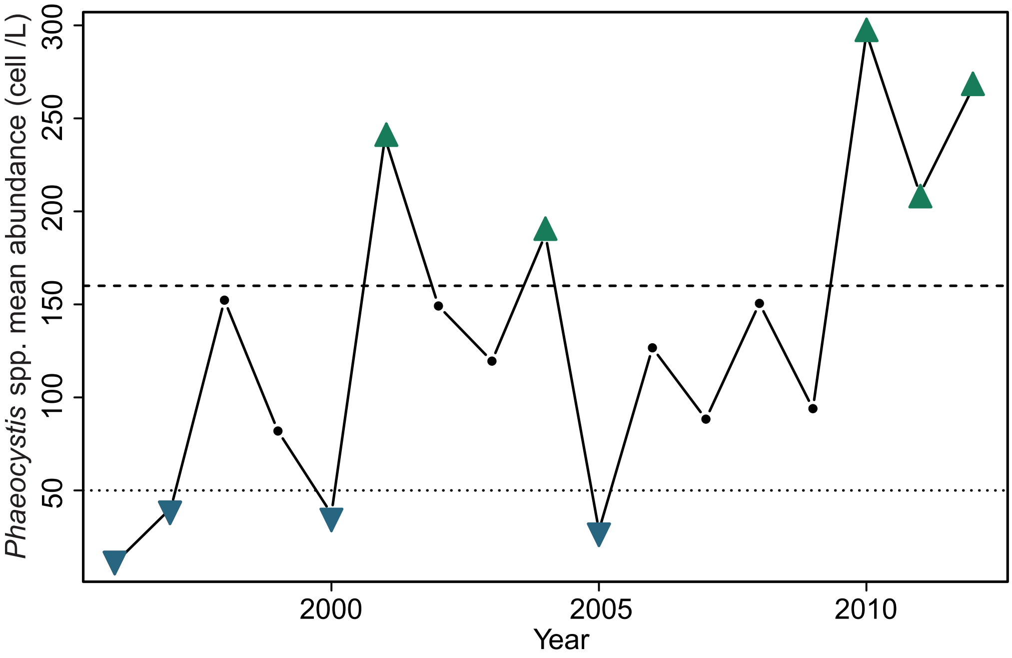

Figure 4.19: Temporal variation of the annual mean abundance of *Phaeocystis* spp. (cell.L^{-1}) from 1996 to 2012. The dashed line represents the upper threshold (160 cell.L^{-1}) and the dotted line represents the lower threshold (50 cell.L^{-1}) then dividing the abundance in three categories (Low, intermediate, high). Only high (green triangle) and low (blue triangle) annual mean abundance events were kept for the rest of the study

revealed that 7 diatom species were correlated to the overall pattern of the community (Gud, Gus, Par, Pss, Ske, Thn, and Thg, with ρ=0.97; See code in Table 4.3) in subset L while 9 diatom species were relevant in subset H (Cha, Dyt, Gud, Gus, Led, Nit, Par, Ske, Thn, with ρ=0.96). Five species, Gud, Gus, Par, Ske, Thn were common to the two contrasting environmental conditions leading to 11 species of interest for the rest of the study. Two species occurred only in subset L (Thg and Pss) and four species occurred only in subset H (Dit, Cha, Led, and Nit)(See code in Table 4.3).

Although the two subsets showed similar increase in temperature and PAR, varying from 5.8 to 19.9°Cand from 8.5 to 6.1 10^3.W.m^2 respectively (Figure 4.20A and 4.20B), differences occurred between the two subsets for turbidity, salinity and nutrient concentrations. Accordingly, subset L, displayed higher turbidity but lower salinity than subset H. (Figure 4.20C-D). Moreover, nutrient concentrations were significantly lower and decreased faster in subset H than in subset L during late winter-early spring (Figure 4.18 E-H). Phosphate concentration had an overall higher concentration in subset L (Figure 4.20F).

The sum of nitrate and nitrite concentrations had similar concentrations in January and December in both L and H subset, but with an overall higher concentration in L than in H (Figure 4.20G). The seasonal trends of silicate concentration were similar in the two subsets, although decreasing faster the rest of the year in subset H than in subset L (Figure 4.20H). The DIN:PO_4 followed a hump shape with a maximum in April (DIN:PO_4: 88) and March (DIN:PO_4: 70) for subset L and H respectively (Figure 4.20I). The DIN:Si was higher in subset L than in H with a maximum in April (DIN:Si: 59) and March (DIN:Si: 30) respectively.

4.3.2 Niche analysis (OMI)

The OMI analysis revealed that the realized niche of 11 diatom species of interest, depicted by the BV-step analysis, and *Phaeocystis* spp. were significant (Table 4.3). The first two axis of the OMI analysis represented 87% of projected inertia, of which OMI 1, represented 74%. OMI1 was mainly explained by nutrients and turbidity (Figure 4.21C), while OMI 2 was mainly explained by PAR, temperature and salinity. The seasonal effect can be pictured by the environmental trajectories of subset H and L (Figure 4.21B). The environmental trajectory of subset H had a higher position and resembled more a full cycle than subset L which went "back on track" (Figure 4.21B).

Ske, Thg and Thn were typical species of late winter-early spring and are, as expected, low in OMI 1 axis (on the left side, Figure 4.21A). Their niches were explained by high nutrient concentrations and turbidity, but low temperature, PAR and salinity. These three species have the highest niche breadth (Tol Ske: 3.52, Thn: 3.35, Thg: 3.14) (Table 4.3). The niches of Dit and Cha, Par and Nit were related to intermediate values of OMI1 (lower values of nutrients and turbidity; Figure 4.21A). They distributed themselves vertically, along the OMI2, by their preferences for higher salinity, temperature and PAR (higher temperature and PAR downwards ; Figure 4.21A). Nit and Par had the lowest marginality (OMI: 0.06 and 0.09 for Nit and Par respectively). The niche of Pss, Gud, Gus and Phae were characterized by low nutrient concentrations and turbidity but differed from each other by salinity, PAR and temperature affinities. Phae niche position was characterized by relative high salinity but intermediate temperature and PAR, while the others were rather defined by lower salinity levels and higher temperature and PAR, along the OMI2 axis. The niche of Led, which is typically a summer diatom species was characterized by the lowest nutrient concentrations and turbidity, high salinity, and intermediate temperature and PAR. As a result, Led was characterized by a

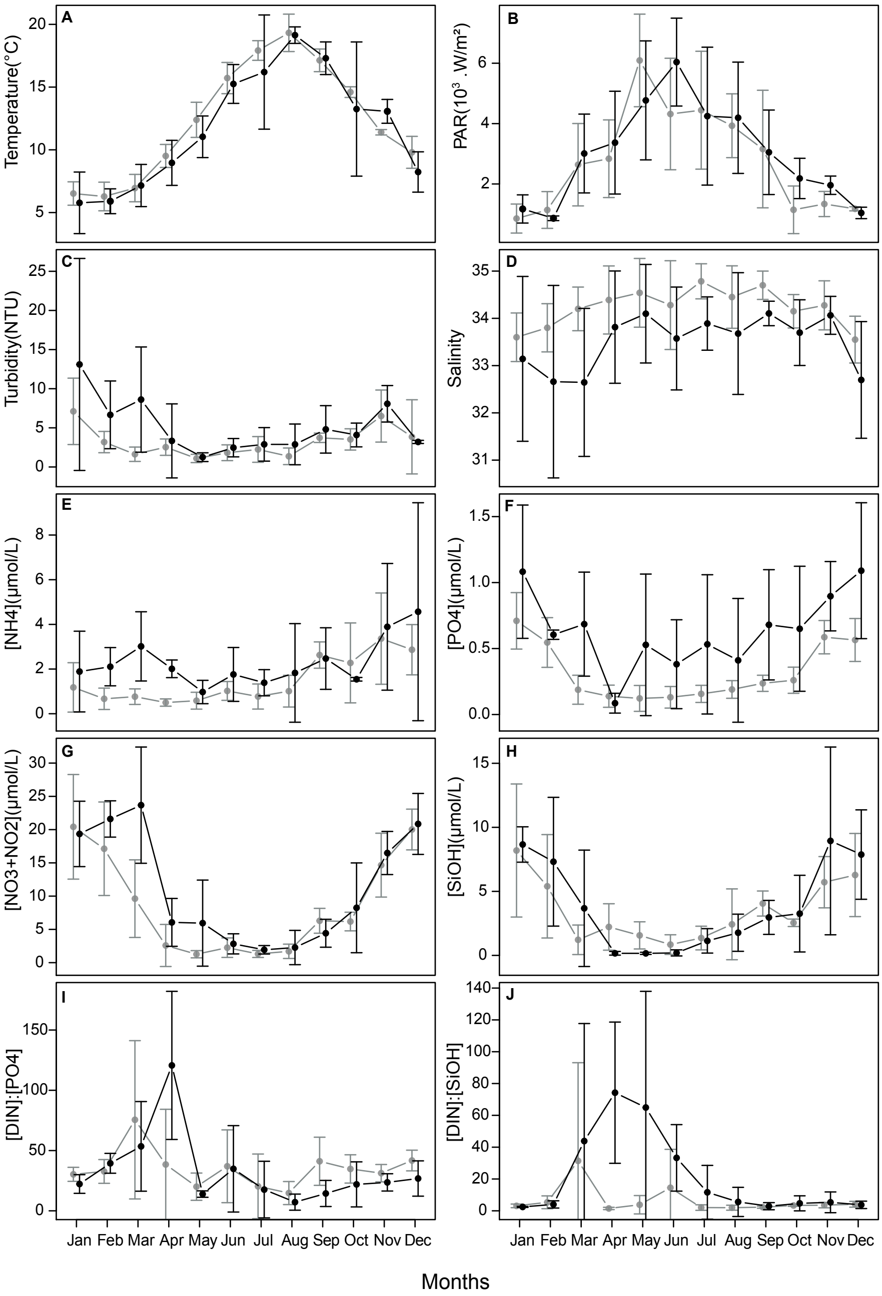

Figure 4.20: Monthly mean (± SD) of each environmental variables for the subset H (grey) and L (black), low and high annual mean abundance of *Phaeocystis* spp. respectively.

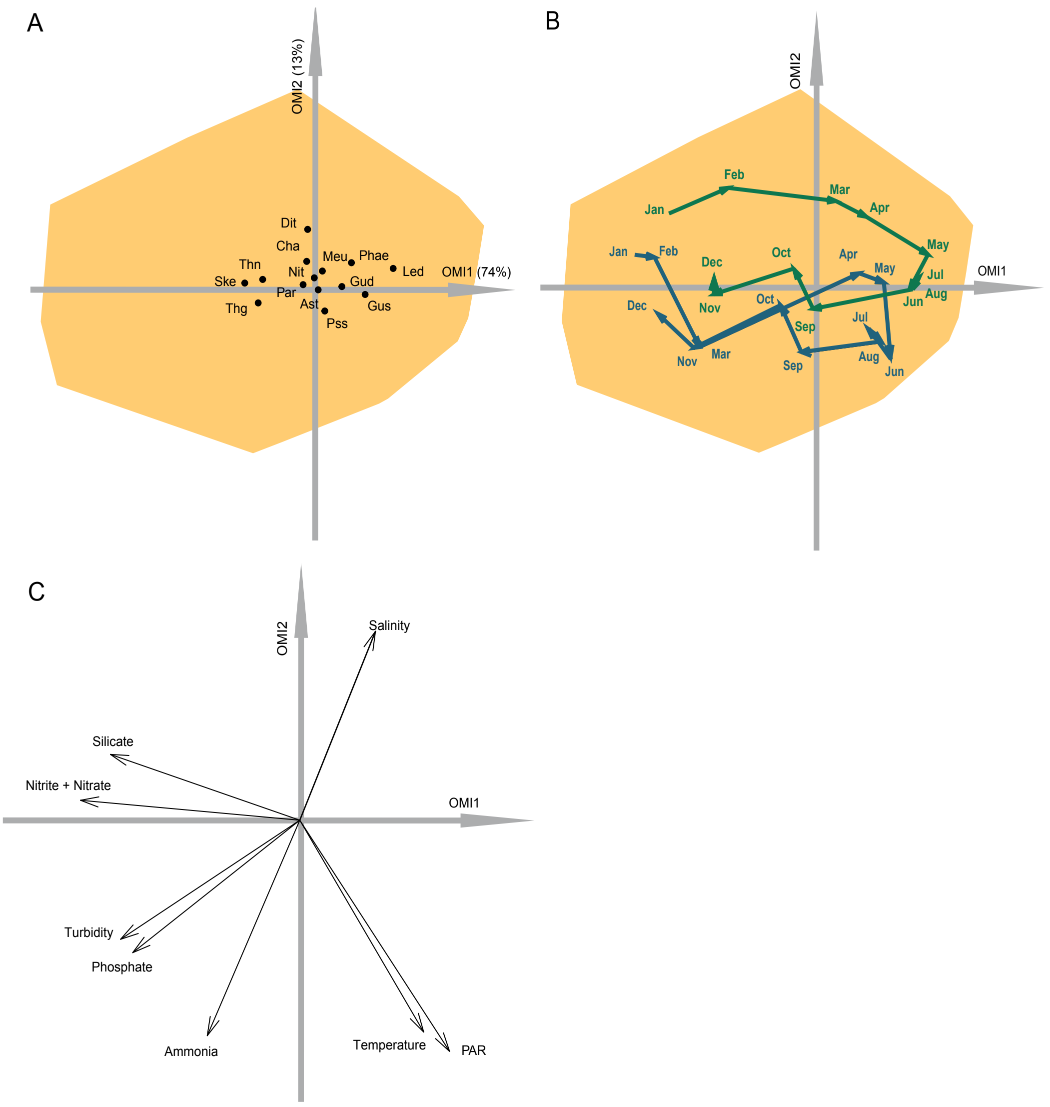

Figure 4.21: OMI analysis of the 11 diatom species and *Phaeocystis* spp. A) The orange polygon represents the overall habitat environmental space. The species labels represent the species niche position (see Table 4.3 for codes). B) The environment trajectory, from January to December, under the two subsets L, blue arrows, and H, green arrows. C) The canonical weights of environmental variables.

Table 4.3: Niche parameters calculated with the OMI analysis for 11 diatoms species and *Phaeocystis* spp. The parameters are the inertia, the marginality (OMI), the tolerance (Tol) and the residual tolerance (Rtol). Cplx: Complex. The P values were calculated with 1000 permutations, see methods for further details.

Species	Code	Inertia	OMI	Tol	Rtol	P
Chaetoceros danicus	Cha	7.09	0.36	0.98	5.76	0.03
Ditylum brightwellii	Dit	7.48	1.07	1.14	5.26	0.00
Guinardia delicatula	Gud	7.28	0.22	2.51	4.56	<0.001
Guinardia striata	Gus	6.65	0.79	1.62	4.24	<0.001
Leptocylindrus danicus	Led	6.61	2.23	1.31	3.07	<0.001
Nitzschia longissima	Nit	7.73	0.06	0.77	6.89	0.05
Paralia sulcata	Par	7.82	0.09	2.24	5.49	0.00
Cplx. $Pseudo-nitzschia\ seriata$	Pss	7.25	0.20	0.96	6.09	0.01
Skeletonema spp.	Ske	10.12	1.64	3.52	4.96	<0.001
Thalassionema nitzschioides	Thn	9.02	0.93	3.35	4.74	<0.001
Thalassiosira gravida	Thg	9.23	1.15	3.14	4.95	<0.001
Phaeocystis spp.	Phae	6.58	0.83	1.36	4.39	<0.001

high marginality (OMI: 2.231).

4.3.3 Subniche calculations (WitOMI)

Phaeocystis spp. subniche position had significantly shifted and the subniche breadth expanded from the subset L to H. (WitOMIG: 2.64 and 2.11 ; Tol: 0.59 and 0.64 for subset L and H respectively) (Figure 4.22). The marginality (WitOMIG) showed that *Phaeocystis* spp. used a more common habitat in subset H than in L. This means that the species has a preference for the environmental habitat conditions found in subset H over L (Figure 4.22). Now considering the subsets independently, the subniche position from the average subset habitat conditions, G_K was much greater in subset L then H (WitOMIG_K: 3.24 and 0.59 from subset L and H respectively). *Phaeocystis* spp. used a more common habitat in subset H, favoring its development (237 cells.L^{-1}, Table 4.4). On the other hand, the habitat preference in subset L, which is atypical for the environmental habitat conditions within subset L, is not well suited for *Phaeocystis* spp. (29 cells.L^{-1}, Table 4.4).

The different WitOMIG values for the common diatom species (Ske, Thn, Par, Gud, Gud), expressed a change in subniche position (Table 4.4). Meanwhile, the tolerance from G, of Gud increased while it decreased for Gus, Par,

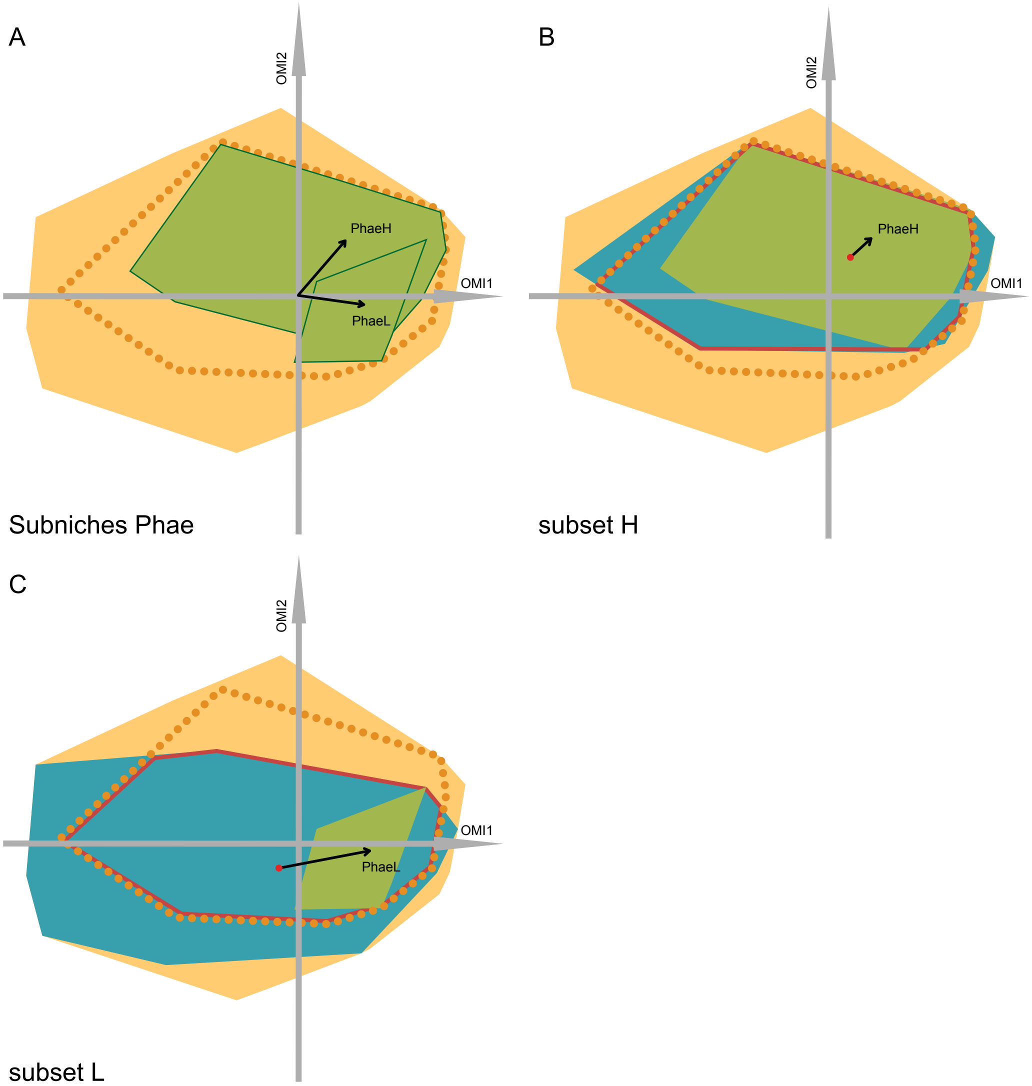

Figure 4.22: *Phaeocystis* spp. subniches dynamics. A) The illustration of the *Phaeocystis* spp. subniches dynamic find within the niche, the dotted orange contour. The green polygon represent *Phaeocystis* spp. subniches. The orange polygon represents the overall habitat environmental space. The labels represents the subniches position and the arrows the marginality. B and C are the graphical representation of *Phaeocystis* spp. subniches within the environmental subsets, blue polygons. The red contour represents *Phaeocystis* spp. existing fundamental subniche. The red dots represent the mean environmental conditions found within each subsets.

Table 4.4: Subniche parameters of the 11 diatom species of interest and *Phaeocystis* spp. The marginality (WitOMI), tolerance (TOL) and mean abundance were calculated under the two subsets, L and H. The niche parameters were calculated from G and G_K. For code see Table 4.3. All subniches were significant ($P \leq 0.001$). - not applicable means that the species were absent in one of the two subsets, or not significant with the BV step analysis. For further details see Materials and Methods.

Code	WitOMI				Tol				Mean abundance	
Origin	G		G_K		G		G_K		(cells.L^{-1})	
Data subset	L	H	L	H	L	H	L	H	L	H
Cha	-	1.34	-	0.31	-	0.56	-	1.95	-	111
Dit	-	1.93	-	0.58	-	0.45	-	1.26	-	100
Gud	0.6	1.26	0.2	0.16	0.62	1.28	2.97	1.97	295	298
Gus	1.09	2.07	1.3	0.65	1.43	0.91	2.05	1.49	226	222
Led	-	4.11	-	2.05	-	0.61	-	0.65	-	118
Nit	-	0.86	-	0.14	-	0.58	-	2.14	-	268
Par	1.48	0.63	0.52	0.16	1.73	0.45	1.68	2.85	138	284
Pss	0.83	-	0.28	-	0.6	-	1.69	-	173	-
Ske	3.17	2.88	1.71	3.85	3.83	2.14	3.86	2.45	206	126
Thn	6.61	0.77	4.36	0.63	2.17	1.19	2.22	3.03	163	197
Thg	2.02	-	0.78	-	3.83	-	4.13	-	139	-
Phae	2.64	2.11	3.24	0.59	0.59	0.64	0.67	0.46	29	237

Ske and Thn (Table 4.4). The low WitOMIG_K values, in the environmental habitat conditions subset H was preferable for Thn, Par, Gud, and Gus, compared to the environmental habitat conditions of subset L. The opposite pattern occurred for Ske (Table 4.4). Ske had a preference for the environmental habitat conditions of subset L. The species mean abundance reflected the species habitat suitability. Ske had a higher mean abundance in subset L. Par, Thn had higher mean abundance in subset H, while Gud and Gus had stable mean abundance (Table 4.4).

Concerning the species that occurred in only one subset, Pss had one of the lowest marginality and intermediate tolerance (WitOMIG_K: 0.28 and Tol: 1.69), while Thg had an intermediate marginality with a high tolerance (WitOMIG_K:0.78 and Tol: 4.13) , in subset L (Table 4.4). In subset H, Nit and Cha had a low, Dit an intermediate, and Led a high marginality (WitOMIG_K: 0.14, 0.31, 0.58, and 2.05 for Nit, Cha, Dit and Led respectively) (Table 4.4). Led had an intermediate tolerance while Nit, Cha and Dit had high tolerance (Table 4.4).

The environmental habitat conditions of subset H had enhanced the common diatoms and *Phaeocystis* spp. mean abundance, as the species had greater affinities with this type of environmental habitat conditions. *Phaeocystis* spp. still managed to reach high abundance despite, the increase of the relevant number of diatom species. *Skeletonema* spp. was the only common diatom species which was disfavored by the change in environmental habitat conditions and better responded to the environmental habitat conditions of the subset L.

A succession of the diatom subniche was observed in the two subsets (Figure 4.23A and B), as expected from the niche analysis (Figure 4.20). In subset L, the late-winter early-spring species (Ske, Thn and Thg) were blooming first because they were affiliated with winter like conditions, *i.e.*, low temperature, PAR and salinity, but high nutrient concentrations and turbidity. Then, Par was second to bloom followed by Pss, Gud, Gus and Phae (Figure 4.23A). Ske was the sole first species to appear in subset H. In addition to Thn, Cha, Dit, Par and Nit appeared secondly. The succession of diatoms continued with Gud, Gus and Led (Figure 4.23B). *Phaeocystis* spp. subniche overlapped most of the diatoms niche position but still managed to have a larger niche breadth than in subset L. The succession diatoms-*Phaeocystis* spp. did not take place in subset H, as *Phaeocystis* spp. managed to develop concomitantly with the diatom species (Figure 4.23B).

4.3.4 Biological reducing factor

Phaeocystis spp. subniche in subset L occupied 19% of the existing fundamental subniche. Therefore the biological constraint was equal to 81% (Figure 4.24B). The subniche occupation of *Phaeocystis* spp. in subset H within the existing fundamental subniche represented 75%. The subniche biological constraint was of 25% of the existing fundamental subniche (Figure 4.24A). Therefore, we can suspect that the unused available conditions of *Phaeocystis* spp. existing fundamental subniche could have been occupied by competing diatom species, such as *Skeletonema* spp., *Thalassionema nitzschioides*, *Thalassiosira gravida* and the *Pseudo-nitzschia seriata* complex (Figure 4.24A). By contrast, we can suspect that *Phaeocystis* spp. subniche overlapped the diatoms subniches in subset H (Figure 4.24B).

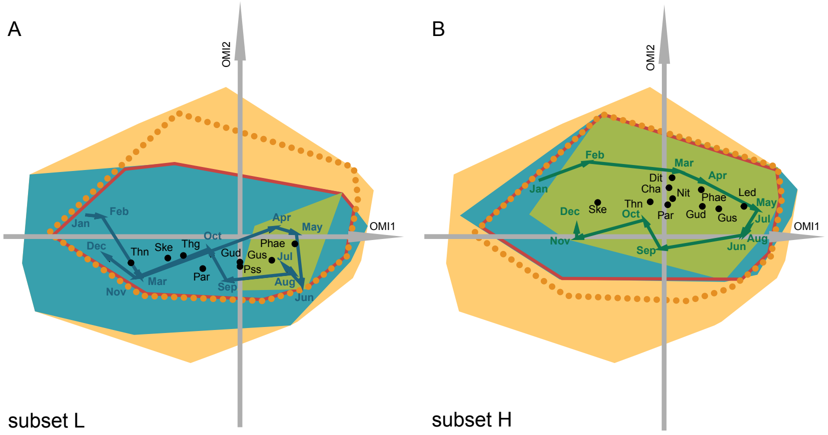

Figure 4.23: *Phaeocystis* spp. subniches within the two subsets L and H. The green polygon represents *Phaeocystis* spp. subniche. The orange polygon represents the habitat conditions space. The dotted orange contour represents *Phaeocystis* spp. realized niche. The red contour represents *Phaeocystis* spp. existing fundamental subniche. The labels represent the subniches position of the relevant species resulting from the BV-step analysis. The arrows represent the trajectory taken by the habitat conditions from January to December under their respective subsets.

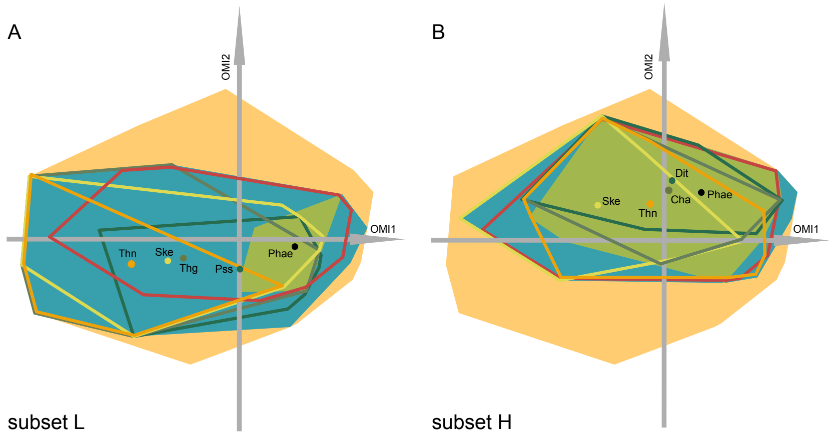

Figure 4.24: *Phaeocystis* spp. and possible competitors subniches within the two subsets L and H. The orange polygon represents the habitat conditions space. The blue polygon represents the subset habitat conditions space. The green polygon represents *Phaeocystis* spp. subniche. The red contour represents *Phaeocystis* spp. existing fundamental subniche. The colored dots and the corresponding polygon represent the subniche position and breadth respectively. Not all relevant species of each subset were represented for the sake of clarity.

4.4 Discussion

The OMI analysis revealed that nutrient concentrations (phosphate, silicate, nitrite, nitrate and ammonia) played an important role in the diatom community distribution (Figure 4.21A and 4.21C). Subset H was characterized both by lower nutrient concentrations and faster decrease than subset L (Figure 4.21E to 4.21H). *Phaeocystis* spp. realized subniche shifted in position and increased in breadth from the subset L to H. The diatom-*Phaeocystis* spp. succession occurred in subset L but not in H. *Phaeocystis* realized subniche seemed to be more controlled by the preceeding diatom community than by the subset habitat conditions. Furthermore, the increasing diversity in the diatom community exerted a lower biological constraint on *Phaeocystis* realized subniche. The results suggest that key diatom species possibly competed for resources with *Phaeocystis* spp., especially for nitrogen, phosphate and light but only when silicate was available. We will first discuss the robustness of actual hypotheses related to *Phaeocystis* spp. niche in literature and second we will discuss the competitive biotic interaction as an explanation to its fluctuating abundances.

4.4.1 *Phaeocystis* spp.hypotheses

The "silicate-*Phaeocystis* hypothesis" [Lancelot et al., 1987; Reid et al., 1990] has historically been a major explanation in the appearance of *Phaeocystis* spp. The silicate concentration in the environment may determine the duration and stability of the diatom community. For instance, in both subsets, *Phaeocystis* spp. started to bloom when the silicate concentration dropped under 1.5 μmol.L^{-1}. This threshold was reached later in April for subset L compared to March for subset H (see Figure 4.20). However the "silicate-*Phaeocystis* hypothesis" [Lancelot et al., 1987; Reid et al., 1990] is only partly verified since *Phaeocystis* was already present, in the subset H in January, but did not bloom until the silicate concentration dropped under the threshold. The lower inorganic P demand of *Phaeocystis* spp. compared to diatoms [Riegman and Noordeloos, 1992] could explain its constant presence in subset H characterised by low phosphate concentration from January to June. On the contrary, the "eutrophication hypothesis", which stipulates that *Phaeocystis* spp abundance increases with high N concentration, was not validated in this study. Subset L, was characterized by higher concentrations of nitrite, nitrate and ammonia than subset H, leading to a dominance of diatoms species but resulting in lower abundances of *Phaeocystis*. Furthermore, even though in subset L, leftover N from diatoms was still high, *Phaeocystis* did not bloom as much.

Phaeocystis spp. might use the excess N leftover by the diatoms for growth but it does not seem to determine the outbreaks of high abundance bloom events. The hypotheses concerning *Phaeocystis* spp. appearance link to N:Si [Tett et al., 1993; Tett and Walne, 1995] and N:P [Riegman and Noordeloos, 1992] were better at predicting the HAB timing. The maximum in N:Si or N:P corresponded to the start of *Phaeocystis* spp. bloom, in both habitat subset conditions.

According to [Borkman et al., 2016], higher salinity characterized the year of high *P. pouchetii* abundance and could also explain the years of high *Phaeocystis* spp. abundance. The higher salinity also reflected a lower precipitation flow rate from rivers, and wind turbulence which can also take part in the turbidity level. The subset H was characterized by a higher salinity and a lower turbidity, than in subset L. The photosynthetically active radiation and temperature had exhibited similar variations during the season. Temperature did not seem to have impacted *Phaeocystis* spp. appearance, because in subset H, *Phaeocystis* spp. was present in January, the coldest month (6.5°C). The higher turbidity level in subset L, suggested that the real amount of photosynthetically active radiation reaching the community was less than in subset H. However, *Phaeocystis* spp. still appeared under low PAR condition. This is in contradiction with the hypothesis suggesting the dominance of *Phaeocystis* spp. over diatoms when conditions resemble early summer, along the Dutch coast[Peperzak, 1993].

4.4.2 Biotic interactions

The unused available conditions in *Phaeocystis* spp. existing fundamental subniches is considered as the subset biotic reducing factor. Predation can be possible as there was no distinction between single cells and colonies of *Phaeocystis* spp. within the data set. *Phaeocystis* spp. colonies are known to reduce predation by zooplankton, mainly due to size mismatch [Daro et al., 2006; Rousseau et al., 2000]. Infection by viruses can also be a cause of the biological constraint. Experimental results showed that *P. pouchetii* cell mortality rates by virus infection can be up to 0.8d^{-1} [Brussaard et al., 2005] but viruses do not infect healthy colonies [Bratbak et al., 1998]. Therefore, the most appropriate biological constraints in this study seems to be competition. The diatom community is directly competing for resources with *Phaeocystis* spp. From late-winter to summer, the succession in blooms of the diatoms and their appearance will depend on their preferences regarding environmental habitat conditions, further driving *Phaeocystis* spp. appearance and bloom. For instance, *Skeletonema* spp., *T. nitzschioides*, and *T. gravida* are known to be bloom forming species [Pratt, 1959; Smayda, 1958]. They are considered as winter diatoms, according to their respective niche positions with preference for high nutrient concentrations and turbidity in association with low temperature, PAR and salinity. Their leading appearance, bloom magnitude and persistence determined the composition of the following community. *Skeletonema* spp. is known to grow up to 25% faster when on sustained ammonia than on nitrate [Suksomjit et al., 2009; Tada et al., 2009]. *T. nitzschioides* has also been shown to grow faster in ammonia and nitrate enrichment conditions [Mochemadkar et al., 2013]. In subset L, the high level of ammonia concentration could have potentially helped *Skeletonema* spp., *T. nitzschioides* and potentially *T. gravida*, which are pioneers, to grow faster and bloom, establishing its dominance in the community [Suksomjit et al., 2009; Tada et al., 2009] (Figure 4.21B). Furthermore, the *P. seriata* complex occurrence is also known to be nitrogen-limited, and more than capable of using ammonia [Fehling et al., 2006]. *Phaeocystis* spp. also grows faster on ammonia than on nitrate [Tungaraza et al., 2003] but seemed to be out-competed by the diatoms in these environmental habitat conditions. Other factors, such as silicate and phosphate were not limiting and favored the diatoms. The establishment of the diatoms species, with a preference for ammonia, possibly out-competed *Phaeocystis* spp., until the concentration of silicate became limiting, succeeded by its bloom.

In subset H, *Phaeocystis* spp. managed to flourish, despite the presence of the 5 same species (*Skeletonema* spp., *T. nitzschioides*, *Paralia sulcata*, *Guinardia delicatula* and *Guinardia striata*) and 4 other species (*Chaetoceros danicus*, *Ditylum brightwellii*, *Nitzschia longissima* and *Leptocylindrus danicus*). The lower concentration of phosphate favored *Phaeocystis* spp. presence, over diatoms, considering its capacity to store phosphate within its colony matrix [Schoemann et al., 2001; Veldhuis et al., 1991], coupled with its lower P demand [Riegman and Noordeloos, 1992]. Moreover, *Phaeocystis* spp. is a good competitor for nitrogen [Riegman, 1995], along with lower concentration of silicate, the diatoms community did not bloom as much as in subset H. Silicate limitation is thought to have resulted in an increase in *Phaeocystis* spp. blooms' magnitude and continuity [Cadée and Hegeman, 1986; Lancelot, 1990; Lancelot et al., 1987]. The silicate limitation dually selected diatom species which are less silicified, such as *Leptocylindrus danicus*, *Chaetoceros danicus* and *Nitzschia longissima* [Hasle et al., 1996]. Furthermore, the N-source dependency of diatom silicate competitiveness, which determines the dominant species of the community [van Ruth, 2012], reinforced the idea that *Skeletonema* spp., *T. nitzschioides*, *T. gravida* and *P. seriata* complex are decisive species for *Phaeocystis* spp. bloom.

The readjustment of the nutrient concentrations, made more than one resources limiting for the diatoms, resulting in a biodiversity increase [Hillebrand et al., 2014], as shown with the BV-step analysis (from 7 to 11 species, from subset L to H). The niche expansion of *Phaeocystis* spp. (Tol: 0.59 and 0.64 for subset L and H respectively) can be partly explained by a relaxation in biological constraint (Table 4.4). The possible decrease in the diatom competitive ability, resulted in the 25% of unused available environmental habitat conditions of *Phaeocystis* spp. existing fundamental subniche.

4.4.3 Further perspectives

Further investigations on the diatom competitive ability can be done experimentally [van Ruth, 2012], and with the trait based approach [Litchman and Klausmeier, 2008]. The major components of the trait based approach are the species traits, environmental gradients, species interaction and performance currency which determines the species niche within the community [McGill et al., 2006]. In this study, the niche and subniche dynamic within the overall environmental habitat and subset environmental habitat conditions were studied for the entire community. Furthermore, we also managed to quantify the biological constraint exerted on *Phaeocystis* spp. subniches. The direct relationships between traits and the species response to the environmental conditions [Lavorel and Garnier, 2002] can give us clues on the mechanisms driving the community composition, in parallel with the patterns of functional trait distribution [De Bello et al., 2009; Weiher et al., 1998], also on how it controls the following *Phaeocystis* spp. bloom. Some methods, which link niche analysis and trait-based approach already exist. The OMI-GAM analysis [Kleyer et al., 2012] determines species responses to environmental conditions, using the OMI analysis [Dolédec et al., 2000] and additionally could explain these responses using generalized additive models (GAM), with the traits as explanatory variables [Kleyer et al., 2012]. Such analysis can help solve the *Phaeocystis* spp. riddle. In the continuity, more precise ecological dynamic models could be built as the diatoms can be split into different functional groups. Models, such as the MIRO model [Lancelot et al., 2014] which also studies the spring-diatom-*Phaeocystis* bloom considered diatoms as a large pool responding homogeneously to nutrient concentrations and/or ratios. As shown in the study, the mechanism driving the bloom of *Phaeocystis* spp. is multifactorial, suggesting a greater consideration of the diatoms diversity, including their respective traits and competitive ability. Trait-based understanding of plankton distribution started with the paradox of the plankton [Hutchinson, 1961]. Margalef was the first to understand the balance between the physical and nutritional forces, relating to different life forms of phytoplankton, with the classical "mandala" [Margalef, 1978, 1979]. Since then, the concept of the "mandala" has found its way into predicting HABs [Smayda and Reynolds, 2001] and nowadays incorporating twelve dimensions [Glibert, 2016]. Herein, the environmental trajectory can help predict the high abundance events of *Phaeocystis* spp. in future "mandala" like models, with the use of the WitOMI calculations.

4.5 Conclusion

The appearance of *Phaeocystis* spp. depends on multiple environmental factors, and moreover, on the preceding diatom community which are first to appear in late winter. Within both subsets, *Phaeocystis* spp. could have potentially realized a large subniche. The reduction and/or expansion of its subniche mostly depended on the winter environmental conditions and on the biological constraint. The diatom competitive ability appearing in late-winter are suspected to take part in the biological constraint of *Phaeocystis* spp. subniche. The establishment of the leading species in the bloom succession, herein *Skeletonema* spp., *Thalassionema nitzschioides* ,*Thalassiosira gravida* seemed to be driven by the nutrient concentration. Under non-limiting P environmental conditions, competition among diatoms for silicate will be N-source dependent. The high concentration of ammonia, allowed a rapid growth and bloom of the later-winter diatom (*i.e. Skeletonema* spp.) (Figure 4.19E) and the Si limits their bloom magnitude. The winter conditions effect on the *Phaeocystis* spp. bloom requires further investigations. The trait-based approach in relation with the community response to the changing environmental conditions seemed to be a promising field for studying the becoming of HAB.

4.6 Acknowledgements

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Chapter 5

Phytoplankton long-term and seasonal diversity-productivity relationships with an invasive species.

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5.1 Introduction

One of the main questions in ecology is how species diversity, productivity and available resources are related. Historically, it was long thought that productivity drives diversity following the Species-Energy Theory (SET) [Wright, 1983] or the Resource-Ratio Theory (RRT) [Tilman, 1982]. SET hypothesizes that available energy controls the variation in species richness, the community size and the probability of stochastic extinction [Wright, 1983]. RRT stipulates that the species coexistence is affected by the imbalance of two or more available resources, increasing possibilities for competitive replacements [Tilman, 1982]. More recently, a new consensus, the "Biodiversity-Ecosystem Functioning" (BEF theory), has been developed by reversing the causality and argues that the diversity is a driver for ecosystem functioning, such as biomass production [Naeem et al., 1994; Gross and Cardinale, 2007; Hillebrand and Matthiessen, 2009]. Later, Cardinale et al. [2009b] were first to combine ecological stoichiometry and the BEF theory, which was later named the Multivariate Productivity-Diversity model (MPD) by Hillebrand and Lehmpfuhl

[2011]. The two key aspects of Cardinale et al. [2009b] concepts were (i) the differentiation between the potential and the realized productivity, and (ii) the separation between the resource availability and imbalance. The former aspect allows to distinguish several pathways between biodiversity and productivity: the resource availability determines the maximum attainable biomass i.e. potential productivity and the quantity of standing biomass i.e. the realized productivity [Hillebrand and Lehmpfuhl, 2011]. The latter aspect, the distinction between the resource availability and the resource imbalance, is defined as the divergence of actual supply ratios from the balanced ratios [Cardinale et al., 2009b], allowing the inclusion of RRT. The general consensus in MPD is that (i) as the resource availability increases, biomass and species richness increases as well, (ii) as resource imbalance increases, both biomass and species richness decrease, (iii) a positive impact of diversity is expected on biomass.

In MPD, productivity and biodiversity are proxied in different ways. The term productivity can be confusing as it is a rate. The standing biomass is often used in literature [Cardinale et al., 2009a,b; Hillebrand and Lehmpfuhl, 2011; Lewandowska et al., 2016] and true productivity is rarely used (but see Lehtinen et al. [2017]). Often, the realized biomass is considered as equal to the productivity as it is the quantity produced at the time when the data was collected [Hillebrand and Lehmpfuhl, 2011]. As for biodiversity, it can be proxied by richness, evenness or other diversity indices and its choice can potentially impact the model. Evenness has been less frequently used in biodiversity-functioning relationships and often neglected in biodiversity experiment in profit of richness [Hillebrand et al., 2008; Gamfeldt et al., 2015]. Both biodiversity aspects should be considered, since evenness responds more rapidly to environmental changes than does richness [Chapin et al., 2000], and evenness is a good indicator for species extinctions risk in a community [Odum, 1969; Chapin et al., 2000; Halloy and Barratt, 2007]. For instance, evenness had been shown to decrease with increasing nutrient supply while species richness increased [Hillebrand et al., 2007; Lewandowska et al., 2016]. Norberg et al. [2001] showed that at the local scale, dominance by a single species (i.e. low evenness) can result in high biomass production when the dominant species has a high resource use efficiency. On the contrary, if the dominance decreases, the productivity should decrease as no other species can become as productive, despite the increase in richness [Matthiessen et al., 2010; Lewandowska et al., 2012; Mulder et al., 2004]. Finally, low evenness can also be responsible for low biomass if the dominating species is subject to high competition [Rohr et al., 2016].

The productivity-diversity relationship has been studied more on terrestrial ecosystems than on aquatic communities due to methodological challenges, such as sampling and taxonomic resolution [Lehtinen et al., 2017]. This statement holds true for freshwater versis marine ecosystems [Blake and Duffy, 2010; Eklöf et al., 2012; Godbold, 2012]. Wille et al. [2008] were the first to show that freshwater phytoplankton diversity exhibits a causal relationship between resource use efficiency (RUE) and productivity, similarly to what was observed for plants. Cardinale et al. [2009b] first applied MPD on freshwater phytoplankton (see above). Only recently, BEF theory [Hodapp et al., 2015] and MPD [Lehtinen et al., 2017; Lewandowska et al., 2016] were used in marine ecosystems. Common unexpected results between these marine studies is a strong negative relationship between evenness and phytoplankton biomass and a positive relationship between richness and biomass [Hodapp et al., 2015; Lehtinen et al., 2017; Lewandowska et al., 2016]. The apparent contrast in diversity-productivity relationships from terrestrial and aquatic communities was suggested to be due to the natural phytoplanktonic communities "bloom-oriented" mode of life [Lehtinen et al., 2017]. The inverse relationship between evenness and biomass is particularly representative of the dynamic succession of few successful species, while the positive link between richness and biomass illustrates the remnant populations of previous blooming taxa [Lehtinen et al., 2017]. Another common relationship in aquatic studies are the positive links between the resource imbalance and richness [Lehtinen et al., 2017; Lewandowska et al., 2016] and/or evenness [Lehtinen et al., 2017; Gamfeldt and Hillebrand, 2011]. This fact is in contradiction with Tilman [1982] RRT and reveals the complexity of the diversity dynamics in aquatic communities. Finally, these relationships can potentially be the result of consumer predation, based on a competition-defense trade-off [Viola et al., 2010] as previously reported in freshwater communities [Hillebrand and Lehmpfuhl, 2011]. In marine ecosystems, the highly variable effect of the predation onto diversity, cascading down the food-web, influences the relationship between different dimensions of biodiversity and ecosystem functioning [O'Connor and Crowe, 2005; Byrnes et al., 2006; Douglass et al., 2008].

Typical resources, used in the MPD, are nitrogen (N), phosphorus (P) and light. Coastal ecosystems around the world are subject to increasing eutrophication in all densely populated areas [Vollenweider, 1992] which translated into increasing concentration of N and P over the past decades [Smith et al., 2003]. N and P being often limitant for phytoplankton growth, compared to light and silicate, eutrophication alters the balance between these resources and affects the primary production in coastal marine systems [Rabalais, 2004]. The more serious cases of aquatic eutrophication can lead to algal blooms, algal scum, increased benthic algal growth, and massive growth of submersed and floating macrophytes [Hallegraeff, 1993; Turner and Rabalais, 1994; Vollenweider, 1992; Bouwman et al., 2005]. During the last decades, the harmful effects of eutrophication in coastal marine systems have been acknowledged and with the potential to have a wide implications for biodiversity, water quality, fisheries, and recreation in industrialized and developing regions [Anderson et al., 2002; Li and Zhang, 1999; Bouwman et al., 2005; Davidson et al., 2012] and is considered to be a major and growing environmental problem [Davidson et al., 2012]. Coastal systems are also more subject to species invasion [Cohen and Carlton, 1998]. Local biodiversity has previously been reported to change, even increase, under the presence of an invasive species, but its impact on the ecosystem functioning as yet to be studied [Sax and Gaines, 2003; Byrnes et al., 2007; Karlson et al., 2011]. Other environmental variables, than resources, can just as equally influence the MPD model which can be updated in the manner of Hodapp et al. [2015] so to include, temperature, kinetic energy and salinity.

The aim of the study was to investigate the environmental response of the MPD relationship, in a native phytoplankton community, including an invasive species, within an eutrophicated coastal marine ecosystem. The diversity-productivity relationships are probably ecosystem dependent [Hillebrand and Lehmpfuhl, 2011] and there is a need to understand the role and effect of temporality [Gamfeldt et al., 2015]. In aquatic ecosystems, seasonality of resource supply and ratio, along with biodiversity dynamics and other environmental variables probably blur the MPD's relationships. A long term data series, over 15 years, was then used to cover many of the different possible interaction between MPD and the environmental variables. Special attention was paid on separating the effect of the seasonal signal and the long-term trend which could bring a new insight into the framework proposed by Cardinale et al. [2009b] with additional variables as in Hodapp et al. [2015].

5.2 Methods

5.2.1 Data

The data was retrieved from Lefebvre et al. [2011], from 1998 to 2012. Information on the phytoplankton species and water chemical composition were collected by the French REPHY-IFREMER network (Réseau de Surveillance du Phytoplancton et des Phycotoxines) on a fortnightly to a monthly basis. The coastal station of Boulogne-sur-mer was selected because the waters are known to be eutrophied and developing harmful algal blooms (*Phaeocystis* spp). Seawater temperature (°C), salinity (PSU), turbidity (NTU), inorganic nutrient concentrations (dissolved inorganic nitrogen, silicate, and phosphate in μmol.L^{-1}) and photosynthetically active radiation (PAR, W.m^{2}), O_2 saturation (mg.L^{-1}), chlorophyll-a and pheopigments (μg.L^{-1}) were measured. Note that PAR is the cumulative sum over the five days preceeding phytoplankton sampling date. Wind speed (m.s^{-1}) was obtained from the French Institute 'Météo France', based on hourly records at the coastal meteorological station of Boulogne-sur-mer, northern France. A wind daily mean speed and stress were calculated. The abundance of each species and genus were retrieved: biovolume were collected for each species and/or genera from [Olenina et al., 2006] first, and if not found, was searched on `http://eol.org/traitbank` by using the R packages "Reol" and "traits" [Banbury and O'Meara, 2014; Chamberlain et al., 2016]. From the website, if several values were found for the same species or genera, the mean of all biovolume were used. We are aware that the biovolumes value can vary for a species due to its plasticity and in response to its environment [Kishimoto et al., 2013; Dokulil et al., 2007], but herein the use of biovolume is an indicator of the mean total biovolume of the community.

5.2.2 Data preliminary processing

As in Hernández-Fariñas et al. [2014], the monthly median of all variables and diversity aspect of species and genera were calculated .We focused on the coastal station 1 of Boulogne-sur-mer because the waters are known to be dominated by *Phaeocystis* spp. in some years. As in Cardinale et al. [2009b], resource availabiliy "a" and resource ratios "θ" were calculated with the log-tranformed nitrogen, phosphate and PAR. The pre-processing calculation separate the quantity of resources "a", of the measurement of imbalance of the resources "θ", which becomes independent [Cardinale et al., 2009b]. The independency of "a" and "θ" is important for the explanatory strength of the model [Henseler et al., 2015]. The biovolume and *Phaeocystis* spp. were also log-transformed due to the large variation of the values. The variables were deseasonalized using the "ts" and "decompose" function of the "stats" packages in R statistical software [R Core Team, 2017]. The observed data were decomposed into seasonal, trend and residual time series with an additive decomposition model by using a moving average of lag 12. Only the trend and seasonal time series were used for the model.

5.2.3 Model setup

The multivariate nature of the data requires a methodology which can be applied to assess fundamental mechanisms while capable to accommodate with multicollinearities, as well as direct and indirect influences. Structural Equation Models (SEMs) are a multivariate approach capable of dealing with the different nature of these dependencies [Arhonditsis et al., 2006; Grace et al., 2010]. SEMs allow the integration of several processes in the same model, analysing a framework of multivariate hypotheses enabling the incorporation of more flexible networks contrarily to a bivariate approach.

The model was composed of five exogenous latent variables, which were described by temperature, kinetic energy (wind velocity, wind stress, turbidity) and chemical conditions (salinity and O_2). Seven endogenous latent variables were distinguished. Two of them illustate the resources availabiliy ("a") and resource imbalance ("θ") .Two are respresenting the diversity aspects of the phytoplankton community, richness and eveness (e.g. expressed by Pielou's evenness and the Shannon index) at species and genus levels [Pielou, 1966; Shannon and Weaver, 1949]. Two endogenous variables represented the ecosytem funtionning, biomass, (used chlorophyll-a and pheopigments as proxies) and total biovolumes (the sum of species biovolume). Finally, a latent variable representing the invasive species was measured by *Phaeocystis* spp's abundance. A total of 93 species and 58 genera were used in the study.

As in Hodapp et al. [2015], we assumed direct causal links between the environmental variables and all endogenous variables. Chemical conditions were indicated by salinity only as it was known to affect the composition of the phytoplankton community [Lionard et al., 2005]. Kinetic energy was measured by wind speed, wind stress and turbidity reflecting the mixing of the water column which can affect the phytoplankton community structure, and diffusion of interstitial sediment nutrients [Diehl et al., 2002]. Temperature affects both phytoplankton growth rates and nutrient remineralisation rate, so we assumed a link between temperature, biovolume, biomass and the invasive species [Thamdrup et al., 1998; Colijn and van Beusekom, 2005; Boyd et al., 2013; Xu et al., 2017]. The invasive species being in competition with the native community and disrupting the ecosytem function, we assumed a direct causal link between biovolume and invasive species, and between invasive species and biomass.

5.2.4 Model analysis

SmartPLS returns standardized path coefficients. Hence, the size of path coefficients can be directly compared and interpreted as the estimated change in an endogenous latent variable for 1 unit of change in an exogenous variable. Although partial least squares regression is capable of dealing with multicollinearity better than ordinary regression [Wold et al., 1984; Abdi, 2007], it is recommended to check for high multicollinearity among exogenous latent variables. For this purpose, we calculated variance inflation factors (VIFs). VIF quantifies the amount of variance inflation of regression coefficient estimates due to multi-collinearity. The interpreation and calculation of the evaluation criteria were done respecting the accepted minimum value of 0.7 for factor loadings, 0.5 for the Average Variance Extracted (AVE), Composite reliability of 0.6, Cronbach's Alpha of 0.6 Hodapp et al. [2015]]. Furthermore, the discriminant validity was assessed by using the maximum accepted value of 0.95 for the Heterotrait-Monotrait Ratio (HTMT) criterion instead of the Fornell-Larcker criterion as it is more performant in detecting discriminant validity [Henseler et al., 2015].

5.3 Results

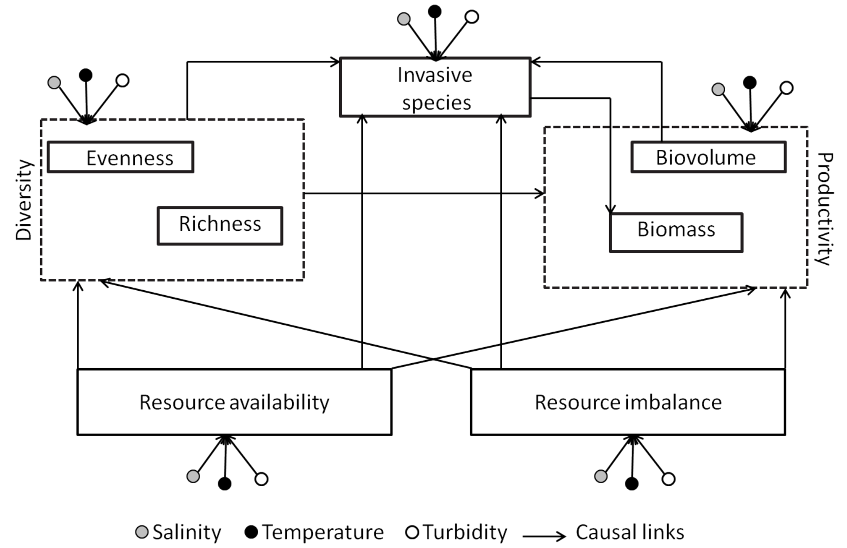

Figure 5.25: Initial model structure according to assumptions. Only latent variables are displayed; indicator variables were omitted for clarity. Arrows depict causal pathways.

In order to obtain a robust model, the O_2 saturation, wind stress and speed were removed from the Kinetic energy and Chemical condition latent variable respectively due to low AVE values [Hulland, 1999]. Otherwise all other criteria were met for the long-term model (Appendix B Table S1 to S4) and the seaonal model (Appendix B Table S5 to S8). Therefore Kinetic energy and Chemical conditions were renamed Turbidity and Salinity respectively (Figure 5.25).

5.3.1 Data long-term trend

The resource availability "a" and imbalance "θ" slightly fluctuated except for a window of two years in the midlle of the series when "a" and "θ" were higher and lower than the common trend, respectively (Figure 5.26D and 5.26E). The phenomenon can be explained by the higher concentration of PO_4 in the system (increase of "a") which rebalances the ratio between resources (decrease of "θ") (Figure 5.26D and 5.26E). The temperature was relatively stable throughtout the study period with a drop in temperature in autumn 2000 (Figure 5.26F). Diversity indices, concerning species and genera, followed the same trend. Turbidity generally decreased while Salinity, and richness increased (Figure 5.26G, 5.26H and 5.26I). Chlorophyll-a generally decreased with a peak in autumn 2008 and the pheopigments had a tendency to decrease (Figure 5.26J). The *Phaeocystis* spp. abundance, seemed to oscillate with, more or less, a three-year period (Figure 5.26K). The total biovolume increased abrutly during the years 1999 to 2000 but seems to have been more stable since (Figure 5.26L). The Shanon diversity index generally increased but with the same apparent three-year period (Figure 5.26M). Finally, the Pielou's eveness also appeared to have a similar oscillations (Figure 5.26N).

5.3.2 Long-term MPD model

In a classical MPD point of view, there is a positive effect of resource availability (a) on evenness and a positive influence of resource imbalance (θ) on evenness and richness (Figure 5.27). It is worth noticing that there was no significant direct effect of a and θ onto biomass and biovolume (Figure 5.27). Evenness and richness impacted biomass negatively and positively, respectively (Figure 5.27).

The invasive species was positively affected by a and θ. Evenness and richness impacted the invasive species negatively and positively, respectively (Figure 5.27). The invasive species had a negative link with biomass (Figure 5.27). Temperature had only one negative affect on biomass. Salinity had a strong influence as it was related to all endogenous variables. Salinity positively af-

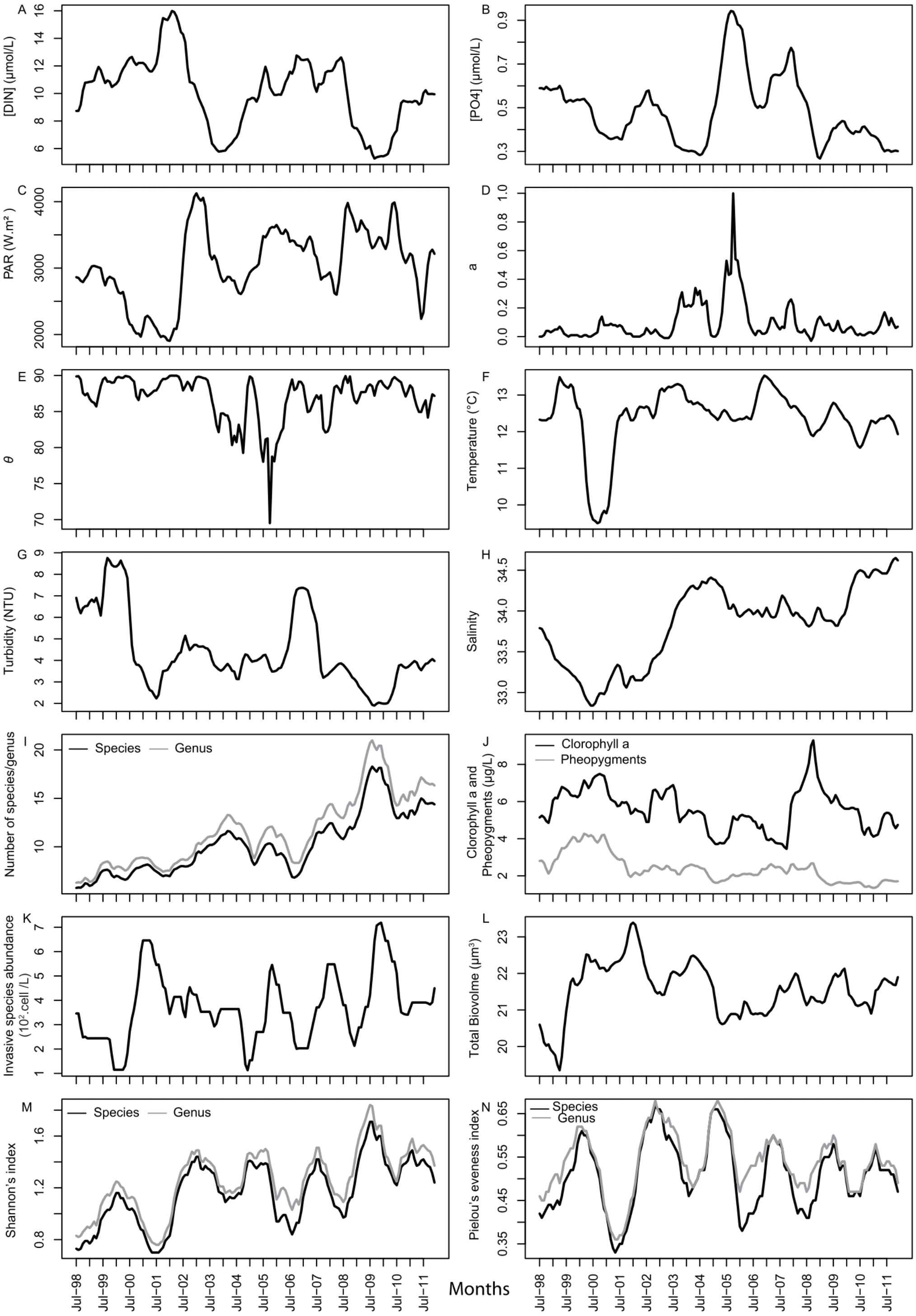

Figure 5.26: Variable trend after being deseasonalized on a monthly basis, from June 1998 to December 2011.

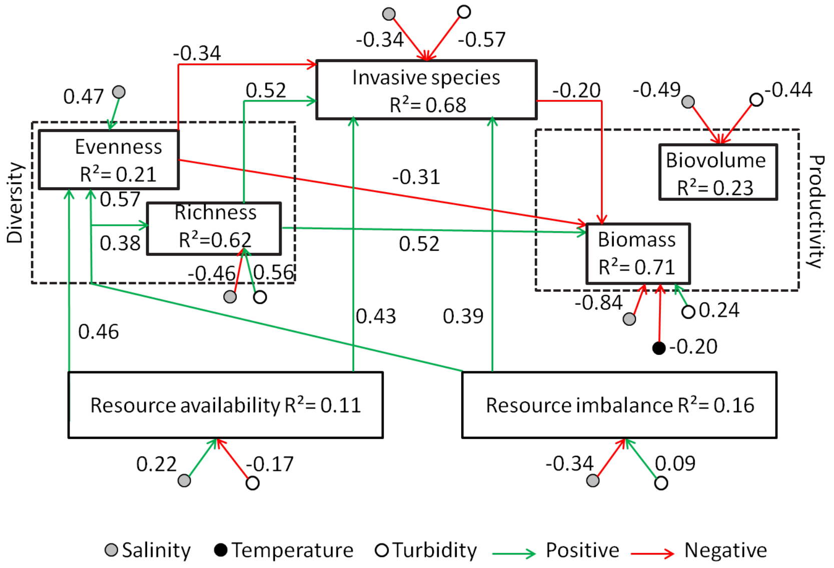

Figure 5.27: Long-term trend final structural model. Only significant pathways are displayed. Path coefficients are placed next to corresponding pathways. R^2 values are displayed for all endogenous variables.

fected richness, evenness, and resource imbalance and negatively all the other endogenous variables (Figure 5.27). Turbidity acts as an opposite to salinity on a, θ, richness and biomass (Figure 5.27). Whereas it had a similar negative effect on biovolume and the invasive species (Figure 5.27).

5.3.3 Data seasonal trend

Nitrogen, Phosphate and turbidity followed a similar trend throughout the year, i.e. a U-shape, decreasing from January until June and increasing again until December (Figure 5.28A, 5.28B and 5.28G). PAR, temperature and salinity had a hump-shape trend with the maximum in summer (Figure 5.28C, 5.28F and 5.28H). No clear trend appeared for resource availability "a" but the resource imbalance "θ" dropped in Spring and Autumn (Figure 5.28D and 5.28E). The number of species and genus peaked twice during the year, in late winter-early spring, and in autumn (Figure 5.28I). Chlorophyll-a and the invasive species peaked in spring, while the pheopigment stayed stable (Figure 5.28J and 5.28K). Biovolume increased from January to March, stable until October and then decreased (Figure 5.28L). Pielou's evenness and Shannon index of diversity, at species and genus levels, dropped in April and steadily increased until December (Figure 5.28M and 5.28N).

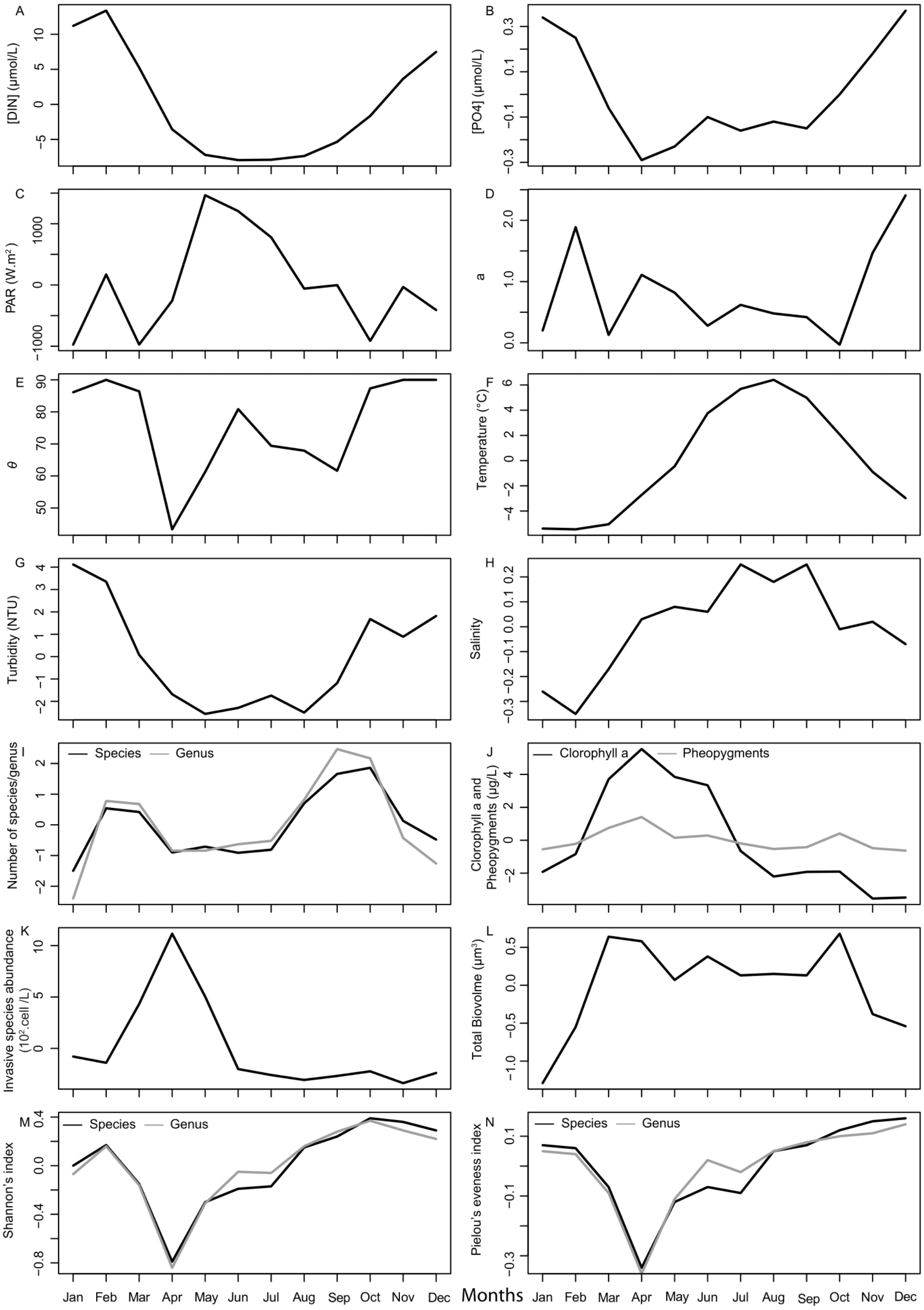

Figure 5.28: Mean monthly seasonal signal for each variables over for one year.

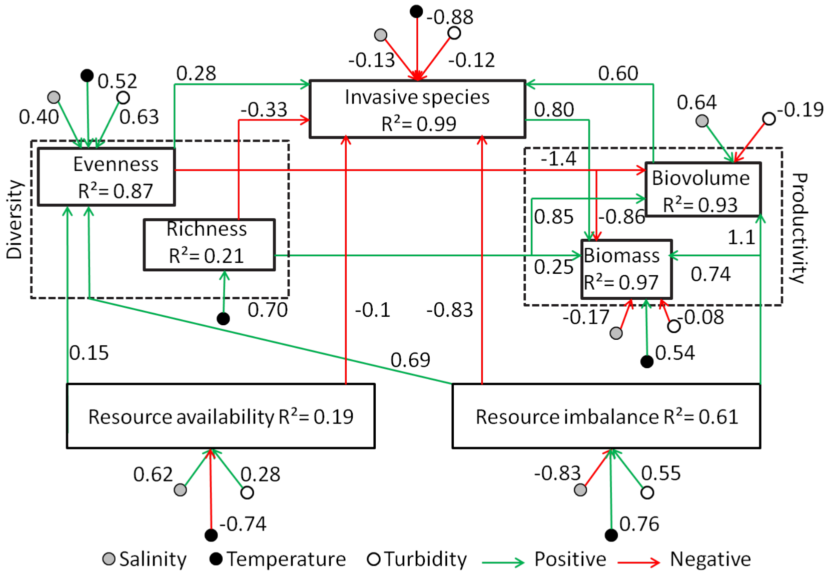

Figure 5.29: Seasonal structural model. Only significant pathways are displayed. Path coefficients are placed next to corresponding pathways. R^2 values are displayed for all endogenous variables.

5.3.4 Seasonal MPD model

Similarly to the long-term, a and θ had a positive influence on evenness. On the contrary, θ had no effect on richness, but had a positive effect on biomass and biovolume (Figure 5.29). Like the long-term MDP, richness and evenness had a positive and negative effect on biomass, respectively. Unlike, they have an equivalent effect on biovolume (Figure 5.29). The causal links towards the invasive species, were all of the opposite sign than in the long-term model (Figure 5.29). Additionally, the biovolume was positively linked to the invasive species (Figure 5.29).

All three exogenous variables had a great influence in the model. Antagonistically to the long-term model, temperature was the main driver (high path coefficients). It had a positive relationship with biomass, along with richness, θ, evenness and biovolume (Figure 5.29). On the other hand, temperature negatively impacted a and the invasive species. Salinity had a similar effect on both models, but it had lost its influence on richness and had the opposite effect on biovolume (Figure 5.29). Turbidity had similar links as salinity on, a, evenness, biomass and the invasive species. Whereas it worked as the opposite with θ and biovolume (Figure 5.29).

5.4 Discussion

The originality of our method was to extract the seasonal and long-term signal from the time-series. It is critical to decompose the data, otherwise, the seasonal signal hides the long-term trend, due to the system's dynamics as in Figure 5.26 and 5.27 of Lefebvre et al. [2011]. The differences between the two models are the number of relationships between the two diversity proxies with both productivity aspects, and the direct links of resource imbalance (θ) with diversity and productivity. In both models, evenness and richness were both linked to biomass negatively and positively respectively. But the seasonal model revealed additional negative and positive links from both diversity proxies to biovolume. These diversity-productivity relationships were already reported in previous studies [Hodapp et al., 2015; Lehtinen et al., 2017; Lewandowska et al., 2016], which confirms the idea that despite separating the highly variable seasonal signal from the long-term trend, these relationships still hold. Other common relationships are the direct link between θ and the two proxies for productivity, which were only revealed in the seasonal model. Moreover, the relations were positive which is opposite of the general consensus findings but corroborate the ones of [Lewandowska et al., 2016] in marine studies. The results comes in line with previous studies but also suggest that the seasonal trend might have played a role in their findings. The positive relationship can be explained by the phytoplankton blooms [Smayda, 1997], characteristic of annual primary productivity in marine system [Winder and Cloern, 2010]. An established phytoplankton response to seasonal increase in temperature and light availability (while nutrient are still available) is the increase biomass during spring bloom [Cushing, 1959; Sommer et al., 1986], corresponding to a rebalancing of resource, i.e. a drop in θ (Figure 5.28E and 5.28J). Furthermore, the spring bloom can also be seen in the last common relationships in aquatic studies: the positive links between the resource imbalance and richness [Lehtinen et al., 2017; Lewandowska et al., 2016] and/or evenness [Lehtinen et al., 2017; Gamfeldt and Hillebrand, 2011]. The resource-diversity relationship was dominated by θ (0.69) over a (0.15) in the seasonal model, but balanced out in the long-term model (γ=0.46 a -> evenness, γ=0.38 θ -> richness and γ=0.57 θ -> evenness). During spring, the dynamic succession of few successful species and the remnant populations of previous blooming taxa [Lehtinen et al., 2017] could explain the positive relation between θ and the diversity. As θ was decreasing in spring, or the resource was more balanced, a drop in Shannon diversity indexes and Pielou's index for evenness can be seen, and the richness started was high (Figure 5.28E, 5.28M, 5.28N). The relationship between the θ and the diversity were strengthened in the long-term model with an additional link to richness. Oppositely, in the long-term model, the relationship between θ and productivity was not existent. These differences between the two models showed that the θ-diversity and the diversity-productivity relationships is strengthen and weakened respectively, on a longer time scale. However the θ-productivity can be considered on short-time scale studies.

Furthermore, in Lewandowska et al. [2016], meta-analysis have shown that the biomass and richness decreased with a higher resource supply (a), but increased in response to resource imbalance (θ). The arguments for the contradiction was explained by the increasing nutrient incorporation by the heterotrophic microbes, other forms of nutrient were not considered (DOP and DON), and light was not used as a resource [Lewandowska et al., 2016]. Despite using light as a resource in our models, as it can become an important resource under repleted nutrient supply [Cardinale et al., 2009b], we still did not found the same results as found by Lewandowska et al. [2016] for the L4 station in the Western English channel. So maybe, as extrapolated by Lewandowska et al. [2016], the organic form of nutrient should be used in future MPD models. This limitation misrepresent the consumption of dissolved organic nutrients, affecting the link between resources and biomass. Furthermore, the resulting relationships could also be the result of an artifact. Even though it has been deseasonalized, the use of *in situ* data encompass the high dynamism of the marine ecosystem which can be subject to an increasing species migration while θ disfavor the native one. Although, previous studies had already shed light on other possible explanations for those relationship. Evenness negative relationship with biomass could be explained by the dominance of a few highly productive species; reducing the dominance by these species decreases the realized productivity [Lewandowska et al., 2016]. The positive relationships between the a and θ with evenness has already been reported by Hillebrand and Lehmpfuhl [2011]. Biotic interactions, such as competition or predation, can potentially favor and/or inhibit the occurrence of some species, lifting the dependency of biomass from the resources. Competition appeared as the first explanation for a phytoplankton community using the same resources, as explained by Tilman [1982] RRT. Additionally, the positive relationship between richness and biomass was also common for both models. The relationship can be attributed to an increasing efficiency in resource use with higher richness, which consequently produces more biomass [Wille et al., 2008; Cardinale et al., 2009b,a; Hillebrand et al., 2007]. The argument is reinforced by Chesson's ideas of stabilizing and equalizing mechanisms for coexistence [Chesson, 2000], when extreme resource supply ratios prevent trade-offs in resource use from stabilizing coexistence. A second explanation for the positive relationship between a and θ with evenness is the effect of predation within the MPD model [Hillebrand and Lehmpfuhl, 2011]. Consumers effect has previously been reported as a limitation within the MPD models [Hillebrand and Lehmpfuhl, 2011]. Experiments had shown that consumers increased evenness if resource conditions promoted dominance but decreased evenness if resource conditions already promoted evenness, as in the model. The mechanism involved is described as the competition-defense trade-off, i.e. the species that profits the most from the resources is also the one that is the most consumed [Viola et al., 2010]. Additionally, the consumers presence could be accounted for a decrease in algal biomass as the subsequent biomass removal increased with increasing resource supply [Elser, 1992; Sarnelle, 1992; Hillebrand, 2002, 2005]. The process could potentially have a large impact in the long-term, especially in the case of trophic cascades [Estes, 1998; Eriksson et al., 2009; Hughes et al., 2013] and mismatch [Sommer et al., 2012; Edwards and Richardson, 2004], which are common in marine studies.

The tight linkage of phytoplankton to the climatic conditions makes their annual cycle highly variable from year-to-year [Cloern and Jassby, 2008; Paerl and Huisman, 2008; Garcia-Soto and Pingree, 2009], and different across systems [Pratt, 1959; Scheffer, 1991; McQuatters-Gollop et al., 2008] and vulnerable to long-term changes. For instance, the negative relation between temperature and biomass can be surprising as it is often associated with the metabolic rates and therefore biomass [Yvon-Durocher and Allen, 2012]. The positive temperature biomass relationship cannot be valid on multidecadal trend. For instance, shifts in earlier bloom timing, with lower biomass, were reported in the Western Scheldt Estuary due to the past 30 years warming [Kromkamp and Van Engeland, 2010]. Similarly, the warm phase of the North Atlantic Oscillation triggered a shift in community composition in the Baltic Sea [Smayda et al., 2004; Alheit et al., 2005]. So changes in community composition can further alter the community optimal temperature ranges [Eppley, 1972; Goldman, 1977; Thomas et al., 2012]. Moreover, the combined effect of temperature and other abiotic changes, such as nutrient, has been reported to negatively effect primary productivity. Under phosphorus limitation, increasing temperature had a negative effect on lake phytoplankton biomass, while the effects were positive during eutrophic conditions [Tadonléké, 2010].Therefore, the long-term and seasonal trend are necessary to understand the temporal MPD relationships of marine phytoplankton. Since phytoplankton fluctuation can be induced by climate change, directly and indirectly, by many processes operating at many time scales. Salinity and turbidity also seemed to have a great impact onto the MPD model in both seasonal and long-term trend. Turbidity is increasing in coastal systems because of erosion and nutrient input [Rabalais, 2004]. It can be considered as synonymous of freshwater input along with nutrient loading from rivers, resuspension of sedimental nutrients and increasing light-limitation [Oliver et al., 2010]. The positive relationship between turbidity and both resource aspects, seemed to be explained by the increasing importance of light resource within the ecosystem. On the other hand, a higher salinity can be a proxy for dryer periods with increasing light availability. Light being an important resource for phytoplankton growth [Currie, 1991; Rosenzweig and Abramsky, 1993; Abrams, 1995; Waide et al., 1999; Mittelbach et al., 2001] it seemed to explain the positive link with evenness, lifting the light limitation on growth and increasing coexistence as in the RRT [Tilman, 1982]. Moreover, light attenuation relation with diversity being humped-shape, it also has the potential to explain the positive relationship of salinity with richness in the long-term trend model [Chalar, 2009]. The indirect effect of light on salinity seemed to corroborate with the positive link with resource availability which decreases the imbalance of resources in repleted conditions. A greater consideration should be taken into the inclusion of precipitation and runoff within future models, as they can directly influence salinity, turbidity, resource input into the system, and therefore the BEF relationship [Thompson et al., 2015; Bouwman et al., 2005].

The coastal ecosystems are often more vulnerable to invasive species due to anthropogenic pressure [Cohen and Carlton, 1998]. The invasive species was directly correlated to the resource availability and imbalance. The increasing resource availability, which also comes in hand with an increase in resource imbalance, as in the case of eutrophication as been reported to favor the occurrence of harmful and nuisance algae worldwide [Davidson et al., 2012]. Herein, the results revealed a positive effect of richness on the invasive species along with a negative effect on evenness. The results revealing the increase in local species richness seemed to be characteristic of species invasion [Sax and Gaines, 2003; Byrnes et al., 2007] but little is known on the effect of increase biodiversity in the system [Byrnes and Stachowicz, 2009; Karlson et al., 2011]. The relationships fits with the RRT theory of Tilman [1982] the increase resource imbalance increases the number of species which includes the invasive species. The negative effect of evenness, can reflect the interactions between native and invasive species that compete for shared resources [Giller, 1984; Korsu et al., 2012]. By competing for resources, it decreases the productivity of the native community explaining the negative relationship between the invasive species and biomass. The result corroborates with the previous finding, but only on a long-term trend. On a seasonal scale, the opposite scenario seemed to be occurring. The increasing of θ and a inhibit its occurrence, along with increasing richness and decreasing evenness. The contradictive scenarios seemed also to change the impact of the invasive species onto the community biomass. In the long-term it negatively impacted the native biomass while with the seasonal signal, it had the opposite effect. Salinity and turbidity cannot explain these changes as they were always negatively related to it. The negative relationships might also be the reflection of resource competition with the native community, due to increase or decrease in light availability, resuspension of sedimental nutrients, or more directly it cannot stand turbulent waters [Oliver et al., 2010]. The opposite scenarios seemed to only be explained by temperature, which was negatively correlated to the invasive species. Herein, the success of the invasive species, over the native community, from a year to another seemed to temperature dependent. In warm years, the higher temperature favor the less productive numerous small native species, at a more even proportion, which are able to inhibit the success of the invasion. On the contrary, cold years favors the invasive species as only a few dominant productive native species compete with it for resources. Therefore, the long-term trend seemed to be driven by the consecutive cold years, as seen in the drop in temperature in Figure 5.25F.

5.5 Conclusion

We have shown that the positive relationship between Resource imbalance and availability to Evenness and in turn negatively related to biomass, also the positive link between richness and biomass [Lewandowska et al., 2016] seemed to be applicable to the coastal marine ecosystem, over seasons and in long-term relationship. Furthermore, we have shown the importance of including other abiotic factors, as in Hodapp et al. [2015] in order to grasp the larger picture of the BEF relationship as they may differ and affect the system differently, at different scales. The inclusion of the invasive species, within the model, shed light onto the variable coming into play and the different relationships allowing the success or the downfall of the invasion. The relationships found within the seasonal model defined the relationship of the long term trend model, which is the consequence successive cold years scenario.

5.6 Acknowledgments

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Chapter 6

Discussion

6.1 Result synthesis

6.1.1 Within outlying mean indexes: refining the OMI analysis for the realized niche

Hutchinson's niche concept was adapted for a greater applicability by revisiting both the Jackson and Overpeck [2000] theory and the Outlying Mean Index analysis [Dolédec et al., 2000]. The intersection between $\mathbf{N}_{\boldsymbol{R}}$ and the sub environmental space $\mathbf{K}$ was used to estimate the biotic constraint (Figure 2.2). A subset of environmental conditions (K), is defined within the environmental gradients E_1 and E_2 and it can be of temporal and/or spatial scales. In each K, the species subniches $\mathbf{S}_{\boldsymbol{R}}$ can be calculated from both, the mean environmental habitat condition of $\mathbf{E}$, G, and from the subset mean habitat conditions G_K. Therefore a subniche, $\mathbf{S}_{\boldsymbol{R}}$, is found within the existing fundamental subniche $\mathbf{S}_{\boldsymbol{P}}$ allowing the observation and quantification of the subset biotic factor $\mathbf{S}_{\boldsymbol{B}}$ constraining the species subniche [Karasiewicz et al., 2017]. All $\mathbf{S}_{\boldsymbol{R}}$, $\mathbf{S}_{\boldsymbol{B}}$ and $\mathbf{S}_{\boldsymbol{P}}$ are comparable as they are all found within $\mathbf{E}$. Along with the subniche concept, a new statistical method was developed based on the Outlying Mean Index (OMI) [Dolédec et al., 2000]. The Within Outlying Mean Indexes, are composed of the calculation of two different indexes Within Outlying Mean Index from G and from G_K (WitOMIG and WitOMIG_K). The index estimations require the calculation of the species frequency relative to each $\mathbf{K}$ subset (with $1 \leq \mathbf{K} \leq N$). Second, the N Fr_K matrices are concatenated to produce the overall species frequency table ($\mathbf{Fr}^*$).Third, the standardized environmental table $\mathbf{Z_0}$ is used in combination with $\mathbf{Fr}^*$ to calculate WitOMIG. In a similar fashion, WitOMIG_K is estimated by combining $\mathbf{Fr}^*$ with $\mathbf{Z}^*$.$\mathbf{Z}^*$ is the result of the concatenation of the N $\mathbf{Z}^*$ corresponding to the independently centered K subsets of the standardized $\mathbf{Z_0}$ [Karasiewicz et al., 2017]. Therefore, the subniche concept is well suited to study the species response under global change in combination with the biotic interaction at a temporal scale. It makes the species, subniches $\mathbf{S}_{\boldsymbol{R}}$, biotic factor, $\mathbf{S}_{\boldsymbol{B}}$ and the subset of environmental conditions comparison possible under any scale chosen [Karasiewicz et al., 2017].

6.1.2 Environmental response of *Phaeocystis* spp. realized niche

After developing the concept and the corresponding statistical methods, we applied the WitOMI analysis and the subniche concept in order to study the response of phytoplankton community under environmental conditions favoring and disfavoring the appearance of HAB. In the coastal waters of the Eastern English Channel (EEC) , the occurrence of *Phaeocystis* spp. and its yearly annual variable blooms, along with the preceeding bloom of diatoms makes it a perfect case study. The OMI analysis revealed that, as expected, the species niches were distributed along the nutrient concentration and turbidity gradients, and with the temperature, Photosynthetic Active radiation (PAR), and salinity gradients. The subset environmental conditions hosting the high abundance of *Phaeocystis* spp. (subset H) was characterized by lower turbidity, nutrient concentration and temperature but higher salinity compared to the subset of low *Phaeocystis* spp. abundance (L). The annual environmental trajectory of subset H resembled more a full cycle than subset L which went "back on track". The diatom community in subset H was richer in species number than in subset L (11 and 7 respectively) with five species common to both subsets (*Guinardia delicatula*, *Guinardia striata*, *Paralia sulcata*, *Skeletonema spp.*, *Thalassionema nitzschioides*). *Phaeocystis* has a smaller realized subniche in events of in subset L than H because of a higher biological constraint (81% and 25% of *Phaeocystis* existing fundamental subniche for subset L and H respectively). ï · The higher diversity of the diatom community, has a weaker biological constraint in subset H than in L. The preceeding key diatom species, such as *Skeletonema spp.*, *Thalassionema nitzschioides* and *Thalassiosira gravida* community seemed to be controlled by the environment. The concentration of silicate, being limiting in subset H, favored other less dominant species competing for resources but still being over competed by *Phaeocystis* spp. Whereas in subset L, the concentration of silicate, as well as nitrogen being higher, the first blooming species, (e.g.*Skeletonema* spp., *Thalassionema nitzschioides*) could establish themselves within the water column for longer time periods, and could possibly out-compete *Phaeocystis.* In subset L, diatoms-*Phaeocystis* spp. spring bloom succession reported by Breton et al. [2006] occurred, whereas *Phaeocystis* was always present in the subset H. The preceeding diatom competitive ability controlled the bloom of *Phaeocystis* which was itself reliant on the winter nutrient stock concentration.

6.1.3 Phytoplankton long-term and seasonal diversity-productivity relationships with an invasive species.

The study revealed that the multivariate diversity-productivity (MPD) relationship, in response to the changing climatic condition and the presence of the harmful algae species differ according to the time-scale. MPD was strengthened in the seasonal cycle by relating both diversity proxies to both productivity proxies. MPD reveals that a few productive species are dominating the community, but biomass production can be further enhanced by increasing richness, as resource used is more efficient. In the long-term model the relationship between the resource imbalance (θ) and the diversity proxies were strengthened. It reveals the importance of the Resource Ratio Theory long-term applicability [Tilman, 1977] on the community diversity. The relationship between θ and productivity was only significant on a seasonal scale suggesting that short time scale relationships can have a large impact on a longer time scale. Temperature, as expected, had a large influence on the seasonal model, being the main driver for phytoplankton seasonality, but had a low impact on the long term. Turbidity and salinity always had a relatively high influence on both models affecting all aspects of the MPD relationship. Turbidity and salinity effect on the relationship might also be an indirect affect of dry and wet periods. The biomass and richness declined with higher resource supply (a), but increased in response to resource imbalance (θ).Despite considering light as resource, as suggested in previous studies [Lewandowska et al., 2016; Cardinale et al., 2009b], the relationship reflects the one of the limitations of the study, the unconsidered consumers. In conditions which promote dominance of a few productive species, consumers can decrease evenness and increase richness. The competition-defense trade-off, could explain the mechanism involved, in addition it will also account for the subsequent biomass loss during increasing a. The seasonal-scale MPD relationship can help explain what it is happening on the long-term. The successive low temperature annual cycle, can explain the success of the invasive species in the long-term. The annual cycle is associated with low salinity and turbidity conditions, will also be related to low levels of resource availability, increasing θ. The depleted resources, but at greater balance, increases community evenness which in turns enhanced the occurrence of the invasive species. The lower temperature, decreasing the species number further led to the appearance of the invasive species. The community diversity conditions are characterized by species of small volume, and thus intensified the invasive species presence. In return, the invasive species occurrence boosted the biomass production. In long-term, the invasive species were positively influence by the a and θ which was expected in cases of eutrophication. Furthermore the long-term increase in species numbers, at equal proportions were less competitive. Consequently, as expected, the invasive species have a negative effect on the primary production in general.

6.2 Perspectives

6.2.1 Methodology improvements

During the thesis, the data of only one sampling station was used. This site had allowed us to study the temporal dynamism and realized niche of the phytoplankton niche community, and their respective diversity-productivity response to the environmental change under events of Harmful Algae Bloom (HAB). The study could be improved by including the following suggestions.

Spatial distribution

The first limitation of the study can be lifted by including a spatial dimension, in parallel to a temporal dimension. The French National Phytoplankton and Phycotoxin Monitoring Network (REPHY) is managed by the French Institute for the Exploitation of the Sea (IFREMER). Its aim is to study: i) the spatial and temporal variability of phytoplankton communities along the French coast, and ii) the potential phycotoxin-producing species and their relationships with toxic shellfish outbreaks. Since 1987, this network has collected information on phytoplankton communities and currently provides a large database covering numerous sites with different hydrological characteristics. Additionally other data-base, such as Helgoland Roads and Continuous Plankton Recorder monitoring surveys, could be used to gather more heterogeneity, in terms of environmental variations and phytoplankton community. Marine ecosystems are heterogeneous because environmental variables (*i.e.* temperature, turbidity, salinity, etc) are subject to permanent disturbances due to hydrodynamic processes and turbulence [Reynolds, 2006] affecting the phytoplankton spatial distribution. On a large scale, oceanic oscillation such as the North Atlantic Oscillation (NAO), along with winds regime and great water currents, as the Golf Stream, have profound effects on phytoplankton distribution and composition [Cullen et al., 2002; Cloern, 1996]. On a smaller scale, such as coastal zones, phytoplankton communities are altered by high nutrient input concentration from local rivers and water masses exchanges between the open seas and deep waters in shallow shores [Reynolds, 2006]. Therefore, if one wants to include a spatial dimension into the niche dynamism study, they should consider the scale of it. Turbulence and hydrodynamic processes are dynamic phenomenon which affect the phytoplankton distribution at all scales [Cloern, 1996].

For instance, Species Distribution Models (SDM) which make predictions on the climate change effect on species' distribution range assume that species have a fixed environmental niche, known 'niche conservatism'. Therefore, it implies that each species' distribution and cycle is mostly defined by environmental conditions [Irwin et al., 2015]. Although there is strong evidence of environmental conditions controlling phytoplankton distribution [Parmesan, 2006; McMahon and Hays, 2006; Thomas et al., 2012; Parmesan and Yohe, 2003; Hays et al., 2005; Beaugrand et al., 2002] it is a simplistic view. Palaeoecological research, along with other studies, revealed that the species are much more resilient to climate change than first thought with fixed environmental niches [Lohbeck et al., 2012; Schlüter et al., 2014; Reusch and Boyd, 2013]. Resilience to climate change can be referred to as 'niche plasticity', and might be caused by the combining effect of biotic and abiotic factors including (a) evolutionary adaptation, (b) genetic variation, (c) phenotypic plasticity, (d) biotic interaction (*e.g* competitors, parasites, prey and predators) responses to changing conditions and (e) phenological changes [Chivers et al., 2017]. As changes in spatial ranges among marine phytoplankton has been reported [Beaugrand et al., 2002; Parmesan and Yohe, 2003; Hays et al., 2005; Sagarin et al., 1999; Edwards and Richardson, 2004; Burrows et al., 2011; Pinsky et al., 2013], it is not known whether they track their preferred environmental conditions or display resilience. In other words, do phytoplankton exhibit niche conservatism [Thomas et al., 2012; Gienapp et al., 2008; Poloczanska et al., 2013] or niche plasticity. Evidence shows that diatoms had a greater tendency for niche plasticity compared to dinoflagellates [Chivers et al., 2017] revealing that the use of Within Outlying Mean index on more than one station, in phytoplankton community study, could lead to more complex interpretation. A greater spatial heterogeneity will come with, for each species, a greater variation in evolutionary adaptation, genetic variation, and phenotypic plasticity which might lead to different responses to global change and biotic interaction altering the phenology. The quote "*more data the better*", in the context of spatial variation in phytoplankton niche, should be used with caution.

The current state of knowledge on the spatio-temporal variation effect on phytoplankton diversity-productivity is very limited. Most studies have been using data resulting small in both time and spatial scale and performed in controlled homogeneous experimental conditions. The MPD varies on a local or regional scale [Chase and Leibold, 2002; Chase and Ryberg, 2004], which concedes the importance of the community spatial dynamics and the constraints exerted by different processes. Theoretical and empirical results reported that the rate of dispersion impact primary production by limiting local and regional coexistence [Loreau et al., 2003; Matthiessen and Hillebrand, 2006]. Hillebrand and Lehmpfuhl [2011] revealed the difference in local and regional diversity-productivity relationship, the meta community, algal biomass increased with increasing resource supply and increasing imbalance, whereas local species richness and evenness decreased with the same conditions. Still a relatively few studies have focused on the impact of the spatial scale and heterogeneity on local extinction, HAB, functional and phylogenetic composition, concomitantly with other aspects of environmental change (especially temperature and eutrophication). Their respective influence on the relationship between diversity and ecosystem functioning, and under natural conditions across spatial and temporal scales requires further investigations. [Naeem et al., 2009; Tomimatsu et al., 2013].

Another limitation which also affects phytoplankton spatial distribution is the depth at which the data is collected. The data used during the studies were collected between the surface and a meter deep but depth is also associated with vertical light, temperature and nutrient concentration gradients. The ability of some phytoplanktonic groups to control their vertical position (*e.g* dinoflagelates) is considered as a competitive advantage as they motile themselves into light and nutrients [Ross and Sharples, 2007]. Their motility allows them to optimize their growth and multiplication contributing to the community's diversity [Ross and Sharples, 2007]. Greater attention should be brought into refining the variables, in particular light. Light availability in the water column should be a measured instead of solar radiation. For similar solar radiation, the light available to the phytoplankton can be altered by the level of water turbidity. Some studies have also revealed the importance of verticality in species' abundance in distribution. The spatial distribution, either vertically or horizontally, reveals to be of great importance for marine phytoplankton to the dynamism of heterogeneity of their environment. More spatial variation comes also with greater complexity in phytoplankton response to global change.

Other variables and resources

A common limitation of the two studies, is the unconsidered different form nutrient. Dissolved organic nitrogen and phosphate (DON and DOP), can become important resources at certain depth where light is depleted. As questioned by Darwin [1845] "*I presume that the numerous lower pelagic animals persist on* *the infusoria, which are known to abound in the open ocean: but on what, in the clear blue water, do these infusoria subsist?"*. The microbial loop was only recently discovered and explored. Research revealed the significance of microbes in the ocean's food web. The idea that bacteria decomposing organic material and remineralizing into inorganic nutrients was only fully accepted in the 1980s [Pomeroy et al., 2007]. In association with other micronutrients, such as zinc, copper and iron, they might help in understanding the phytoplankton water column distribution. Some species might be more dependent on the microbial loop, in depleted nutrient winter stock conditions, as in summer. The DOP and DON could be used as a proxy for microbial recycling in the MPD model or as a environmental variable in the WitOMI analysis. The micronutrients can be limiting for growth as they are also essential resources. They can also be added as resources in the MPD model and niche analysis for a greater species niche partitioning and mechanistic knowledge of the diversity-productivity relationship. Another limitation, which mostly affects the diversity-productivity study, is the understanding of direct and indirect effect of environmental variables. As mentioned, the salinity variation might be an indirect affect of dry and wet periods, which can partly be considered by considering precipitation as an environmental variable. Phytoplankton response to precipitation has revealed to depend upon the season and region [Thompson et al., 2015]. Winter precipitation has a tendency to reduce chlorophyll *a*, diatoms and chrysophytes, but summer precipitation increases chlorophyll *a* and chlorophytes. In wet regions, more precipitations favored chlorophyll *a* but decreased dinoflagellate in autumn and diatoms in spring. On the opposite, dry regions experiencing less precipitation in spring and summer made decrease the abundances of chlorophytes [Thompson et al., 2015]. The variability of phytoplankton patterns in association with seasonal and year-to-year precipitation cycles increase the predictions capacity of community composition and structure of estuarine and coastal waters.

Beyond these practical concerns, many fundamental studies in ecology have been using phytoplankton as a model system. Hutchinson [1961] "paradox of the plankton" questionned how numerous phytoplankton species can coexist on only little resources, contradicting the competitive exclusion principle. The "trait-based approaches" has gained interest in ecology [Lavorel and Garnier, 2002; McGill et al., 2006; Westoby and Wright, 2006], because it has potential to give a mechanistic understanding on the ecological communities organization and can be used for further prediction of community organization under global change.

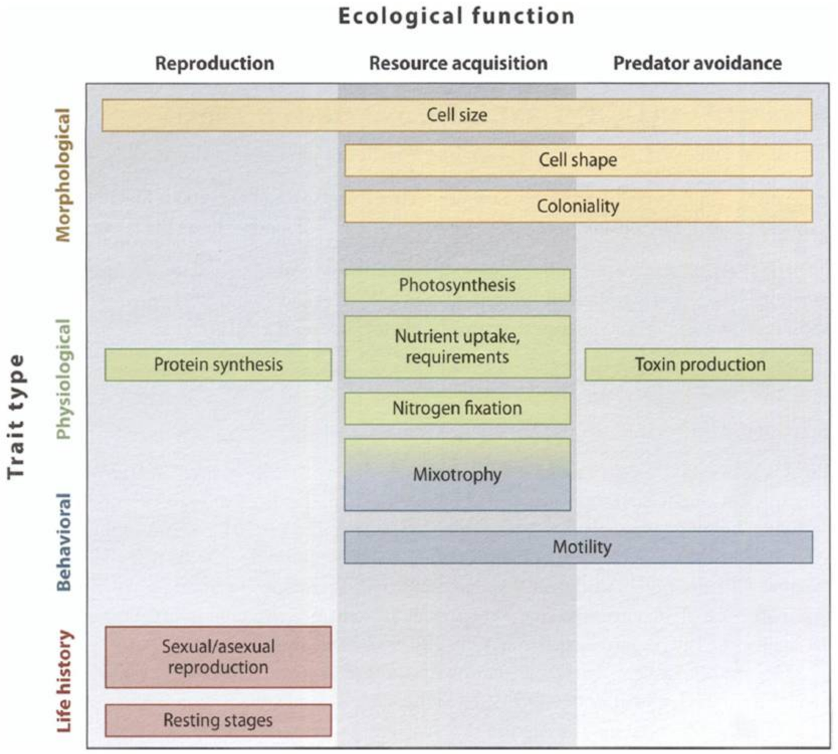

Figure 6.30: Litchman et al. 2008 summary of phytoplankton trait which can affect different ecological functions

6.2.2 Functional niche and diversity

The thesis was focusing on the empirical view of the niche dynamism and diversity-productivity relationship of phytoplankton community. The understanding of the mechanism involved could be done by using Litchman and Klausmeier [2008] "trait-based approach". The four major components of the "trait-based"" approaches are the species traits, environmental gradients, species interactions, and performance currencies [McGill et al., 2006]. Despite the difficulty in other ecosystems to define and measure the traits that impact the species ecological niches, for phytoplankton these traits remain relatively simple to define and measure [Litchman and Klausmeier, 2008].

The recent interest for making predictions on community responses to global change, and their effect on ecosystem functioning have reshaped the way of classifying species [Petchey and Gaston, 2006]. Hence, it is not the species' traits that control their growth, reproduction and survival, but their functional response traits [Violle et al., 2007]. Trait-based approach allows, therefore, grouping species with comparable morphological (size, shape, and coloniality), and/or physiological (maximum growth rate, half-constant nutrient uptake, minimum nutrient quota, maximal nutrient uptake rate, light use efficiency, photosynthesis efficiency, etc) and/or phenological characteristics. All may help to reveal the optimal ecological strategies along environmental gradients [Petar et al., 2014; Caroni et al., 2012; Naselli-Flores and Barone, 2012], and has allowed to get a deeper insight into the mechanisms controlling the community structure for a better understanding of the ecosystem functioning and biodiversity changes [Ebeling et al., 2014]. Furthermore, functional diversity (*i.e.* the extent of traits differences among co-occurring species) has been proposed as an important characteristic of a community composition [Tilman, 2001; Hooper et al., 2005]. Research has shown that biodiversity-functional diversity relationships are complex and ecosystem dependent [Cadotte et al., 2011], concealing selection and complementary effects [Tilman, 1999]. The functional important aspects of species diversity are now more commonly represented by functional traits composition than by other more traditional groups, such as phylogeny [Diaz and Cabido, 2001]. The direct relationships between traits and the functioning of a species [Lavorel and Garnier, 2002] can give us clues (1) on the mechanisms driving the community composition with the patterns of functional trait distribution [Weiher et al., 1998; De Bello et al., 2009] and (2) how it controls the dynamic of the community, or the spring bloom succession. The Within Outlying Mean Index (WitOMI), could help reveal the dynamism of the community functional niches.

Although linking the niche concept with the trait-based approach is attractive, its application can reveal to be difficult as it first requires the identification of the relevant environmental axes defining the species niche. Concerning the phytoplankton community, the environmental conditions defining them is well documented as previously explained. Once the environmental gradients are determined, the most common method to calculate species niche is to analyze species abundances (or presence-absence) and define the niche using further statistical techniques, as the Outlying Mean Index [Dolédec et al., 2000] ,used during the thesis [Guisan and Thuiller, 2005]. Instead of the species abundance, species trait values can be used to analyse their respective responses along the environmental gradients. Second, the identification and quantification of the species trait that respond to those environmental variables can reveal to be more difficult. Despite the Litchman and Klausmeier [2008] summary, the traits defined in the study are not known for all species and mostly change during the phytoplankton life-cycle. Furthermore, the values for traits measured are often done in experimental conditions [Litchman and Klausmeier, 2008] and might not be representative of the *in situ* values. As species and individuals differ in trait values [Litchman and Klausmeier, 2008; Litchman et al., 2007], the quantitative knowledge and time-series of traits values among species could contribute to the niche differentiation between species, as well as their respective impacts on coexistence and diversity [Chase and Leibold, 2003]. As not all species traits are known or sampled yet, Bruggeman [2011] has developed a model that can help counter the gaps. As most phytoplankton traits are more or less conserved in evolution, thus the species traits' value can be found in its evolutionary history along with common correlations between traits. The trait value estimation considered the species phylogenetic relationships between species types, and the approximation by the power-law relationships (e.g., allometric scaling laws) between traits [Bruggeman, 2011]. The model could be used to complete trait data set for further analysis.

Nevertheless, these studies in phytoplankton ecology focused on responsive traits (traits that explain community structure) to the environmental variability. However, it has already been shown on land, that traits of different plant species can explain both the response of a community to environmental changes and their effects on ecosystems [Lavorel and Garnier, 2002]. Now, this notion of effect traits as well as the relation between functional effect groups and functional response groups are still poorly explored [Pakeman, 2011]. This is an important task to evaluate if community acts as a filter between environmental change and ecosystem functioning. To distinguish between the response functional group and effect functional group, several methods are available. Different statistical analyses (*e.g.* Cluster regression, RDA-sRegTree, RDA-mRegTree, OMI-GAM, RLQ,double CCA) already exist to define the response functional niches of a community but can also be applied for effect functional group, as summarized in Kleyer et al. [2012]. For instance, the RLQ [Dray et al., 2014] is a three-table ordination method testing the relations between species traits and abiotic variables (R, abiotic variables; L, species abundances; Q, species traits). The statistical triplet had mostly been used for studying functional response of species trait but can be applied to study the effect functional species trait by replacing the abiotic variable table (R) by the ecosystem one wants to study. Similarly, the OMI analysis [Dolédec et al., 2000] has been updated for functional trait research with an additional Generalized Additive Model [Burnham and Anderson, 2003; Thuiller et al., 2007], making the so-called OMI-GAM [Kleyer et al., 2012]. It is a three-component statistical analysis:

1. Determining the species response to the environmental gradients (OMI analysis)

2. Modeling the traits contribution to the response (GAM)
3. Clustering the species according to the responsive species-trait models (Cluster analysis)

The method could also be applied to understand the contribution of species traits onto the ecosystem functioning. The dynamism of the functional niche can potentially be studied, with the WitOMI, by applying an adapted version of the second and third components. One of the advantages of the WitOMI analysis is the quantification of biotic interaction [Karasiewicz et al., 2017], which is one major component of the trait-based approach [Litchman and Klausmeier, 2008]. The biotic interaction will interfer with the traits value of each species within a community, consequently affecting the prevalence of the functional trait among the community.

The trait-based approach could also be used in relation with the Biodiversity-Ecosystem Functioning (BEF) theory [Gamfeldt et al., 2015]. Species richness of a community do not illustrate the functional redundancy of the assemblage and the inclusion of functional could solve this issue [Griffin et al., 2009, 2013; Best et al., 2013; Cadotte, 2013]. Furthermore, it could also help in estimating the performances of the phytoplankton with certain traits values. The performance of the species, with a characteristic set of traits, will vary along environmental gradients. Phytoplankton traits and performances are more often measured in laboratory experiments, but does it reflect their natural performances? A structural equation modelling can be developed to understand the response of causal relationships between the taxa's traits and its performance to environmental changes. The equations resulting from the model of each taxa could then be used to estimate the community performance. The performance for each species can be estimated and, along the functional niche, it will give the opportunity to investigate key trade-offs structuring the community. Some trade-offs are known to contribute to species diversity, [Kneitel and Chase, 2004] possibly driving seasonal succession [Reynolds, 1984; Sommer et al., 1986] are:

- Between maximum growth rate and competitive ability, also known as the *r*-*K* strategy dichotomy [Kilham, 1980; MacArthur, 1967; Sommer, 1981].
- Between competitive abilities for different resources. The trade-off can potentially explain species shifts across supply ratio gradients and the species coexistence as resources [Leibold, 1997; Passarge et al., 2006; Tilman, 1982],

- Between competitive abilities and grazer resistance [Grover, 1995; Leibold, 1989, 1996] has the potential to explain species replacements along nutrient gradients as well as the coexistence [Leibold, 1996],

The results of the methods, the potential implication of the competition for resources within the community, and the role played by grazers, during successive bloom still remain to be tested experimentally.

6.2.3 Biotic interactions

Lavorel et al. [2013] proposed a conceptual framework which proposed the application of the Litchman and Klausmeier [2008] trait-based approach to predict the effect of the changing environmental conditions on the ecosystem service delivered by the different trophic levels. The concept is an extension of the "response-effect model" which quantifies the dependence of the ecosystem service to environmental change by studying the correlation between the "effect traits" (i.e. defined the delivery of the ecosystem service) and the "response trait" (i.e determine the response of the community to environmental factors) [Lavorel and Garnier, 2002; Suding et al., 2008]. Despite being developed for terrestrial ecosystems, the framework could be adapted to the marine ecosystem for single or multiple -trophic level systems. Figure the adaptation of the conceptual framework developed by Lavorel et al. [2013] which could be used as a conceptual tool to integrate the functional trait, with the environmental response, ecosystem functioning discussed previously, and biotic interaction. Future studies could be held to generate hypotheses on the response of the whole system with a model such as Structural Equation Modelling (SEM). As discussed previously, the response and effect traits could be determined by different statistical. The conceptual framework proposed here requires quantitative data on biotic interactions. The biotic interactions, which are of main interest in thesis are competition (e.g. species 1 and 2 are primary producers), and grazing (e.g. species 1 and 2 are a primary producer and a consumer) (Figure 6.2.3). Biotic interactions are hardly measurable *in situ* which implies to test its effect on the phytoplanktonic niche dynamism and diversity-productivity relationship in response to global change, in an experiment.

Competition experiment

In chapter 3, the WitOMI analysis was used to study the niche dynamism of the phytoplankton community under environmental conditions of high (H) and low (L) abundance of *Phaeocystis* spp. The results reveal that the preceeding diatom, especially *Skeletonema spp.*, *Thalassionema nitzschioides* and

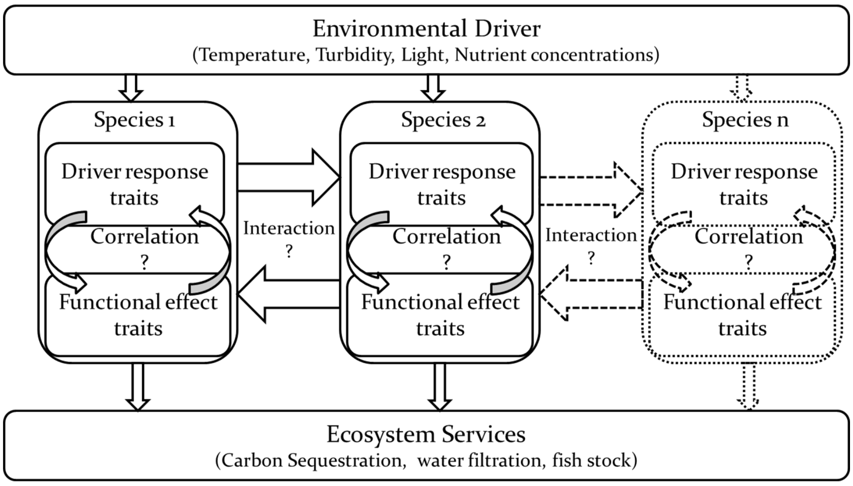

Figure 6.31: Conceptual framework inspired from Lavorel et al. 2013. The method includes the functional responses and effects between two species, from the same or from different trophic levels, to predict changes in ecosystem functioning

Thalassiosira gravida, can potentially out-compete *Phaeocystis* spp. and reduce its realized subniche. The diatom-competition hypothesis remains to be tested, in an experimental set up. The "biotic interaction" experimental set up would aim to recreate the two subset environmental conditions described in chapter 3. The environmental condition of subset H was characterized by lower turbidity, so therefore more light available, along with depleted nutrient concentration and temperature but higher salinity than in subset L. A multispecies experiment, with the *Skeletonema spp.*, *Thalassionema nitzschioides*, *Thalassiosira gravida* and *Phaeocystis* spp. could be run in chemostats, with a steady decrease in nutrient supply and increasing temperature and light availability. Similarly to the multispecies experiment, monoculture of each species could be used as controls under both environmental conditions. Samples could be collected daily to measure the abundance of each species but also their respective traits (size, shape, surface to volume ratio, coloniality). Moreover, the water chemistry, as the N, P and Si ratio should be measured. The experiments will end when the nutrient is not supplied anymore. The data collected will be analysed with the WitOMI analysis to measure the species subniche dynamism and the corresponding biotic constraint, which in this case could only be competition. In addition with the measured traits, their variation in value could help us understand their performances (as growth rate, nutrient uptake rate) which would also be measured, with greater accuracy, could be used to create models. The monoculture will help us understand the implication of the abundance and traits value variations in structuring the community via competition. Furthermore the performances measured in the monoculture would be used to understand how the community is performing as a unit, and what are the contributions of each species. The experiment might provide answers on the community structure with the study of the r-K strategy dichotomy [Kilham, 1980; MacArthur, 1967; Sommer, 1981] and the trade-off between competitive abilities for different resources [Leibold, 1997; Passarge et al., 2006; Tilman, 1982]. An essential biotic interaction also greatly influences phytoplankton community structure and composition as to be investigated, grazing.

Grazing rate

In chapter 4, we have seen that if the environmental conditions favored the dominance of a few productive species, the consumers may be the reason for decreasing evenness and increasing species richness within the community. The *in situ* measurement of the consumers grazing rate on the phytoplankton community is possible via a simple experiment with the natural community. Landry and Hassett [1982] developed the dilution experiment to measure the herbivory of microzooplankton in natural marine communities. The dilution of the natural community decreases the possible encounters between the primary producers and the consumers. The idea consists of diluting the natural community, at different proportions, with filtered seawater. The dilution series is then used to estimate the grazing rate as the phytoplankton growth rate increase by increasing the dilution. The apparent growth rate is extrapolated with the highly diluted natural community, which is assumed to grow grazers. Grazing rate is estimated as the slope of a regression of apparent phytoplankton growth in the dilutions series against the dilution factor. The dilution experiment depend upon a few assumptions:

1. Phytoplankton growth rate is not limited by nutrients nor by density dependence
2. Phytoplankton growth rate is exponential
3. The consumers' grazing rate is linear to the phytoplankton concentration.

The dilution experiment requires little manipulation. In depleted nutrient conditions, nutrient levels could be increased to meet the expectation of assumption 1. The dilution experiment, which has become standard protocol for the grazing rate estimation [Landry, 1993], could be done routinely when the samples are collected for phytoplankton monitoring. A time on the community grazing rate would be extremely valuable. In association, the temporal changes in consumers biomass, abundance and taxa population, the data collected would be used to estimate the trophic efficiency between phytoplankton and grazers, which would influence the microzooplankton consumption by higher trophic levels [Dolan et al., 2000]. The trophic efficiency between phytoplankton and grazers can also be affected by the phytoplankton response to consumers.

Induced defense

Not all phytoplankton are defenseless primary producers when confronted to consumers. Numerous taxa have evolved constitutive or inducible defense against grazing. Phytoplankton species trait flexibility, or phenotypic plasticity, impacts on their edibility. The plasticity includes variation in morphology, performances and biochemical composition. Some of these traits been reported as a defense mechanism against grazers. Oppositely to constitutive which is fixed, the induced defenses provide a ductile protection against the several species, allowing a species to phenotypically adjust to different consumers [Tollrian and Harvell, 1999]. The (induced) defense can be regulated towards the most threatening consumers, in the present or near future. The ability to adapt its defensive response to different degrees of predation risk is particularly useful when in presence of more than one consumer. The algal response (*e.g.* single celled or large colonies) will depend on which consumer poses the biggest threat according to the grazers' algae size preference [Long et al., 2007]. Consumers feeding success mostly depend on phytoplankton's size, shape, cell wall structure and of its ability to produce toxins [Van Donk et al., 2011]. The defenses would come at a cost for the species. The costs can be of a physiological performance nature, as for the trade-off between maximum growth rate and competitive ability, the r-K strategy dichotomy [Kilham, 1980; MacArthur, 1967; Sommer, 1981]. The costs can also be of ecological nature. For instance, colony formation would enhance the colony's sinking rate down to the euphotic zone [Lürling and Van Donk, 2000; Verschoor et al., 2009], having a negative impact on the species competitive ability. The defensive capability of a phytoplankton species against consumers will therefore impact its performance, its competitive ability and consequently affect the food web [Agrawal, 1998; Van Der Stap et al., 2007, van der Stap et al. [2008], van der Stap et al. [2009]; Van Donk, 2007]. In the case study, the diatoms are known to form colonies and have been reported to survive the gut passage of copepods [Nejstgaard et al., 2007; Kruse et al., 2009] by increasing silification of their cell wall by chemical cue response to copepod [Pondaven et al., 2007]. They are also known to produce chemicals affecting the reproductive success of copepods [Leflaive and Ten-Hage, 2009; Ianora and Miralto, 2010], which can be possibly induced by consumers when damaged [Pohnert, 2000]. *Phaeocystis* spp. polymorphic life cycle including stages of solitary cells and gelatinous colonies [Rousseau et al., 1994, 2007]. *Phaeocystis* spp. capacity to form colony is highly plastic, and capable of changing the colony size in response of the different chemical cues from different consumer species [Wang et al., 2015]. Size-mismatch is *Phaeocystis* spp. main strategy to avoid grazers [Hamm et al., 1999; Nejstgaard et al., 2007], significantly reducing its mortality by morphological plastic responses [Long et al., 2007; Jakobsen and Tang, 2002]. Colony formation and enlargement seemed to be responsible for the species success in marine systems [Nejstgaard et al., 2007; Tang, 2003]. Furthermore, when confronted to grazing by copepods, *Phaeocystis* spp. decreases its colony numbers by a significant 60–90%. Therefore, it suggests the prior acquisition of knowledge on the natural consumer's diversity and the types of chemical induction cues. Van Donk et al. [2011] has distinguished three main types of induction cues:

1. Chemical cues released from a lysed cells of the same species that have not been in contact with herbivore's digestive system, known as mechanical damage cue.
2. Chemical cues released by consumers in absence of a particular prey species (i.e. when feeding on a different species), also known as herbivory-released cues.
3. Chemical cues that are released when species cells and/or their contents come into contact with the feeding apparatus and digestive system of the grazer, also known as feeding-related chemical cues.

The type of chemical cue which induces the phytoplankton defense mechanism can easily be tested in an experimental setup as proposed by Van Donk et al. [2011]. Different medium conditioned by each type of chemical cues can be added to a monoculture, revealing how the species defense is induced.

The hypothesis that the biotic interaction plays a significant role in phytoplankton response to global change goes in lines with the idea that biodiversity as a role in trophic interactions in association with ecosystem processes [Reich et al., 2001; Tilman et al., 2006]. The studies results implies in association with competition, grazing is involved in the process of phytoplankton response to global change. The trade-off between competitive abilities and grazer resistance [Grover, 1995; Leibold, 1989, 1996] could also be tested in the "Biotic interaction experiment". The study could help understand the impact of high abundance of *Phaeocystis* spp. on the rest of the food web. Along with competition, the presence of grazers and /or chemical cues produced by grazing has the potential to increase the *Phaeocystis* spp. colony size. The data collected during the experiment would be analysed with the WitOMI analysis, to reveal community subniche dynamism, along with species functional trait, with and without grazers. The biotic constraint variation would be quantified and describe with greater precision as the biotic interactions are controlled. The data can be summarized after by the conceptual framework of Figure .

Chapter 7

General Conclusion

The aim of the thesis was to describe and to measure the temporal responses and causalities of the phytoplankton community structure, under global changes, with the occurrence of a harmful algae. The investigation was carried out by dividing it into three questions:

1. Can a niche concept and a statistical method be developed to allow the observation and quantification of the species' niche response to global changes? Can the biotic interaction affecting the species' niche be observed and quantified?

Hutchinson [1961] niche concept was adapted by decomposing Jackson and Overpeck [2000] theoretical concept in association with the Dolédec et al. [2000] Outlying Mean Index (OMI). The statistical method was done by including Calenge et al. [2005] K-select decomposition prior the ordination of the OMI analysis. It has led to the Within Outlying Mean Indexes (WitOMI) which calculated, within the same ordination, the species subniche position and breadth to the overall habitat condition (WitOMIG), and from a subset of habitat conditions. The decomposed realized niche, $\mathbf{N}_{\boldsymbol{R}}$, and environmental space $\mathbf{E}$, allowed the quantification and observation of the realised subniche, $\mathbf{S}_{\boldsymbol{R}}$, dynamism under subset of environmental conditions, $\mathbf{K}$. The decomposition permit the observation and quantification of the impact of biological interaction on a species subniche, under subset of environmental conditions.

2. What is the response of the phytoplankton community structure under HAB or no HAB conditions? What environmental conditions explain the occurrence of a harmful algae?

Lower temperature, light availability, higher salinity, with lower winter nutrient stock increased diatom richness and *Phaeocystis* spp abundance. All hypotheses, which are supposed to predict the occurrence of *Phaeocystis* spp. (i.e. the "silicate-*Phaeocystis* hypothesis", "eutrophication hypothesis") appears to be true but incomplete. The different hypothesis either predict the bloom timing and/or the magnitude. Under condition of low *Phaeocystis* abundance, the species was subjected to high biological constraint. It is suspected to come from some diatom species which compete for resources. The nutrients being of higher concentration, the diatoms were not nutrient-limited for growth. The environmental conditions favored the dominance of a few species, such as *Skeletonema* spp., *Thalassionema nitzschioides* and *Thalassiosira gravida*. The "diatom-competition" hypothesis should have a greater consideration in future research.

3. How global change and the invasive species affect the diversity-productivity relationship in a short-term and long-term scales?

The investigation of the diversity-productivity relationship revealed that the seasonal relationship can explain the success of the invasive species, under long-term global change. In the seasonal-term, temperature co-varying with light and nutrients, had the greatest influence on the diversity-productivity relationship. In the long-term, the diversity-productivity relationship was more influenced by turbidity and salinity. Successive cold years with high resource imbalance favored the invasive species occurrence as only a few dominant productive native species compete with it for resources. In the long term, the invasive species reduced the phytoplankton biomass as it increases the number of small size taxa. Additionally, the result suggested a role played by grazers as the species evenness increases as more resources are available. A competition-defense trade-off probably occured.

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Appendix

Appendix 1: WitOMI results and species' code

Table S1: Hydraulic requirement parameters of the 57 invertebrate taxa sampled in spring and autumn. Inertia = total variability; OMI = outlying mean index. P number of random permutations (out of 1000) that yielded a higher value than the observed marginality (OMI, WitOMIG or WitOMIG_K) (the value in **bold** characters are significant, $P < 0.05$). Tol = tolerance, Rtol = residual tolerance. I. = inertia; G (G_k) are the subset marginality WitOMIG (WitOMIG_K) ; $-$ = NA. The WitOMI cannot be calculated when the OMI is not significant (See Discussion for further details). The species is the one use as example for Figure 2.4D, 2.4E, and 2.4F (Species code in Appendix S1; Table S3).

Season	All					Spring					Autumn					Spring					Autumn				
Code	I.	OMI	Tol	Rtol	P	I.	G	Tol	Rtol	P	I.	G	Tol	Rtol	P	I.	G_K	Tol	Rtol	P	I.	G_K	Tol	Rtol	P
AFLU	5.54	1.63	1.16	2.75	**0.05**	5.59	2.46	0.54	2.59	0.00	5.05	4.99	0.04	0.02	0.00	5.89	2.76	0.70	2.43	0.00	5.05	4.99	0.04	0.02	0.00
ANTO	6.26	2.86	0.48	2.92	**0.01**	6.26	2.86	0.48	2.92	0.00	-	-	-	-	-	7.08	3.68	0.41	3.00	0.00	-	-	-	-	-
ATSP	5.26	0.77	1.94	2.54	0.10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BASP	4.95	0.15	0.92	3.88	**0.00**	5.22	0.37	1.28	3.57	0.01	4.02	0.95	0.86	2.21	0.00	4.89	0.04	2.11	2.74	0.01	4.02	0.95	0.86	2.21	0.00
BIMI	6.44	2.67	1.22	2.56	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
BFAS	5.52	1.63	0.83	3.06	**0.00**	5.52	1.63	0.83	3.06	0.00	-	-	-	-	-	4.86	0.97	1.62	2.27	0.00	-	-	-	-	-
CASP	4.75	2.09	0.70	1.96	**0.00**	3.82	2.28	0.45	1.09	0.00	5.17	2.46	0.75	1.96	0.00	3.98	2.44	0.46	1.08	0.00	5.17	2.46	0.75	1.96	0.00
CESP	5.99	1.36	1.74	2.89	0.14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CERA	5.24	0.44	1.56	3.24	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CLEP	5.03	0.44	1.38	3.21	**0.00**	5.04	0.48	0.96	3.60	0.01	4.99	1.70	1.40	1.89	0.00	4.68	0.12	2.26	2.30	0.00	4.99	1.70	1.40	1.89	0.00
CMAR	5.30	2.09	1.10	2.10	**0.00**	5.36	2.17	0.96	2.24	0.00	4.97	3.47	0.60	0.90	0.00	4.80	1.60	1.55	1.65	0.00	4.97	3.47	0.60	0.90	0.00
CHIR	4.44	0.49	1.52	2.42	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
CPIC	5.51	2.83	0.52	2.16	**0.00**	5.51	2.83	0.52	2.16	0.00	-	-	-	-	-	5.72	3.04	0.56	2.12	0.00	-	-	-	-	-
DRSP	4.50	1.07	1.90	1.52	**0.04**	8.57	3.37	2.26	2.94	0.00	3.75	2.11	0.71	0.93	0.00	7.42	2.22	2.13	3.08	0.00	3.75	2.11	0.71	0.93	0.00
DUSP	5.33	0.14	1.74	3.45	**0.05**	5.85	0.59	1.64	3.61	0.00	4.78	1.01	1.72	2.05	0.00	5.38	0.12	3.08	2.18	0.00	4.78	1.01	1.72	2.05	0.00
ECSP	5.35	0.33	1.47	3.55	**0.00**	5.33	0.53	1.48	3.32	0.01	5.49	0.57	1.22	3.70	0.00	4.86	0.06	2.57	2.24	0.01	5.49	0.57	1.22	3.70	0.00
ECTE	5.46	3.09	0.12	2.25	0.12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ELMA	3.18	0.79	0.04	2.35	0.86	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EPEO	5.68	1.27	0.75	3.66	0.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
EVIR	5.30	0.34	1.28	3.68	**0.04**	5.30	0.34	1.28	3.68	0.01	-	-	-	-	-	5.20	0.24	2.07	2.89	0.00	-	-	-	-	-
EPAR	269	3.93	0.14	0.80	3.00	0.26	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	- -
EPYG	4.77	0.14	1.02	3.61	**0.02**	4.77	0.32	0.50	3.95	0.01	4.77	0.47	0.54	3.75	0.00	4.54	0.09	1.10	3.36	0.00	4.77	0.47	0.54	3.75	0.00
ESSP	4.86	0.14	0.86	3.86	**0.00**	5.04	0.65	1.45	2.94	0.00	4.74	0.49	0.47	3.78	0.00	5.00	0.61	1.58	2.81	0.00	4.74	0.49	0.47	3.78	0.00
EGEN	5.05	1.91	0.86	2.28	**0.00**	5.05	1.91	0.86	2.28	0.00	-	-	-	-	-	5.01	1.87	0.91	2.23	0.00	-	-	-	-	-
GASP	5.69	0.36	1.17	4.16	**0.05**	5.87	0.43	1.09	4.35	0.01	2.58	0.62	0.35	1.62	0.00	5.51	0.07	2.19	3.25	0.01	2.58	0.62	0.35	1.62	0.00
HEXO	5.22	0.38	1.25	3.60	**0.00**	5.30	0.44	1.05	3.81	0.01	4.64	2.02	0.82	1.80	0.00	4.92	0.07	2.49	2.37	0.01	4.64	2.02	0.82	1.80	0.00
HPEL	5.24	0.36	1.20	3.69	0.00	5.32	0.45	0.99	3.89	0.01	4.46	2.37	0.30	1.78	0.00	4.93	0.06	2.58	2.30	0.01	4.46	2.37	0.30	1.78	0.00
HYDR	3.57	1.48	0.42	1.67	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
HYSP	5.42	0.34	1.01	4.07	**0.00**	5.44	0.42	0.98	4.05	0.01	5.12	0.76	1.38	2.98	0.00	5.03	0.01	1.85	3.18	0.01	5.12	0.76	1.38	2.98	0.00
HYDS	6.18	2.75	0.83	2.59	**0.03**	6.18	2.75	0.83	2.59	0.00	-	-	-	-	-	7.16	3.73	0.75	2.67	0.00	-	-	-	-	-
LEPT	5.34	2.74	0.47	2.13	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
LESP	4.42	0.31	0.90	3.21	**0.04**	4.61	0.45	1.09	3.07	0.01	2.63	1.24	0.26	1.13	0.00	4.40	0.24	1.31	2.85	0.00	2.63	1.24	0.26	1.13	0.00
LOPAad	4.97	1.20	1.97	1.79	**0.01**	4.97	1.20	1.97	1.79	0.00	-	-	-	-	-	4.87	1.10	2.04	1.73	0.00	-	-	-	-	-
LOPAla	4.57	0.48	1.25	2.85	**0.00**	5.11	0.37	0.47	4.27	0.01	3.72	1.91	0.31	1.50	0.00	4.88	0.14	1.21	3.53	0.01	3.72	1.91	0.31	1.50	0.00
MPOW	5.77	1.21	2.07	2.49	0.27	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
MYSA	4.20	3.34	0.28	0.58	0.24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORHE	5.58	1.77	0.89	2.92	**0.00**	5.58	1.77	0.89	2.92	0.00	-	-	-	-	-	4.93	1.12	1.73	2.08	0.00	-	-	-	-	-
ONSP	5.18	1.10	1.74	2.34	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
ORTH	5.12	0.23	1.26	3.63	**0.00**	5.39	0.39	0.91	4.09	0.01	4.35	0.90	1.57	1.88	0.00	5.01	0.01	2.50	2.50	0.01	4.35	0.90	1.57	1.88	0.00
ORSP	6.83	1.32	2.33	3.18	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OTROad	5.32	0.32	0.79	4.21	**0.02**	5.25	0.41	0.98	3.87	0.01	6.23	2.59	1.00	2.64	0.00	5.01	0.16	1.60	3.25	0.01	6.23	2.59	1.00	2.64	0.00
OTROla	5.52	0.23	1.21	4.08	0.06	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PISI	4.43	0.37	1.12	2.94	0.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
POLY	6.09	1.16	2.02	2.91	0.07	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
PBIF	6.95	3.46	0.59	2.90	**0.01**	8.24	7.16	0.33	0.76	0.00	5.87	3.73	0.79	1.36	0.00	9.48	8.39	0.35	0.74	0.00	5.87	3.73	0.79	1.36	0.00
PPUS	5.23	0.14	0.91	4.18	0.15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RASP	4.76	0.13	0.81	3.82	0.97	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
RHIP	6.91	6.12	0.52	0.27	**0.00**	6.91	6.12	0.52	0.27	0.00	-	-	-	-	-	6.36	5.57	0.54	0.25	0.00	-	-	-	-	-
RHYP	5.93	1.93	1.14	2.86	**0.00**	5.93	1.93	1.14	2.86	0.00	-	-	-	-	-	5.28	1.28	1.61	2.39	0.00	-	-	-	-	-
SIGN	5.51	0.53	1.71	3.26	**0.00**	5.51	0.53	1.71	3.26	0.01	-	-	-	-	-	5.30	0.32	2.08	2.90	0.00	-	-	-	-	-
SARG	5.69	0.24	1.27	4.19	**0.02**	6.12	2.03	1.66	2.42	0.00	5.24	0.83	2.00	2.41	0.00	5.44	1.36	1.34	2.74	0.00	5.24	0.83	2.00	2.41	0.00
SIMU	5.34	0.51	1.24	3.59	**0.00**	5.63	0.58	0.94	4.12	0.00	4.38	2.45	0.87	1.06	0.00	5.11	0.06	1.82	3.24	0.01	4.38	2.45	0.87	1.06	0.00
STEN	6.27	0.57	1.59	4.11	0.38	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SCAN	6.36	1.40	1.40	3.56	**0.02**	6.30	3.00	0.45	2.84	0.00	6.47	0.98	0.62	4.87	0.00	6.54	3.25	0.56	2.74	0.00	6.47	0.98	0.62	4.87	0.00
TANYP	4.88	0.73	1.69	2.46	**0.02**	4.88	0.73	1.69	2.46	0.01	-	-	-	-	-	4.95	0.80	1.92	2.23	0.00	-	-	-	-	-
TANYT	5.34	0.17	1.32	3.85	**0.03**	5.48	0.32	0.91	4.25	0.01	4.46	1.41	0.79	2.26	0.00	5.22	0.06	1.52	3.64	0.01	4.46	1.41	0.79	2.26	0.00
TFLU	6.94	2.03	1.56	3.36	0.11	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Table S2: Physical habitat preference parameters of the 12 fish taxa sampled in ten Mediterranean tributaries of the Rhône River. Inertia = total variability; OMI = outlying mean index. P number of random permutations (out of 1000) that yielded a higher value than the observed marginality (OMI, WitOMIG or WitOMIG_K) (the value in **bold** characters are significant, P <0.05). Tol = tolerance, Rtol = residual tolerance. I. = inertia; G (G_k) are the subset marginality WitOMIG (WitOMIG_K). $-$ = NA. The WitOMI cannot be calculated when the OMI is not significant(See Discussion for further details). The species is the one use as example for Figure 2.5D, 2.5E, and 2.5F (Species code in Table S4 in appendix S1).

Altitude	All					Upstream					Downstream					Upstream					Downstream				
Code	I.	OMI	Tol	Rtol	P	I.	G	Tol	Rtol	P	I.	G	Tol	Rtol	P	I.	G_K	Tol	Rtol	P	S.I.	G_K	Tol	Rtol	P
SCU	5.50	2.15	1.50	1.85	0.08	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
OTR	5.71	0.08	2.43	3.21	**0.00**	4.74	1.12	1.62	2.01	**0.00**	8.44	4.14	1.09	3.21	**0.00**	3.62	0.00	0.96	2.66	**0.00**	4.47	0.18	1.69	2.60	**0.00**
YTR	5.77	0.26	1.69	3.81	**0.00**	4.92	1.15	1.67	2.10	**0.00**	9.17	5.58	1.59	1.99	**0.00**	3.77	0.00	0.75	3.02	**0.00**	4.98	1.40	1.22	2.37	**0.00**
MIN	5.32	0.45	2.52	2.35	**0.00**	2.82	0.33	0.96	1.54	**0.00**	8.51	4.61	0.81	3.08	**0.00**	2.79	0.30	1.01	1.48	**0.00**	3.93	0.04	0.88	3.01	**0.00**
STO	5.91	0.77	2.41	2.73	**0.00**	2.86	0.20	0.67	1.98	**0.00**	9.28	4.93	0.88	3.48	**0.00**	3.17	0.51	0.78	1.87	**0.00**	4.38	0.03	1.24	3.11	**0.00**
BLA	4.99	0.46	2.27	2.26	**0.00**	2.31	0.20	0.71	1.40	**0.00**	8.61	4.53	0.88	3.19	**0.00**	2.51	0.40	0.73	1.38	**0.00**	4.09	0.02	0.68	3.40	**0.00**
SBA	3.71	0.07	0.51	3.13	0.77	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
SON	6.38	4.89	0.75	0.75	**0.03**	-	-	-	-	-	6.38	4.89	0.75	0.75	**0.00**	-	-	-	-	-	2.80	1.31	0.13	1.37	**0.00**
NAS	12.60	10.20	1.62	0.78	**0.00**	-	-	-	-	-	12.60	10.20	1.62	0.78	**0.00**	-	-	-	-	-	4.40	2.00	1.33	1.07	**0.00**
GUD	8.43	4.31	0.95	3.17	**0.00**	1.16	0.25	0.47	0.44	**0.00**	9.47	5.52	0.51	3.44	**0.00**	2.53	1.62	0.02	0.89	**0.00**	4.04	0.09	0.98	2.97	**0.00**
CHU	5.58	1.58	1.69	2.31	**0.00**	1.27	0.03	0.13	1.11	**0.00**	8.61	4.53	0.88	3.19	**0.00**	2.34	1.10	0.28	0.96	**0.00**	4.09	0.02	0.68	3.40	**0.00**
STR	9.92	5.28	1.19	3.46	**0.00**	-	-	-	-	-	11.07	6.86	0.58	3.62	**0.00**	-	-	-	-	-	4.63	0.43	0.84	3.37	**0.00**
BAR	8.34	3.83	1.30	3.21	**0.00**	1.66	0.52	0.07	1.07	**0.00**	9.46	5.26	0.58	3.62	**0.00**	2.60	1.45	0.88	0.27	**0.00**	4.28	0.07	0.60	3.60	**0.00**

Table S3: Invertebrate code from Mérigoux and Dolédec [2004].

Species	Code
Ancylus fluviatilis Müller	AFLU
Antocha sp.	ANTO
Athripsodes sp.	ATSP
Baetis sp.	BASP
Bidessus minutissimus	BIMI
Blephariceraa fasciata (Westwood)	BFAS
Caenis sp.	CASP
Ceraclea sp.	CESP
Ceratopogoninae	CERA
Cheumatopsyche lepida (Pictet)	CLEP
Chimarra marginata (Linnaeus)	CMAR
Chironomini	CHIR
Choroterpes picteti Eaton	CPIC
Dryops sp.	DRSP
Dugesia sp.	DUSP
Ecdyonurus sp.	ECSP
Ecnomus tenellus	ECTE
Elmis maugetii (l)	ELMA
Epeorus sp.	EPEO
Ephoron virgo (Olivier)	EVIR
E. parallelepipedus (a)	EPAR
Esolus spp. (l)	ESSP
E. pygmaeus (a) (Ph. Müller)	EPYG
Euleuctra geniculata Stephens	EGEN
Gammarus spp.	GASP
Hydropsyche spp.	HYSP
H. exocellata Dufour	HEXO
H. pellucidula (Curtis)	HPEL
Hydra sp.	HYDR
Hydroptila sp.	HYDS
Leptocerus tineiformis	LEPT
Leuctra sp.	LESP
Limnius opacus (a) Ph. Müller	LOPAad
L. opacus (l) Ph. Müller	LOPAla
Micronecta poweri	MPOW
Mystacides azurea	MYSA
Oligoneuriella rhenana (Imhoff)	ORHE
Onychogomphus sp.	ONSP
Orthocladiinae	ORTH
Orthotrichia sp.	ORSP
Oulimnius troglodytes (a) (Gyllenhal)	OTROad
O. troglotydes (l)	OTROla
Pisidium sp.	PISI
Polycentrus flavomaculatus	POLY
Procloeon bifidum (Bengtsson)	PBIF
Psychomyiia pusilla	PPUS
Radix sp.	RASP
Rhyacophila sp.	RHYP
Rhithrogena sp.	RHIP
Serratella ignita (Poda)	SIGN
Setodes argentipunctellus McLachlan	SARG
Simuliidae	SIMU
Stenelmis canaliculata (a)	STEN
S. canaliculata (l)	SCAN
Tanypodinae	TANYP
Tanytarsini	TANYT
Theodoxus fluviatilis	TFLU

Table S4: Fish code from Dolédec et al. [2000];† Young of the year.

Species	Code
Sculpin (*Cottus gobio*)	SCU
Older trout (*Salmo trutta*)	OTR
Y-O-Y† trout (*Salmo trutta*)	YTR
Minnow (*Phoxinus phoxinus*)	MIN
Stone loach (*Nemacheilus barbatulus*)	STO
Blageon (*Telestes soufia*)	BLA
Southwestern barbel (*Barbus meridionalis*	SBA
Southwestern nase (*Chondrostoma toxostoma*)	SON
Nase (*Chondrostoma nasus*)	NAS
Gudgjeon (*Gobio gobio*)	GUD
Chub (*Leuciscus cephalus*)	CHU
Streambleak (*Alburnoides bipunctatus*)	STR
Barbel (*Barbus barbus*)	BAR

Appendix 2: Model validity assesement

Table S1: Outer loadings of all measurement models. Outer loadings only exist for relationships between latent variables (columns) and their respective manifest variables (rows). All remaining cells are left blank.Biom: Biomass; Biov: Biovolume; Inv.spp: Invasive species; Turb: Turbidity; Res.ava: Resource availability; Res.imb: Resource imbalance; Rich: Richness; Eve: Evenness; Sali: Salinity; Temp: Temperature; Chloro: Chlorophyll a; gen: genus; sp: species; H: Shannon index of diveristy; J: Pielou's evenness; S: number of species; Pheo: pheopigments; *Phae*: *Phaeocystis* spp. abundance; a: measure of resource availability; θ: degree of resource imbalance.

	Inv.spp	Res.ava	Biom	Eve	Turb	Biov	Res.imb	Rich	Sali	Temp
Chloro			0.831							
Hgen				0.969						
Hsp				0.964						
Jgen				0.857						
Jsp				0.817						
Pheo			0.911							
Phaeo	1									
Sali									1	
Sgen								0.999		
Ssp								0.999		
Temp										1
Turb					1					
a		1								
θ							1			
totbiov						1				

Table S2: The long-term model evaluation criteria for the validity assessment of the measurement part of the model. RUE: resource use efficien cy; AVE: average variance extracted.

	Cronback's Alpha	Composite Reliability	AVE
Invasive spp,	1.00	1.00	1.00
Resource availability	1.00	1.00	1.00
Biomass	0.69	0.86	0.76
Evenness	0.93	0.95	0.82
Turbidity	1.00	1.00	1.00
Biovolume	1.00	1.00	1.00
Resource imbalance	1.00	1.00	1.00
Richness	1.00	1.00	1.00
Salinity	1.00	1.00	1.00
Temperature	1.00	1.00	1.00

Table S3: The long-term model Heterotrait-Monotrait Ratio (HTMT) criterion. Biom: Biomass; Biov: Biovolume; Inv.spp: Invasive species; Turb: Turbidity; Res.ava: Resource availability; Res.imb: Resource imbalance; Rich: Richness; Eve: Evenness; Sali: Salinity; Temp: Temperature.

	Inv.spp.	Res.ava	Biom	Eve	Turb	Biov	Res.imb	Rich
Res ava	0.15							
Biom	0.24	0.28						
Even	0.29	0.07	0.44					
Turb	0.72	0.25	0.41	0.33				
Biov	0.29	0.09	0.25	0.06	0.31			
Res imb	0.07	0.95	0.36	0.06	0.21	0.16		
Rich	0.45	0.12	0.48	0.46	0.64	0.1	0.13	
Sali	0.05	0.29	0.9	0.35	0.38	0.26	0.39	0.64
Temp	0.22	0.08	0.51	0.25	0.15	0.25	0.15	0.07

Table S4: Effect sizes (f^2) of all exogenous variables on the corresponding endogenous constructs in the long-term model.

Endogenous	Exogenous	f^2
Invasive spp.	Biomass	0.045
Resource availability	Invasive spp.	0.043
	Evenness	0.021
Evenness	Biomass	0.155
	Invasive spp.	0.201
Turbidity	Invasive spp.	0.411
	Resource availability	0.025
	Biomass	0.068
	Resource imbalance	0.008
	Biovolume	0.123
	Richness	0.400
Resource imbalance	Invasive spp.	0.032
	Richness	0.028
	Evenness	0.030
Richness	Biomass	0.208
Salinity	Invasive spp.	0.122
	Resource availability	0.037
	Biomass	0.824
	Evenness	0.162
	Biovolume	0.131
	Resource imbalance	0.098
	Richness	0.467
Temperature	Biomass	0.108

Table S5: Outer loadings of all measurement models. Outer loadings only exist for relationships between latent variables (columns) and their respective manifest variables (rows). All remaining cells are left blank.Biom: Biomass; Biov: Biovolume; Inv.spp: Invasive species; Turb: Turbidity; Res.ava: Resource availability; Res.imb: Resource imbalance; Rich: Richness; Eve: Evenness; Sali: Salinity; Temp: Temperature; Chloro: Chlorophyll a; gen: genus; sp: species; H: Shannon index of diveristy; J: Pielou's evenness; S: number of species; Pheo: pheopigments; *Phae*: *Phaeocystis* spp. abundance; a: measure of resource availability; θ: degree of resource imbalance.

	Biom	Biov	Eve	Inv.spp	Turb	Res.ava	Res.imb	Rich	Sali	Temp
Chloro	0.96									
Hgen			0.99							
Hsp			0.99							
Jgen			0.98							
Jsp			0.98							
Pheo	0.96									
Phae				1						
Sali									1	
Sgen								0.99		
Ssp								0.99		
Temp										1
Turb					1					
a						1				
θ							1			
totbiov		1								

Table S6: The seasonal model evaluation criteria for the validity assessment of the measurement part of the model. RUE: resource use efficien cy; AVE: average variance extracted.

	Cronback's Alpha	Composite Reliability	AVE
Biomass	0.92	0.96	0.92
Biovolume	1.00	1.00	1.00
Eveness	0.99	0.99	0.97
Invasive spp	1.00	1.00	1.00
Turbidity	1.00	1.00	1.00
Resource availability	1.00	1.00	1.00
Resource imbalance	1.00	1.00	1.00
Richness	0.98	0.99	0.98
Salinity	1.00	1.00	1.00
Temperature	1.00	1.00	1.00

Table S7: The seasonal model Heterotrait-Monotrait Ratio (HTMT) criterion. Biom: Biomass; Biov: Biovolume; Inv.spp: Invasive species; Turb: Turbidity; Res.ava: Resource availability; Res.imb: Resource imbalance; Rich: Richness; Eve: Evenness; Sali: Salinity; Temp: Temperature.

	Biom	Biov	Eveness	Inv.spp	Turb	Res.ava	Res.imb	Rich
Biov	0.68							
Eve	0.91	0.39						
Inv spp	0.90	0.36	0.9					
Turb	0.44	0.66	0.47	0.26				
Res ava	0.29	0.42	0.13	0.03	0.28			
Res imb	0.53	0.42	0.73	0.61	0.7	0.16		
Rich	0.18	0.48	0.44	0.29	0.1	0.23	0.08	
Sali	0.02	0.48	0.09	0.12	0.81	0.26	0.59	0.22
Temp	0.19	0.42	0.16	0.42	0.68	0.38	0.35	0.37

Table S8: Effect sizes (f^2) of all exogenous variables on the corresponding endogenous constructs in the seasonal model.

Endogenous	Exogenous	f^2
Invasive spp.	Biomass	0.54
Biovolume	Invasive spp.	4.76
Resource availability	Invasive spp.	1.13
	Evenness	0.13
Evenness	Biomass	0.99
	Biovolume	2.64
	Invasive spp.	0.37
Turbidity	Invasive spp.	0.32
	Resource availability	0.03
	Biomass	0.02
	Resource imbalance	0.27
	Evenness	0.77
	Biovolume	0.07
Resource imbalance	Invasive spp.	5.52
	Evenness	1.31
	Biovolume	2.17
	Biomass	1.74
Richness	Biomass	0.62
	Biovolume	5.87
	Invasive spp.	1.62
Salinity	Invasive spp.	0.20
	Resource availability	0.07
	Biomass	0.05
	Evenness	0.11
	Biovolume	0.46
	Resource imbalance	0.21
Temperature	Biomass	0.23
	Evenness	0.28
	Invasive spp.	15.69
	Resource availability	0.15
	Resource imbalance	0.29
	Richness	0.08

Publications

Within outlying mean indexes: refining the OMI analysis for the realized niche decomposition

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ABSTRACT

The ecological niche concept has regained interest under environmental change (e.g., climate change, eutrophication, and habitat destruction), especially to study the impacts on niche shift and conservatism. Here, we propose the within outlying mean indexes (WitOMI), which refine the outlying mean index (OMI) analysis by using its properties in combination with the *K*-select analysis species marginality decomposition. The purpose is to decompose the ecological niche into subniches associated with the experimental design, i.e., taking into account temporal and/or spatial subsets. WitOMI emphasize the habitat conditions that contribute (1) to the definition of species' niches using all available conditions and, at the same time, (2) to the delineation of species' subniches according to given subsets of dates or sites. The latter aspect allows addressing niche dynamics by highlighting the influence of atypical habitat conditions on species at a given time and/or space. Then, (3) the biological constraint exerted on the species subniche becomes observable within Euclidean space as the difference between the existing fundamental subniche and the realized subniche. We illustrate the decomposition of published OMI analyses, using spatial and temporal examples. The species assemblage's subniches are comparable to the same environmental gradient, producing a more accurate and precise description of the assemblage niche distribution under environmental change. The WitOMI calculations are available in the open-access R package "subniche."

Subjects Biogeography, Ecology, Statistics
Keywords Biological constraint, Niche dynamic, Marginality, Community, Spatio-temporal, Subniche, Habitat

INTRODUCTION

The ecological niche concept has been reactivated due to increasing concern over global environmental change, making the niche shift and the conservatism between different areas and time periods important fields of study (*Peterson, 2011*). The ecological niche of a species can be decomposed into two related components (*Hutchinson, 1957*). First, the fundamental niche is the n-dimensional hypervolume within which the population

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of a species can persist, survive, and reproduce indefinitely, and it is not constrained by any biological interactions. Second, the realized niche is the proportion of the fundamental niche within which the species actually persist, i.e., taking into account the effect of abiotic and biological interactions. The fundamental niche cannot be measured by observation, but rather by broad examination of species' physiological requirements using mechanistic approaches (*Peterson et al., 2011*). On the contrary, the realized niche, in a community context, is the "differential habitat preferences of species" (*Ter Braak & Verdonschot, 1995*) and can be estimated by correlative approaches (*Peterson et al., 2011*).

However, the lack of study on the role of biotic interactions (e.g., competition, predation, mutualism, dispersal, and colonization) is a major limitation for defining species' niches appropriately (*Davis et al., 1998*; *Soberón & Nakamura, 2009*). Studies have shown that incorporating biotic factors can lead to better predictions of species' distributions (*Heikkinen et al., 2007*), yet, despite this evidence, biotic factors are still underused and greater assessment is required to fully understand species' niche dynamics (*Soberón & Nakamura, 2009*). According to *Jackson & Overpeck (2000)*, the constraints exerted on the realized niche by biotic process are the differences between the potential niche (i.e., the intersection between the fundamental niche and the realized environmental space (*Soberón & Nakamura, 2009*)) and the realized niche; the realized environmental space being "the portion of the total n-dimensional environmental space that is actually represented [...] within a specified region at a given time" (*Jackson & Overpeck, 2000*). Later on, the potential niche was renamed "the existing fundamental niche" by *Peterson et al. (2011)*. Therefore, the biotic interactions are the differences between the existing fundamental niche and the realized niche. The role of biotic interactions is not directly measurable by observation, as it requires an estimation of the fundamental niche. However, in order to estimate biological interactions, adaptation of the concept of the existing fundamental niche concept can be applied to the decomposed realized niche, which can be measured by observation. This concept requires the decomposition of the realized environmental space, **E**, into subsets of the realized environmental space, **K**, so that **K** is a subset of **E** (Fig. 1). **K** represents the available conditions found within **E**, at a smaller time and/or spatial scale than in **E**. Now considering $\mathbf{N}_R$, the realized niche, found within **E**, as the best estimation of the "fundamental niche" of the species under **K**, the intersection between **K** and $\mathbf{N}_R$ represents the existing fundamental subniche, $\mathbf{S}_P$ (Fig. 1). The existing fundamental subniche corresponds to the abiotically reduced part of $\mathbf{N}_R$ by **K**. Therefore, $\mathbf{S}_P$ includes the subset biotic factor, $\mathbf{S}_B$, reducing $\mathbf{S}_P$ into the realized subniche, $\mathbf{S}_R$ (Fig. 1). In summary:

$$\mathbf{S}_R \bigcup \mathbf{S}_B = \mathbf{S}_P = \mathrm{K} \bigcap \mathbf{N}_R$$

$\mathbf{S}_B$ can be caused by negative biological interactions (e.g., predation, competition, parasitism, etc.) but also can be due to dispersal limitation from the species itself (i.e., lack of time for migration) or occupancy by another species (*Peterson et al., 2011*) (Fig. 1).

The realized niche can be measured directly from the n-dimensional hypervolume (*Blonder et al., 2014*) but ordination techniques are also well suited to investigate species

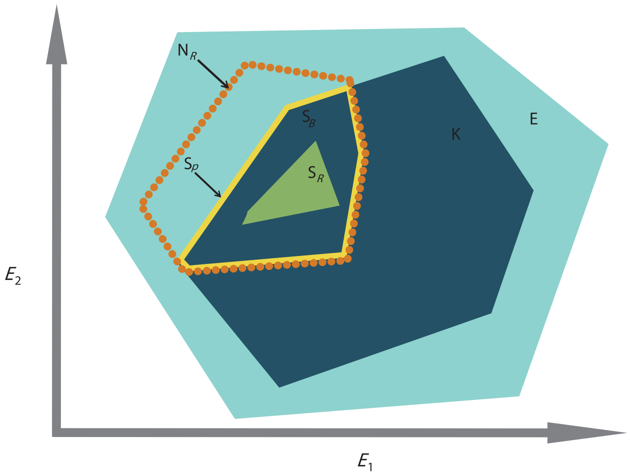

Figure 1 The concept of the existing fundamental niche and biotic interactions of *Jackson & Overpeck (2000)* adapted to the calculation of the realized subniche S_R. E_1 and E_2 are the environmental gradients calculated after an ordination technique. E is the realized environmental space (filled light blue minimum convex polygon). $\mathbf{N}_R$ is the species realized niche (dotted orange contour). **K** is the subset realized environmental space (dark blue minimum convex polygon). $\mathbf{S}_P$ is the existing fundamental subniche (the yellow contour)—a union of $\mathbf{S}_B$ and $\mathbf{S}_R$. $\mathbf{S}_B$ is the subset biotic reducing factor (the part of **K** found within the orange contour), or biological constraint, and $\mathbf{S}_R$ is the realized subniche (the green minimum convex polygon).

and environmental relationships. The outlying mean index (OMI) analysis is an ordination technique designed to explicitly take into account the ecological niche of each species within a community (*Dolédec, Chessel & Gimaret-Carpentier, 2000*). The OMI analysis seeks combinations of environmental variables that maximize average species marginality, i.e., the squared Euclidean distance between the mean habitat conditions used by a species and the mean habitat conditions of the sampling domain (the sampling domain can be defined on a temporal and/or spatial scale). Ecologically, as *Hernández-Fariñas et al. (2015)* stipulated “species with high values have marginal niches (occur in less common habitats in the studied region), and those with low values have non-marginal niches (occur in typical habitats in the region).” In other terms, in OMI analysis, the position of each species in the multidimensional space depends on its niche deviation from a uniformly distributed theoretical species, which would occur under all available habitat conditions (i.e., ubiquitous). In addition, the technique provides information on species’ niche breadth or tolerance where “high tolerance values are associated with taxa occurring in a wide range of environmental conditions (generalist taxa) while low values of tolerance imply that the taxa are distributed across a limited range of environmental conditions (specialist taxa)” (*Hernández-Fariñas et al., 2015*).

Beside OMI analysis, the *K*-select analysis is another ordination technique which is also based on marginality (*Calenge, Dufour & Maillard, 2005*). The *K*-select analysis consists of a non-centered principal component analysis calculated on a table containing the marginality vector coordinates of a species population for the habitat variables (*Calenge, Dufour & Maillard, 2005*). The output of the *K*-select analysis is a

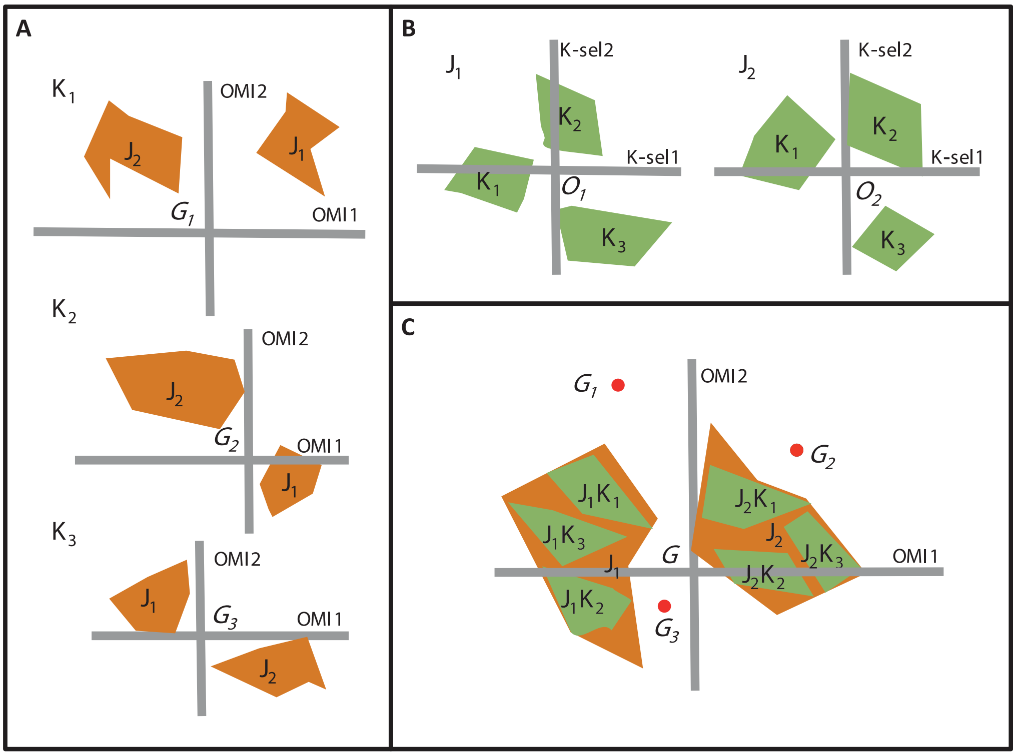

Figure 2 The difference between the OMI analysis, K-select analysis and WitOMI calculations. (A) OMI analyses performed on three hypothetical subsets (K_1, K_2, and K_3) and two species (j_1, j_2). The three positions of the two species niches with their corresponding minimum convex polygon (i.e., niche breadth) are not comparable across subsets (K_1, K_2, and K_3) because ordination is performed for each subset, creating new origins, G_1, G_2, and G_3 (i.e., equivalent to the average habitat conditions used by the community). (B) Separate *K*-select analyses performed for each species, j_1 and j_2, in the three subsets, K_1, K_2, and K_3. The resulting niches for each subset of the two species are not comparable because the origins O_1 and O_2 represent the average habitat used by the species j_1 and j_2, respectively. (C) Species' niche position and breadth analyzed with the OMI analysis. WitOMI, further decompose the species niche into subniches ($j_1 K_1$, $j_1 K_2$, $j_1 K_3$ and $j_2 K_1$, $j_2 K_2$, $j_2 K_3$ for j_1 and j_2, respectively) and indexes can be calculated from *G*, WitOMIG. The black dots (G_1, G_2, and G_3), representing the average subset used by one assemblage, are used to calculate subniche indexes, WitOMIG_K.

multicollinearity of habitat variables for which the marginality is the greatest; in other words, a synthesis of the variables which contribute most to habitat selection. The main difference between the two techniques concerns the weighting of the sampling units (SUs), i.e., one unit of the sampling domain. The OMI analysis assumes the equal availability of SUs (i.e., colonizable) to all monitored species regardless of time and/or space, whereas the *K*-select analysis considers an equal availability of SUs within each subset (i.e., group of SUs) of the sampling domain (e.g., seasons within a year or sites within a region for one species) (*Thomas & Taylor, 1990*). Let us consider an assemblage of two species (j_1 and j_2) collected within a sampling domain divided into three subsets (K_1, K_2, and K_3). To study species' niche dynamics within the community over the three subsets, one can perform three separate OMI analyses, i.e., one for each subset (Fig. 2A) or two *K*-select analyses, i.e., one for each species (Fig. 2B). However, whichever of the two analyses used, a new environmental gradient is created for each analysis performed.

To study niche dynamics, some researchers have used several distinct OMI analyses on habitat condition subsets. For example, *Grüner et al. (2011)* performed 40 OMI analyses (one per year) on a time series of three phytoplankton species to depict their temporal niche trajectories. *Hof, Rahbek & Araújo (2010)* performed 14 OMI analyses (one per region and per family) to assess the phylogenetic relatedness between different amphibian families and genera within each geographical region. *Mérigoux & Dolédec (2004)* performed two OMI analyses on freshwater invertebrates (one per season, spring and autumn) to address seasonal shifts in the hydraulic niche of taxa. One drawback of these approaches lies in the available habitat conditions (as defined by *Dolédec, Chessel & Gimaret-Carpentier (2000)*), which may greatly vary between each subset, impacting the calculations of indexes such as marginalities and tolerances (Fig. 2A). As a result, the observed changes in marginalities can be partly attributed to temporal (annual for *Grüner et al. (2011)* and seasonal for *Mérigoux & Dolédec (2004)*) or spatial changes (*Hof, Rahbek & Araújo, 2010*) in average habitat conditions used by taxa in the assemblage. Hence, performing separate OMI analyses on different habitat condition subsets, using the same domain of habitat conditions, does not make the species' niches comparable across subsets, because average habitat conditions most likely vary from one subset to another. To our best knowledge, *K*-select analyses have not yet been performed on species assemblages, but rather on several populations of one species (reindeer) (*Pape & Löffler, 2015*). In this case study, the authors performed nine *K*-select analyses (one population per season), creating nine different habitat gradients (*Pape & Löffler, 2015*). However, the average habitat conditions used changed for each ordination, giving different meanings to the marginality values for each analysis, making comparisons between seasons inaccurate.

Here, our main goal is to provide a method to estimate the dynamics of the realized subniches, $\mathbf{S}_R$, of each species of an assemblage, compared to G, representing the overall average habitat condition found in **E**. Furthermore, the subniche can also be compared to G_K, which represents the average subset habitat conditions found in **K**. We therefore, propose to combine the properties of the OMI analysis (maximizing the average species marginality within a community) and the *K*-select marginality decomposition within a species (maximizing the species marginality within subsets, i.e., the subniche). Our proposal allows comparing the ecological niche and ecological subniches of species in the n-dimensional environmental space, by fixing the ecological conditions using the OMI analysis (Fig. 2C) and then decomposing the occupation of the realized niche in the same manner as the preliminary calculations of *K*-select analysis. In addition, it describes the possible subniche shift and/or conservatism of species within an assemblage across temporal and/or spatial subsets within the habitat conditions of the sampling domain. Finally, the difference between the existing fundamental subniche, $\mathbf{S}_P$, and the realized subniche, $\mathbf{S}_R$, would therefore correspond to the observed biological constraint, $\mathbf{S}_B$. We illustrate the potential of this method using published studies including both a temporal case (seasonality; see *Mérigoux & Dolédec (2004)*) and a spatial case (longitudinal stream gradient; see *Dolédec, Chessel & Gimaret-Carpentier (2000)*).

THE WITOMI CONCEPT

The OMI measures the marginality of a species (i.e., the weighted average of SUs used by the species) from the average condition of the sampling domain, G (*Dolédec, Chessel & Gimaret-Carpentier, 2000*). OMI originates from the combinations of $\mathbf{Z}_0$, the standardized environmental variable table, and **Fr**, the species frequency table. Here, we aim to estimate the niche occupation dynamics of each species within the community, at different subsets of habitat conditions within the sampling domain. In other words, we aim to scrutinize the subniches of species within a community in the same reference plane, made by the resulting factorial axes from the OMI analysis. The subniche is defined hereafter, as a subset of habitat conditions used by a species.

Inspired by the OMI analysis (*Dolédec, Chessel & Gimaret-Carpentier, 2000*) and the decomposition of marginalities used in K-select analysis (*Calenge, Dufour & Maillard, 2005*), we propose to calculate two additional marginalities. First, the WitOMI to G (WitOMIG) is the species marginality (i.e., the weighted average of SUs of a given subset used by the species) to the average habitat conditions of the sampling domain (G; see Eq. S9 in Appendix S1). Second, the WitOMI to G_K (WitOMIG_K) is the species marginality compared to the average habitat condition used by the community in a K subset habitat conditions (G_K; see Eq. S20 in Appendix S1).

To obtain WitOMIG, we first calculate the species frequency relative to each **K** subset (with $1 \leq \mathbf{K} \leq N$). Second, the N $\mathbf{Fr}_K$ matrices are concatenated to yield the overall species frequency table (Fr*). Third, the standardized environmental table $\mathbf{Z}_0$ is used in combination with (Fr*) to calculate WitOMIG following the Eq. (S9) in Appendix S1.

The calculation of WitOMIG_K first requires centering each of the K subsets of the standardized environmental table $\mathbf{Z}_0(n \times p)$, independently yielding several matrices $\mathbf{Z}_{K^*}$. The N $\mathbf{Z}_{K^*}$ are then concatenated to yield another environmental table $\mathbf{Z}^*$. Finally, $\mathbf{Z}^*$ is used in combination with (Fr*) to calculate WitOMIG_K following the Eq. (S20) in Appendix S1.

Outlying mean index analysis is then used as the reference ordination technique. The subniche coordinates in the n-dimensional space, $\mathbb{R}^p$, are projected onto the OMI factorial plane by multiplying their values by the corresponding eigenvectors. As a result, the niche and the subniche parameters (marginality and tolerance) of the species are all in the same reference factorial plane.

Within outlying mean index to G and the WitOMIG_K calculations are shown in Appendix S1, and do not include the OMI calculations and the OMI analysis, which are fully described in *Dolédec, Chessel & Gimaret-Carpentier (2000)*. The WitOMI calculations, as well as other computational tools, are available in the "subniche" package for R software (*R Core Team, 2013*) and can be downloaded for free at the http://cran.r-project.org. The "subniche" tutorial is available at https://github.com/KarasiewiczStephane/WitOMI.

Statistical significance

The statistical test for significance of the species marginality in the K subsets, which is inspired from *Dolédec, Chessel & Gimaret-Carpentier (2000)*, uses a Monte Carlo test

(*Manly, 1991*). First, the significance of the subset habitat conditions K was calculated by considering the equiprobability of $n!$ permutations of the habitat conditions table Z_0. We compared the observed average of subset habitat conditions, G_K, to the distribution of the 1,000 permutations values following the null hypothesis that G_K is not different from overall average habitat conditions, represented by G.

The significance of the species marginalities from the average habitat condition G, WitOMIG, and from the average subset habitat conditions G_K, WitOMIG_K, were calculated by considering the equiprobability of $k!$ permutations of the species profile $\mathbf{Fr}_K$. Second, a comparison of the observed WitOMIG (Eq. S9 in Appendix S1), and WitOMIG_K (Eq. S20 in Appendix S1) with the distribution of the 1,000 permutations values, found under the K subset, following the null hypothesis that the species within a subset is uninfluenced by its overall average habitat conditions (ubiquitous), for WitOMIG and by subset habitat conditions for WitOMIG_K, respectively. Third, the means of the observed WitOMIG and WitOMIG_K across the K subset were compared to their respective simulated mean.

Graphical display

The graphical display of the species' realized niche and subniche can be obtained by projecting the available SUs of matrix $\mathbf{Z}_0$ on the first two factorial axes of the OMI analysis (OMI1 and OMI2 in Figs. 3 and 4),

$$\mathbf{Z}_0^{\mathbf{u}} = \mathbf{Z}_0 \times \mathbf{u}$$

with $\mathbf{u}$ being the eigenvectors chosen after the OMI analysis and $\mathbf{Z}_0^{\mathbf{u}}$ corresponding to the matrix of coordinates of all available SUs projected onto the OMI analysis plane.

The graph origin is the center of gravity of all available SUs, G, which represents mean overall habitat conditions. Similarly, the subset origin, G_K, is the barycenter of available k SUs within the K subset, since $\mathbf{Z}_{K^*}$ is centered. The species niche and subniche positions correspond to the weighted mean of coordinates, whose weight is equal to the species frequency (see section "species frequency table," Appendix S1). Finally, the minimum convex polygon's contour of available SUs (black in Figs. 3 and 4) and of used SUs (blue and the purple dotted and dashed in Figs. 3 and 4) complete the realized niche and subniche breadth representation of species. The minimum convex polygons were drawn with the package "ade4" for R software (*Dray & Dufour, 2007*). The species niche and subniche positions and their respective minimum convex polygons, relative to the origins, give us an idea about the habitat conditions used by species within the constraining habitat highlighted by the OMI analysis.

ECOLOGICAL APPLICATION

To illustrate the potential of combining the OMI analysis with the WitOMI we used two data sets that address the question of subniche dynamics according to temporal or spatial characteristics of the habitat.

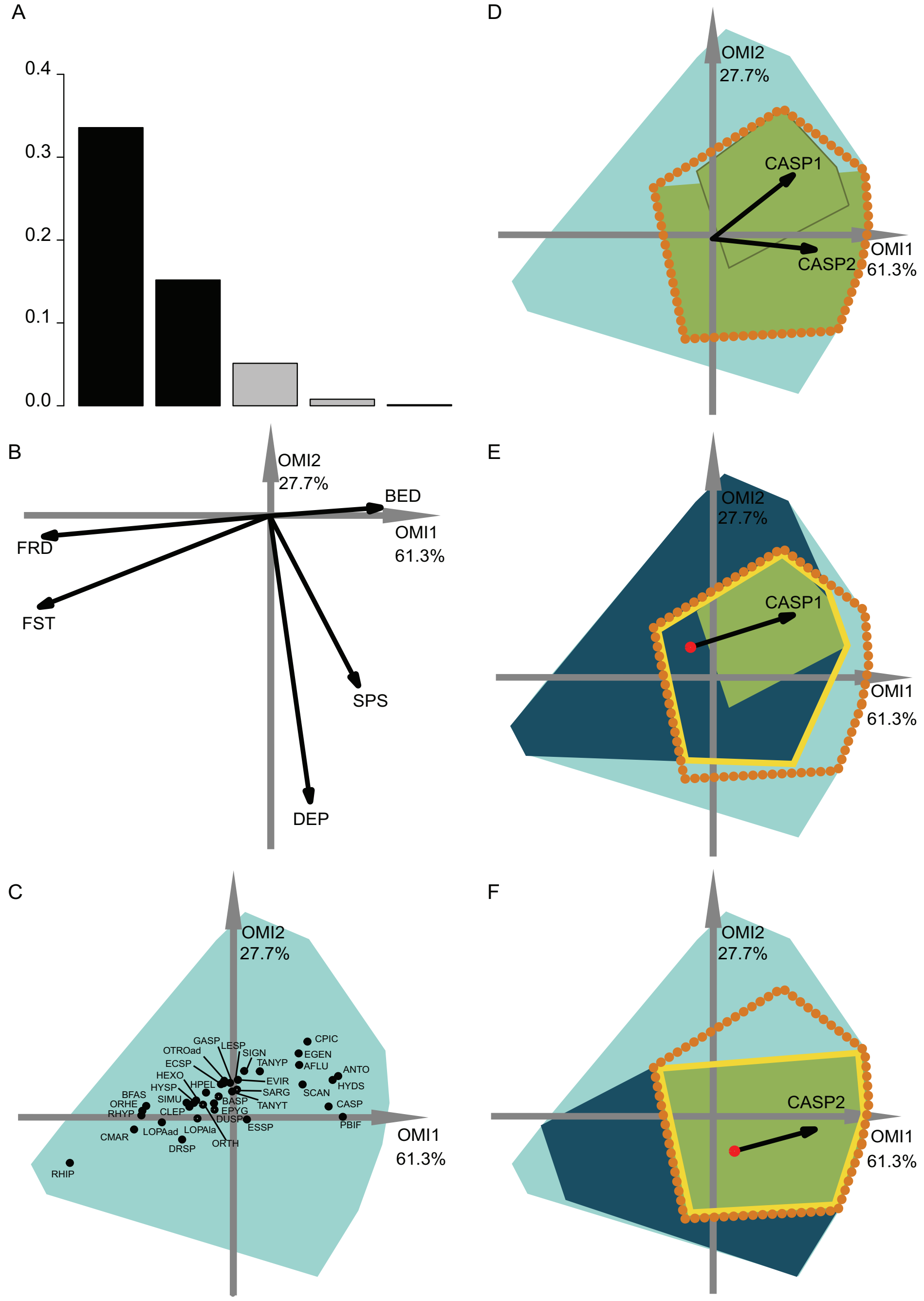

Figure 3 OMI analysis of the invertebrate community and the WitOMI. (A) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axes. The black bars are the chosen factorial axis, OMI1 and OMI2. (B) Canonical weights of environmental variables (FRD, froude; FST, hemisphere number; BED, bed roughness; SPS, substratum particle size, DEP, depth). (C) Representation of the statistically significant species' realized niche positions on the first two factorial axes (Appendix S2; Table S1) (see codes in Appendix S2; Table S3). The light blue minimum convex polygons represent the habitat conditions constraint of all SUs domain. (D) The realized subniches dynamism of *Caenis* sp. (CASP) is the green minimum convex polygon, subsetting the realized niche, the orange dotted polygon. The arrows represent the WitOMIG. (E and F) Represent the *Caenis* sp. Realized subniches under the subset habitat conditions *K*, the dark blue polygon, subsetting the existing fundamental subniche (the yellow contour), encountered in spring and autumn for (E) and (F), respectively. The red dots represent the suborigin, G_K and the arrows represent the WitOMIG_K.

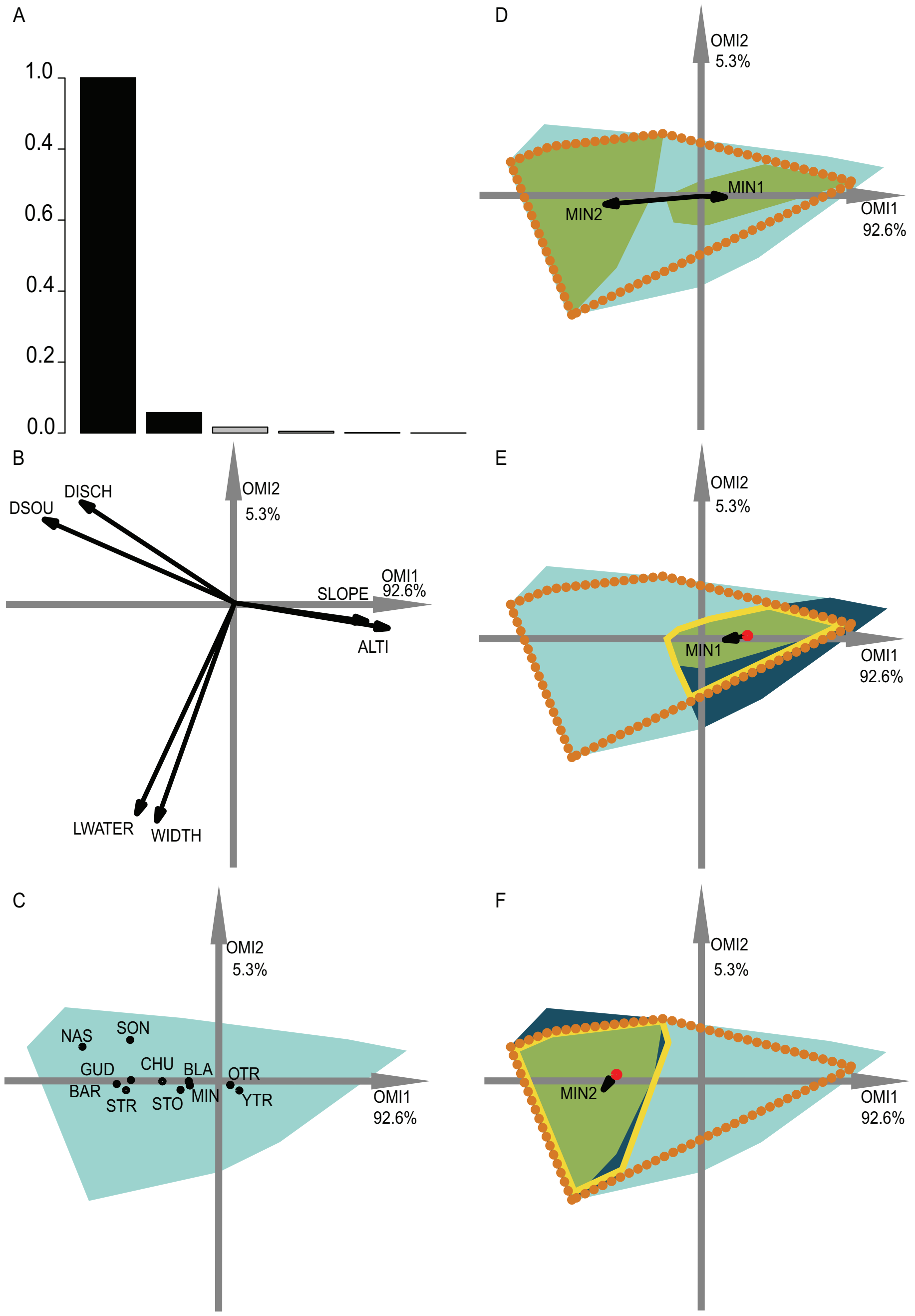

Figure 4 **OMI analysis of the streamfish and the WitOMI.** (A) Bar chart of the eigenvalues, measuring the mean marginality explained by each factorial axes. The black bars are the chosen factorial axis OMI1 and OMI2. (B) Canonical weights of environmental variables (DSOU, distance to the source; DISCH, mean annual discharge; LWATER, lowest monthly discharge occurring every five years; WIDTH, mean stream width; SLOPE, slope; ALTI, altitude). (C) The realized niche position on the first two factorial axes of the significant species (Appendix S2; Table S2) (see codes in Appendix S2; Table S4). The light blue minimum convex polygons represent the habitat conditions constraint of all SUs domain. (D) The realized subniche dynamics of Minnow (*Phoxinus phoxinus*) are the green minimum convex polygons, subsetting the realized niche, the orange dotted minimum convex polygon. The arrows represent the WitOMIG. (E and F) Represent the Minnow (*Phoxinus phoxinus*) realized subniches under the habitat conditions constraint, the dark blue minimum convex polygon, subsetting the existing fundamental subniche (the yellow contour), encountered upstream and downstream for (E) and (F), respectively. The red dots represent the suborigin G_K and the arrows the WitOMIG_K.

Temporal subniche dynamics

The first data set investigated the hydraulic requirement of 57 invertebrate taxa (*Mérigoux & Dolédec, 2004*). Herein, instead of performing an OMI analysis for each season (i.e., spring and autumn as done by authors) we performed one for the entire year. A total of 35 out of 57 taxa had significant OMI (Appendix S2; Table S1). We selected the first two OMI axes, which represented 89% of the explained variability (Fig. 3A), in order to represent the subniches. As depicted by *Mérigoux & Dolédec (2004)*, the first axis shows that FST hemisphere number and Froude number are the most influential hydraulic parameters on the species' realized niche (Figs. 3B and 4C). WitOMI were then calculated for spring and autumn for each of the 35 significant species. All WitOMI (WitOMIG and WitOMIG_K) were significant (Appendix S2; Table S1).

As an example, *Caenis* sp. used an uncommon habitat (OMI = 2.09) compared to the rest of the community (Appendix S2; Table S1). *Caenis* sp. has a preference for high bed roughness compared to most species (Figs. 3B and 3C). A similar pattern can be found with its realized subniches (WitOMIG = 2.28 and 2.24 for spring and autumn, respectively) (Appendix S2; Table S1). The realized subniche positions demonstrate a shift, seemingly caused by the increasing depth in autumn (Fig. 3D). *Caenis* sp. tolerance also showed an increase from spring to autumn (Tol = 0.45 and 0.75, respectively) (Appendix S2; Table S1). Now considering each season separately, *Caenis* sp. occupied different parts of its realized niche (Figs. 3E and 3F). *Caenis* sp. thus used a more atypical habitat compared to the one used by the assemblage in spring and autumn (WitOMIG_K = 2.44 and 2.46) (Appendix S2; Table S1). Despite the seasonal habitat change, the marginality of the habitat used by the species stayed similar. The tolerance also increased when considering the two habitat conditions separately (Tol = 0.46 and 0.75). *Caenis* sp. occupied a greater part of its existing fundamental subniche in autumn than in spring, which suggests more appropriate abiotic conditions or less constraint by biotic interactions.

In spring, the *Caenis* sp. realized subniche (the green minimum convex polygon, Fig. 3E) did not fully occupy the intersection between the niche (orange dotted contour) and the subset habitat condition (dark blue minimum convex polygon) (i.e., existing fundamental subniche). Herein, the empty part of the existing fundamental subniche therefore corresponds to the biological constraint exerted on the species realized subniche. The decreasing biological constraint exerted on the *Caenis* sp. realized subniche from spring to autumn seems to be correlated with the decreasing number of species having a significant marginality (35 to 23 from spring to autumn).

Spatial subniche dynamics

The second data set investigated the fish assemblages used by *Dolédec, Chessel & Gimaret-Carpentier (2000)*. We selected the first two OMI axes, which represented 97.9% of the explained variability, in order to represent the realized subniches (Fig. 4A). We divided the data along the first axis, which is mostly defined by altitude and slope, considering distinct upstream and downstream habitat conditions. All of the WitOMI (WitOMIG and WitOMIG_K) were significant (Appendix S2; Table S2).

As an example, minnow (*Phoxinus phoxinus*), was distributed over the entire longitudinal gradient and used common habitat (OMI = 0.45). However, the used habitat was more marginal downstream than upstream (WitOMIG = 0.33 and 4.61 for upstream and downstream, respectively) (Fig. 4D) (Appendix S2; Table S2). In addition, we observed a shift in the species' marginality and tolerance within its realized niche (Fig. 4D). The reason for the realized subniche change in marginality and tolerance can be explained by the difference between upstream and downstream subset average habitat conditions (red dot, Figs. 4E and 4F) and subset habitat condition constraints (dark blue minimum convex polygon, Figs. 4E and 4F), impacting the species' realized niche. Focusing on the upstream and downstream habitat conditions separately, minnow's marginality upstream was higher than downstream (WitOMIG_K = 0.3 and 0.04 for upstream and downstream, respectively) (Appendix S2; Table S2). In both conditions, the species used a similar habitat to the one used by the assemblage. Furthermore, upstream conditions seemed to have greater constraint on the species realized niche occupation, contracting the minnow realized subniche breadth (Fig. 4E), whereas downstream conditions allowed the species to occupy a greater part of its existing fundamental subniche (Fig. 4F).

In addition, both young and adult trout were found along the entire longitudinal gradient with a preference for upstream conditions (WitOMIG_K = 0 for old and young trout, respectively) (Appendix S2; Table S2). Minnow, stone loach and chub were mostly found downstream while the nase, southwestern nase and streambleak species were exclusive to downstream average habitat conditions (Appendix S2; Table S2). These results were coherent with those of *Dolédec, Chessel & Gimaret-Carpentier (2000)* on the same data set (Fig. 4C). In addition, WitOMI showed that the conditions found downstream offered greater habitat variability because other environmental variables, aside from altitude and slope, influenced species' subniches. The greater variability of habitat downstream permitted hosting more species than upstream, where trout appeared to use most of the habitat conditions.

DISCUSSION

The WitOMI offer new interpretations to niche dynamics by considering subsets of habitat conditions within which the species' realized subniches are developed. WitOMI complement the OMI approach by shifting how realized niches are perceived along fluctuating habitat conditions. WitOMI make all realized subniches comparable along the same environmental gradient as they all refer to the same OMI analysis. The realized subniche parameters can be explained by the average habitat conditions used by the assemblage over the entire sampling domain, WitOMIG, and by the average habitat conditions used within a subset of SUs WitOMIG_K. The advantage of decomposing the realized niche into realized subniches is that the WitOMI are simple measures, which integrate the species realized subniche specialization from the habitat studied (WitOMIG) and from the decomposed habitat (WitOMIG_K), giving additional hints on the role played by different environmental variables. However, our approach has the same experimental limitation as the OMI analysis. The environmental variables used may

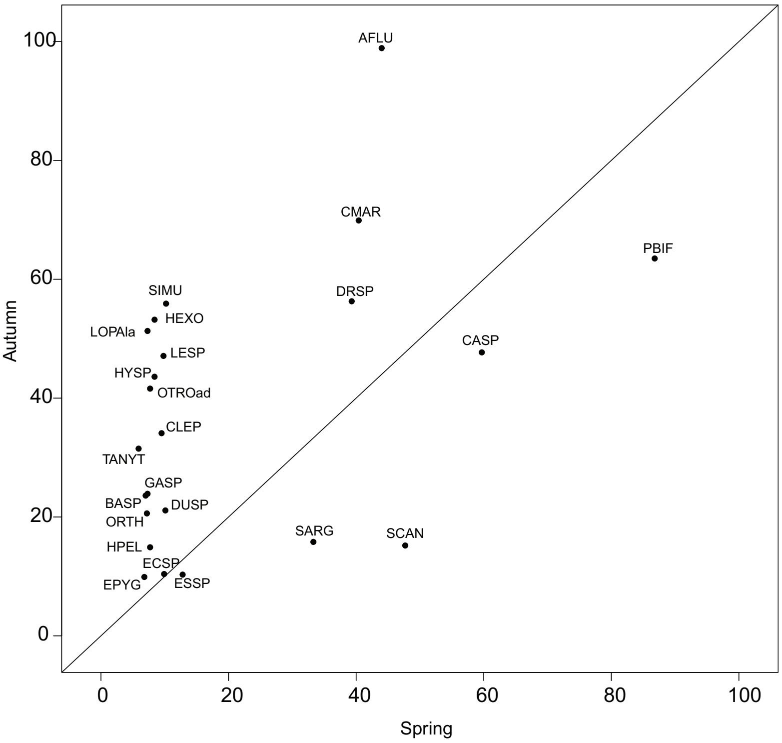

Figure 5 Within outlying mean index to *G* values (as percentage of the total variability, Appendix S2; Table S1) of the 23 significant taxa common to both seasons. Names are abbreviated using codes as given in Appendix S2; Table S3.

not be sufficient to define the realized niche parameters, making the decomposition of the realized niche into realized subniches irrelevant.

The reference species, which represents a theoretical ubiquitous species using the overall average habitat conditions of a sampling domain, helped quantify the shift in realized subniches. The utilization of G as a reference smoothens the atypical conditions, avoiding an over-interpretation of habitat condition effects on the species' niches. Reconsidering the results of *Mérigoux & Dolédec (2004)*, who performed a separate OMI analysis on each season, we found less species common to both seasons with a significant marginality (23 herein and 35 in *Mérigoux & Dolédec (2004)*). Nonetheless, the pattern found in Fig. 5 was similar to the one found in Fig. 2 of the authors, i.e., with more species in autumn having significant marginality than in spring, thus underlying the fluctuating effect of hydraulic constraints advocated by the authors (Appendix S2; Table S1). The WitOMI thus provide more relevant comparable values. In addition, the use of G_K, which can be representative of more variable conditions, can provide additional information about the environmental variables driving the species niche and community composition.

However, the method is limited by the number of SUs defining the sampling domain. This limitation underlines the inapplicability of the WitOMI to an unsignificant realized niche of the OMI analysis. WitOMI are also limited by the number of subsets used to

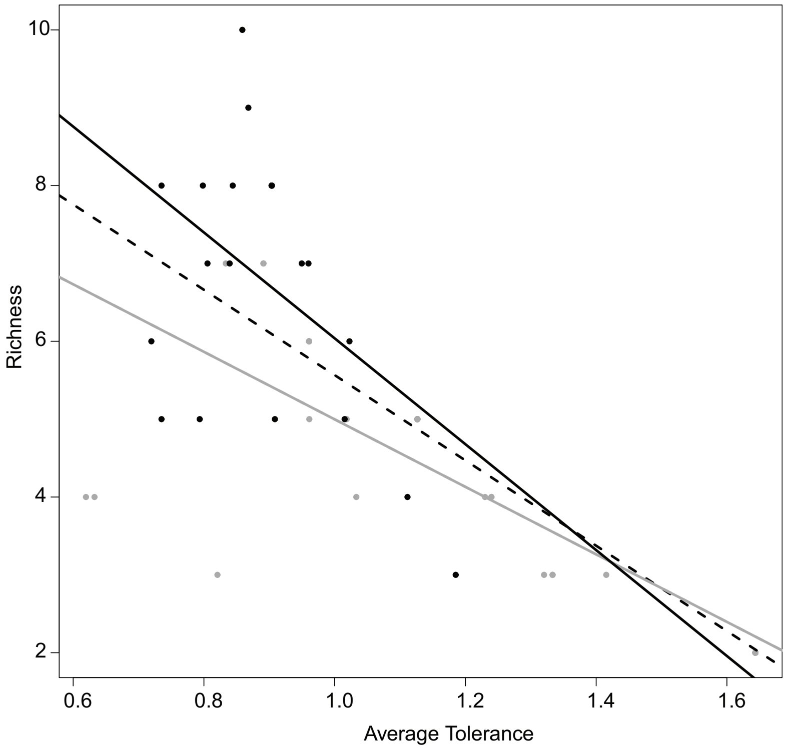

Figure 6 Relation between the average tolerance values of sites upstream and downstream, and their fish species richness. Overall, dashed black line, $R^2 = 0.64$ with $P < 0.001$; upstream, grey line, $R^2 = 0.68$ with $P < 0.001$; downstream, plain black line, $R^2 = 0.21$ with $P = 0.034$.

decompose the sampling domain. In the ecological application, we used two subsets of habitat conditions to decompose the realized niche into two realized subniches. The K SUs defining a subset have an impact on the subniche parameters' significance. Even if it was not the case in our study, a low number of SUs within subsets can cause the test of significance to give a low probability of estimating subset habitat conditions (G_K).

Realized subniches can be compared to their respective subset origins, the subset theoretical ubiquitous species using the most general subset of habitat conditions, in how they differ from G. This comparison provides a more detailed interpretation in the realized niche shift. For instance, similar to *Dolédec, Chessel & Gimaret-Carpentier (2000)*, there was a negative relationship between species richness and realized niche breadth (Fig. 6). The negative relationship was greater upstream ($R^2 = 0.68$ and 0.21 for upstream and downstream, respectively) (Fig. 6). In other words, there was increasing competition upstream because the most common species (with the lowest WitOMIG_K) found upstream, the trout (WitOMI$G_K = 0$ for upstream), has a broad realized subniche upstream (Tol = 1.62 and 1.09 for upstream and downstream, respectively), which decreases species diversity (8 and 11 species for up and downstream, respectively). In this spatial example, the WitOMIG_K allows assessing which species were common upstream, giving a more accurate description of the fish distribution pattern (*Dolédec, Chessel & Gimaret-Carpentier, 2000*), and community structure.

The subsets of habitat conditions and the two WitOMI can be tested with random permutations to assess whether subset habitat conditions and the species marginality are significantly different from what would be expected by chance. They follow the null hypothesis that the subset habitat conditions G_K are not different from the overall habitat conditions G, and that a species is not influenced by habitat conditions for WitOMIG, or by the subset of habitat conditions for WitOMIG_K. Lack of significance in the permutation test can be explained by the defined subset conditions, which might not be appropriate enough, making G_K weakly relevant and the WitOMI unsignificant. This emphasizes the need for a reference habitat condition and a significant realized niche $\mathbf{N}_R$ (e.g., OMI analysis), which can be further decomposed to study realized subniche dynamics. The total inertia of the species (see Eq. 13 in Appendix S1) characterizes the decomposition of the realized niche, $\mathbf{N}_R$, calculated with the OMI analysis, into the species realized subniches, $\mathbf{S}_R$, within the subset habitat conditions, G_K.

The decomposition of the realized niche allows estimating the biological constraints, $\mathbf{S}_B$, exerted on a species (e.g., *Caenis* sp.) in our temporal example. The comparison between the subniche, $\mathbf{S}_R$, and the existing fundamental subniche, $\mathbf{S}_P$, revealed an unused part of $\mathbf{S}_P$ which can be attributed to biological constraints. The quantification of biological constraints is dependent on the envelope chosen to represent the niches and subniches. Quoting *Guisan et al. (2014)*, the niche envelope is "the envelope of conditions in multivariate environmental space defining a species niche. The boundary of the envelope can be defined in many different ways, e.g., percentiles; *Broennimann et al. (2012)*." In this study we used the minimum convex polygon. Therefore, our quantification of the biological constraints, $\mathbf{S}_B$, consisted of measuring the difference between the area of $\mathbf{S}_P$ and $\mathbf{S}_R$. The biological constraints can be given in percentage of the $\mathbf{S}_P$ area but is the minimum convex polygon truly the best envelope? For example, *Blonder et al. (2014)* developed a method to calculate the n-dimensional hypervolume which can be used to quantify the hypervolume of $\mathbf{N}_R$, $\mathbf{S}_R$, $\mathbf{S}_P$, and the biological constraints. As suggested by *Blonder et al. (2014)*, hypervolume might have holes, which may be the equivalent of the biological constraints of a species niche estimated, within the n-dimensional hypervolume. This perspective could bring further insight into the invasive species strategy as explained in *Blonder (2016)*. $\mathbf{S}_B$, which is now quantifiable under subset habitat conditions, can be of a different nature. It can either be due to negative biological interactions, or dispersal limitation (*Peterson et al., 2011*). As a result, caution should be taken while interpreting the nature of $\mathbf{S}_B$.

The description of the subset conditions of the different variables can reveal how the community responds to changing habitat conditions. We can imagine the case where the shifted species' realized subniches do not shift in the same direction as the suborigins. What mechanisms would be involved in species realizing their niches? Would the community be threatened by a changing environment? These questions emphasize the need for using the WitOMI that enables comparing different species' realized niches in a community under changing habitat conditions. Our proposed refinement of the OMI analysis allows us to make hypotheses on the mechanisms involved in a species realizing its niche. The ecophysiological requirements of species should vary with changing habitat conditions, since species must respond to the environmental variation in order to survive. *Kleyer et al. (2012)* recently developed this idea using the outlying mean index followed by generalized additive modeling (OMI-GAM). First, the method consists of using the OMI analysis to determine the species' responses to habitat conditions and their realized niche positions and breadths. Second, traits are used as explanatory variables in a GAM to explain the above species responses. The OMI-GAM thus answers the question "How do trait expressions of species respond to environmental gradients?" Similarly, the WitOMI could be used as a first step of OMI-GAM to study trait expressions within different habitat conditions and to reveal shifts in species life-strategies via a change in the functional trait hierarchy.

The main strength of WitOMI is that they can be applied to any species, population, community, or ecosystem. Regarding the previous example, reanalyzing the data with the WitOMI, should improve the accuracy and details of the results (*Hof, Rahbek & Araújo, 2010*; *Grüner et al., 2011*; *Pape & Löffler, 2015*). This proposal can be used in various aspects of ecology, such as the structure and dynamics of populations and interactions among individuals of the same or different species. In the context of global change, the methods can reveal the response of individuals and groups of organisms, and the organization of biological communities (*Hof, Rahbek & Araújo, 2010*; *Grüner et al., 2011*). The WitOMI can be used as a statistical basis for future ecological niche models such as modeling the potential of an invasive species to establish itself in a new ecosystem (*Broennimann et al., 2012*; *Guisan et al., 2014*). As a perspective, the WitOMI can be applied to study community responses to environmental change, including the impacts of possible community resource-competition.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare that they have no competing interests.

Author Contributions

- Stéphane Karasiewicz conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, wrote the paper, prepared figures and/or tables, reviewed drafts of the paper.
- Sylvain Dolédec conceived and designed the experiments, wrote the paper, reviewed drafts of the paper.
- Sébastien Lefebvre conceived and designed the experiments, analyzed the data, wrote the paper, reviewed drafts of the paper.

Data Availability

The following information was supplied regarding data availability:

The data used are RDA files and are named “ardecheinv” and “drome.” The data, along with the WitOMI calculations as well as other computational tools, are available in the “subniche” package and can be downloaded for free on the CRAN repository http://cran.r-project.org or on Github (https://github.com/KarasiewiczStephane/WitOMI).

Supplemental Information

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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* (WitOMI*G* 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

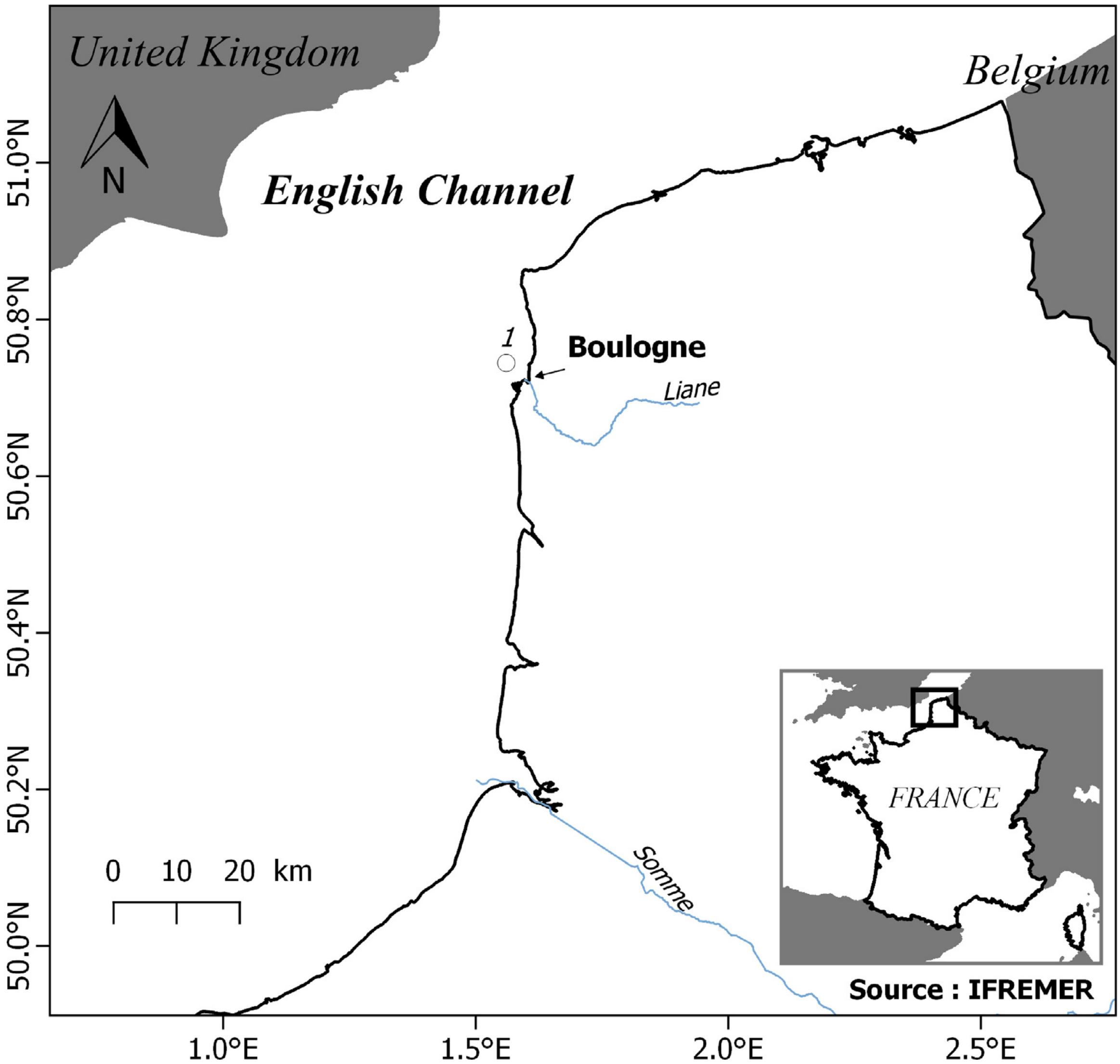

Fig. 1. Map of North of France with the main station location of the French REPHY-IFREMER network.

Carlo permutation procedure (Manly, 1997) with 10,000 permutations.

2.4. Biological constraint

The existing fundamental subniche, $\mathbf{S}_P$, corresponds to the realized niche, $\mathbf{N}_R$, which is reduced abiotically by the subset habitat conditions, **K**. Therefore, $\mathbf{S}_P$ includes the subset biotic factor, $\mathbf{S}_B$, reducing $\mathbf{S}_P$ into the realized subniche, $\mathbf{S}_R$ (Fig. 2). In summary:

$$\mathbf{S}_R \cup \mathbf{S}_B = \mathbf{S}_P = \mathbf{K} \cap \mathbf{N}_R$$

$\mathbf{S}_B$ represents negative biological interactions (e.g., predation, competition, parasitism, etc.), the species dispersal limitation (i.e., lack of time for migration), or occupancy by another species (Peterson, 2011) (Fig. 3). The $\mathbf{S}_B$ unit is in percentage of $\mathbf{S}_P$, and represents the biological constraint exerted on the subniche. Therefore, under the subset habitat conditions H or L, the biological constraint exerted on *Phaeocystis* spp. subniches, and the effect of some other unselected abiotic variables, can be discussed.

All analyses and graphical representations were performed using R software (R Core Team, 2013) with the packages "ade4" (Dray and Dufour, 2007) and "subniche" available for free on the CRAN repository www.cran.r-project.org and on GitHub www.github.com/KarasiewiczStephane/WitOMI.

3. Results

3.1. Subset habitat conditions

Low ($<$50 cells L^{-1}) and high ($>$160 cells L^{-1}) mean annual *Phaeocystis* spp. abundance events (named hereafter subset L and H) occurred on four and five occasions, respectively (L: 1996, 1997, 2000, and 2005, H: 2001, 2004, and 2010-2012; Fig. 3). The non-random BV-step analysis revealed that 7 diatom species were correlated to the overall pattern of the community (Gud, Gus, Par, Pss, Ske, Thn, and Thg, with $\rho = 0.97$; see code in Table 1) in subset L, while 9 diatom species were relevant in subset H (Cha, Dyt, Gud, Gus, Led, Nit, Par, Ske, and Thn, with $\rho = 0.96$). Five species, Gud, Gus, Par, Ske, Thn were common to the two contrasting environmental conditions, leading to 11 species of interest for the rest of the study. Two species occurred only in subset L (Thg and Pss) and four species occurred only in subset H (Dit, Cha, Led, and Nit) (see code in Table 1).

Although the two subsets showed similar increases in temperature and PAR, varying from 5.8 to 19.9 °C and from 8.5

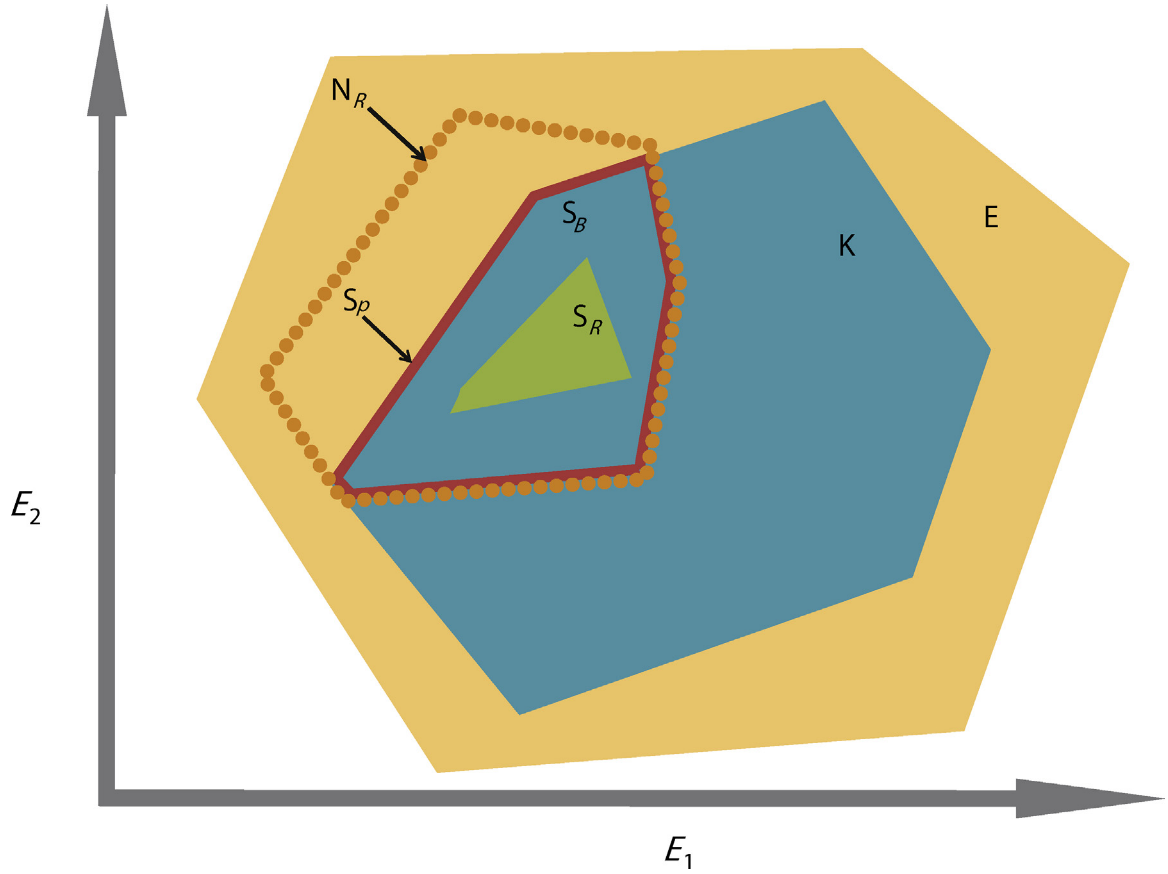

Fig. 2. The subniche concept from Karasiewicz et al. (2017). **E**$_1$ and **E**$_2$ are the environmental gradients calculated after an ordination technique. **E** is the realized environmental space (filled light orange minimum convex polygon). **N**$_R$ is the species' realized niche (dotted dark orange contour). **K** is the subset realized environmental space (blue minimum convex polygon). **S**$_P$ is the existing fundamental subniche (the red contour) – a union of **S**$_B$ and **S**$_R$. **S**$_B$ is the subset biotic reducing factor (the part of **K** found within the orange contour), or biological constraint, and **S**$_R$ is the realized subniche (the green minimum convex polygon). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

to 6.1 × 10^3 W m^2 respectively (Fig. 4A and B), the two subsets differed in turbidity, salinity and nutrient concentrations. Accordingly, subset L displayed higher turbidity but lower salinity than subset H (Fig. 4C and D). Moreover, nutrient concentrations were significantly lower and decreased faster in subset H than in subset L during late winter-early spring (Fig. 2E–H). Phosphate concentration had an overall higher concentration in subset L (Fig. 4F). The sum of nitrate and nitrite concentrations was similar in January and December in both subset L and H, but the overall concentration was higher in subset L than in H (Fig. 4G). The seasonal trends of

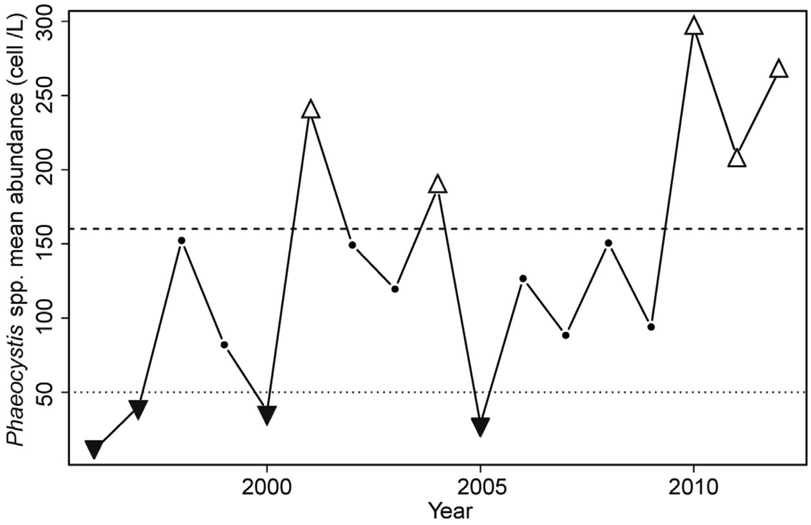

Fig. 3. Temporal variation of the annual mean abundance of *Phaeocystis* spp. (cells L^{-1}) from 1996 to 2012. The dashed line represents the upper threshold (160 cells L^{-1}) and the dotted line represents the lower threshold (50 cells L^{-1}). Abundance was then divided the abundance in three categories (low, intermediate, high). Only high (empty triangles) and low (filled triangles) annual mean abundance events were kept for the rest of the study.

silicate concentration were similar in the two subsets, although it decreased faster the rest of the year in subset H than in subset L (Fig. 4H). The DIN:PO$_4$ followed a unimodal trend with a maximum in April (DIN:PO$_4$: 88) and March (DIN:PO$_4$: 70) for subset L and H respectively (Fig. 4I). The DIN:Si was higher in subset L than in H with a maximum in April (DIN:Si: 59) and March (DIN:Si: 30) respectively.

3.2. Niche analysis (OMI)

The OMI analysis revealed that the realized niches of the 11 diatom species of interest, depicted by the BV-step analysis, and of *Phaeocystis* spp. were significant (Table 1). The first two axis of the OMI analysis represented 87% of projected inertia, of which OMI1 represented 74%. OMI1 was mainly explained by nutrients and turbidity (Fig. 5C), while OMI2 was mainly explained by PAR, temperature and salinity. The seasonal effect can be visualized by the environmental trajectories of subset H and L (Fig. 5B). The environmental trajectory of subset H had a higher position and better resembled a full cycle than subset L, which went “back on track” (Fig. 5B).

The species Ske, Thg and Thn were typical of late winter-early spring and were, as expected, low on the OMI1 axis (on the left side, Fig. 5A). Their niches were explained by high nutrient concentrations and turbidity, but low temperature, PAR and salinity. These three species have the highest niche breadth (Tol Ske: 3.52, Thn: 3.35, Thg: 3.14) (Table 1). The niches of Dit and Cha, Par and Nit were related to intermediate values of OMI1 (lower values of nutrients and turbidity; Fig. 5A). They distributed themselves vertically along the OMI2 by their preferences for higher salinity, temperature and PAR (higher temperature and PAR downwards; Fig. 5A). The species with the lowest marginality were Nit and Par (OMI: 0.06 and 0.09 for Nit and Par respectively). The niches of Pss, Gud, Gus and Phae were characterized by low nutrient concentrations and turbidity but differed from each other in salinity, PAR and temperature affinities. The niche position of Phae was characterized by relatively high salinity but intermediate temperature and PAR, while the other species were rather defined by lower salinity and higher temperature and PAR along the OMI2 axis. The niche of Led, which is typically a summer diatom species was characterized by the lowest nutrient concentrations and turbidity, high salinity, and intermediate temperature and PAR. As a result, Led was characterized by a high marginality (OMI: 2.231).

Table 1
Niche parameters calculated with the OMI analysis for 11 diatoms species and *Phaeocystis* spp. The parameters are the inertia, the marginality (OMI), the tolerance (Tol) and the residual tolerance (Rtol). The *P* values were calculated with 1000 permutations, see methods for further details.

Species	Code	Inertia	OMI	Tol	Rtol	*P*
Chaetoceros danicus	Cha	7.09	0.36	0.98	5.76	0.03
Ditylum brightwellii	Dit	7.48	1.07	1.14	5.26	0.00
Guinardia delicatula	Gud	7.28	0.22	2.51	4.56	<0.001
Guinardia striata	Gus	6.65	0.79	1.62	4.24	<0.001
Leptocylindrus danicus	Led	6.61	2.23	1.31	3.07	<0.001
Nitzschia longissima	Nit	7.73	0.06	0.77	6.89	0.05
Paralia sulcata	Par	7.82	0.09	2.24	5.49	0.00
Pseudo-nitzschia seriata complex	Pss	7.25	0.20	0.96	6.09	0.01
Skeletonema spp.	Ske	10.12	1.64	3.52	4.96	<0.001
Thalassionema nitzschioides	Thn	9.02	0.93	3.35	4.74	<0.001
Thalassiosira gravida	Thg	9.23	1.15	3.14	4.95	<0.001
Phaeocystis spp.	Phae	6.58	0.83	1.36	4.39	<0.001

3.3. Subniche calculations (WitOMI)

Phaeocystis spp.'s subniche position significantly shifted and the subniche breadth expanded from subset L to H (WitOMIG: 2.64 and 2.11; Tol: 0.59 and 0.64 for subset L and H respectively) (Fig. 6). The marginality (WitOMIG) showed that *Phaeocystis* spp. used a more common habitat in subset H than in L. This suggest that the species has a preference for the environmental habitat conditions found in subset H over L (Fig. 6). Considering the subsets independently, the subniche position from the average subset habitat conditions, G_K was much greater in subset L than H (WitOMIG_K: 3.24 and 0.59 from subset L and H respectively). In subset H, *Phaeocystis* spp. used a more common habitat favoring its development (237 cells L^{-1}, Table 2). On the other hand, the habitat preference in subset L, which is atypical for the environmental habitat conditions within subset L, is not well suited for *Phaeocystis* spp. (29 cells L^{-1}, Table 2).

The different WitOMIG values for the common diatom species (Ske, Thn, Par, Gud, Gud), expressed a change in subniche position (Table 2). Meanwhile, the tolerance from G increased for Gud, while it decreased for Gus, Par, Ske and Thn (Table 2). The low WitOMIG_K values in the environmental habitat conditions subset H were preferable for Thn, Par, Gud, and Gus, compared to the environmental habitat conditions of subset L. The opposite pattern occurred for Ske (Table 2). Ske had a preference for the environmental habitat conditions of subset L, as the species' mean abundance, which was higher in subset L, likely reflected the species' habitat suitability. The species Par and Thn had higher mean abundance in subset H, while Gud and Gus had stable mean abundances (Table 2).

Concerning species that occurred in only one subset, Pss had one of the lowest marginalities and intermediate tolerance (WitOMIG_K: 0.28 and Tol: 1.69), while Thg had an intermediate marginality with high tolerance (WitOMIG_K:0.78 and Tol: 4.13), in subset L (Table 2). In subset H, marginality of low for Nit and Cha, intermediate for Dit, and high for Led (WitOMIG_K: 0.14, 0.31, 0.58, and 2.05 for Nit, Cha, Dit and Led respectively) (Table 2). Led had an intermediate tolerance while Nit, Cha and Dit had high tolerance in subset H (Table 2).

The environmental habitat conditions of subset H enhanced the common diatoms and *Phaeocystis* spp. mean abundances, as these species had greater affinities for these environmental habitat conditions. *Phaeocystis* spp. still managed to reach high abundance despite the increase of the relevant number of diatom species. *Skeletonema* spp. was the only common diatom species that was disfavored by the change in environmental habitat conditions, and better responded to the environmental habitat conditions of subset L.

A succession of the diatom subniche was observed in the two habitat subsets (Fig. 7A and B), as expected from the niche analysis (Fig. 4). In subset L, the late-winter early-spring species (Ske, Thn and Thg) were blooming first because they were affiliated with winter like conditions, i.e., low temperature, PAR and salinity, but high nutrient concentrations and turbidity. Then, Par was second to bloom followed by Pss, Gud, Gus and Phae (Fig. 7A). The first species to appear in subset H was Ske, while Thn, Cha, Dit, Par and Nit appeared second. The succession of diatoms continued with Gud, Gus and Led (Fig. 7B). In subset H, the subniche of *Phaeocystis* spp. overlapped most of the diatoms' niche positions, but still managed to have a larger niche breadth than in subset L. The diatom-*Phaeocystis* spp. succession did not take place in subset H, as *Phaeocystis* spp. managed to develop concomitantly with the diatom species (Fig. 7B).

3.4. Biological reducing factor

The *Phaeocystis* spp. subniche in subset L occupied 19% of the existing fundamental subniche. Therefore the biological constraint was equal to 81% (Fig. 8B). The subniche occupation of *Phaeocystis* spp. in subset H within the existing fundamental subniche,

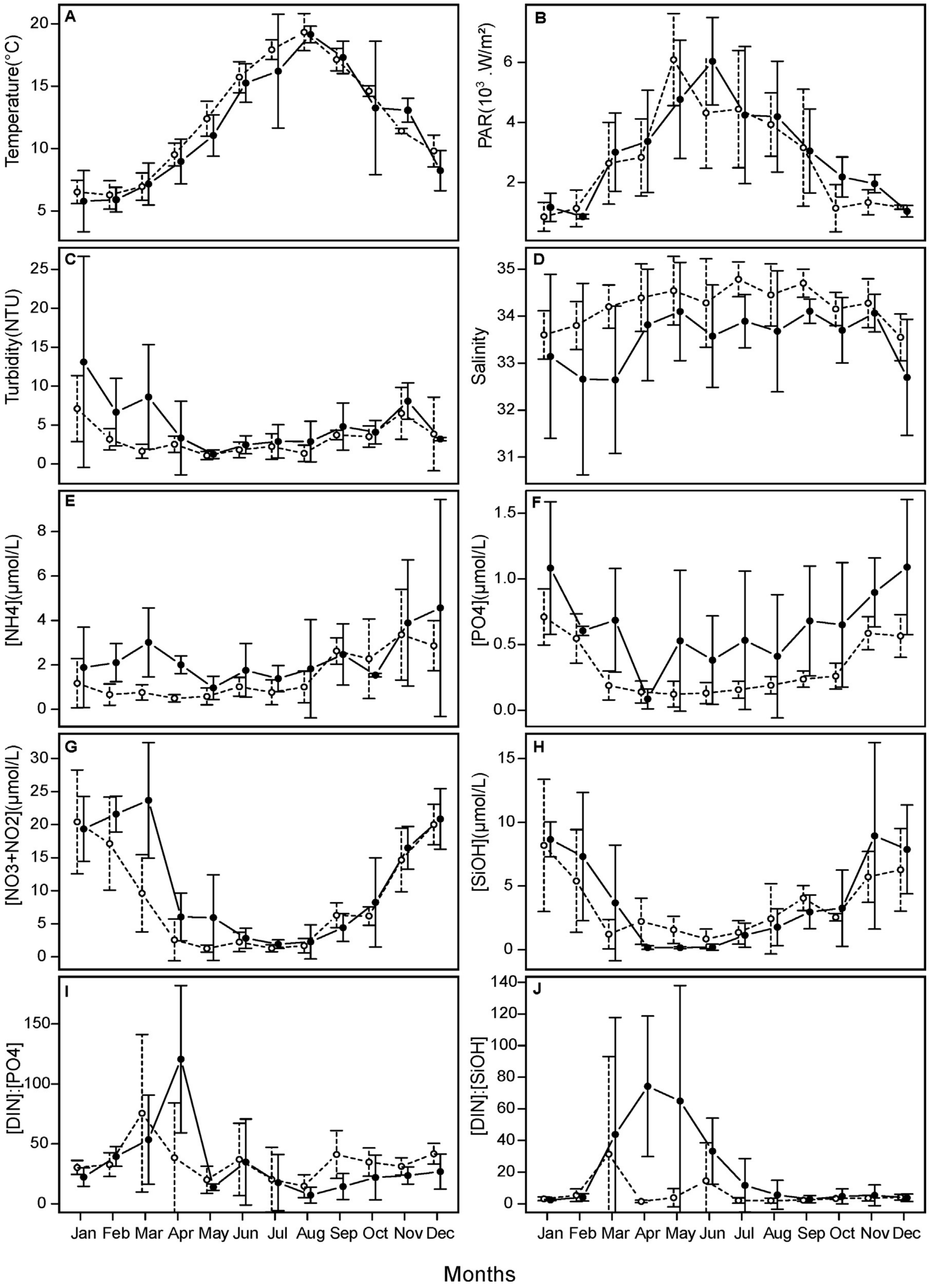

Fig. 4. Monthly mean (±SD) of each environmental variable for the subset H (empty circles) and L (filled circles), low and high annual mean abundance of *Phaeocystis* spp., respectively.

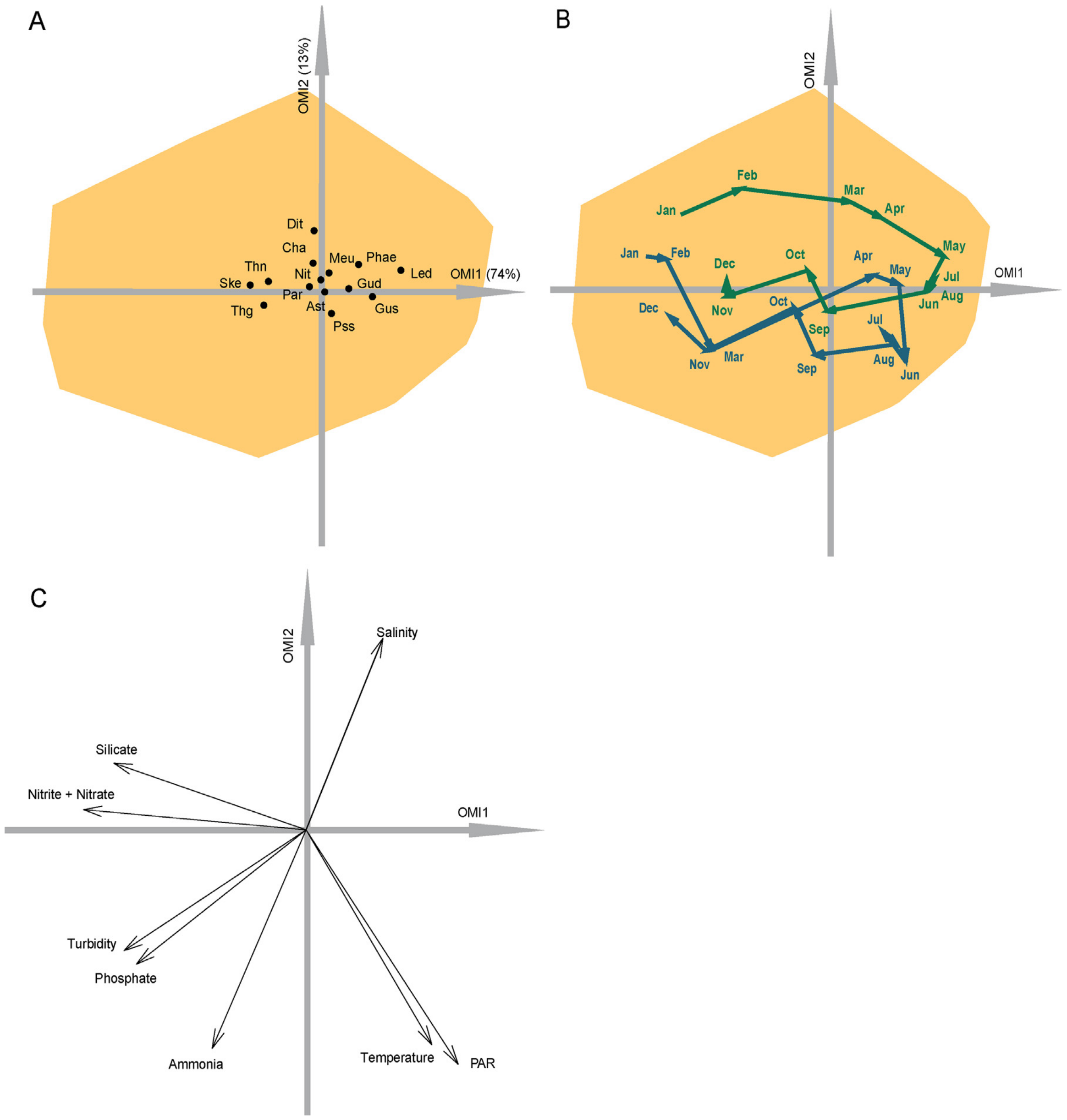

Fig. 5. OMI analysis of the 11 diatom species and *Phaeocystis* spp. (A) The orange polygon represents the overall habitat environmental space. The species' labels represent the species' niche positions (see Table 1 for codes). (B) The environment trajectory, from January to December, under the two subsets L (blue arrows) and H (green arrows). (C) The canonical weights of environmental variables. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

represented 75%. Thus, the subniche biological constraint was of 25% of the existing fundamental subniche (Fig. 8A). Therefore, the unused available conditions of the *Phaeocystis* spp. existing fundamental subniche could have been occupied by competing diatom species, such as *Skeletonema* spp., *Thalassionema nitzschioides*, *Thalassiosira gravida* and the *Pseudo-nitzschia seriata* complex (Fig. 8A). By contrast, the *Phaeocystis* spp. subniche overlapped the diatoms subniches in subset H (Fig. 8B).

4. Discussion

The OMI analysis revealed that nutrient concentrations (phosphate, silicate, nitrite, nitrate and ammonia) played an important role in the diatom community distribution (Fig. 5A and C). Subset H was characterized both by lower nutrient concentrations and faster decreases than subset L (Fig. 5E–H). Therefore, the realized subniche of *Phaeocystis* spp. shifted in position and increased in breadth from subset L to H. The diatom-*Phaeocystis* spp. succession occurred in subset L but not in H. The realized subniche of *Phaeocystis* spp. seemed to be more controlled by the preceeding diatom community than by the subset habitat conditions. Furthermore, the increasing diversity in the diatom community exerted a lower biological constraint on the *Phaeocystis* spp. realized subniche. The results suggest that key diatom species possibly competed for resources with *Phaeocystis* spp., especially nitrogen, phosphate and light, but only when silicate was available.

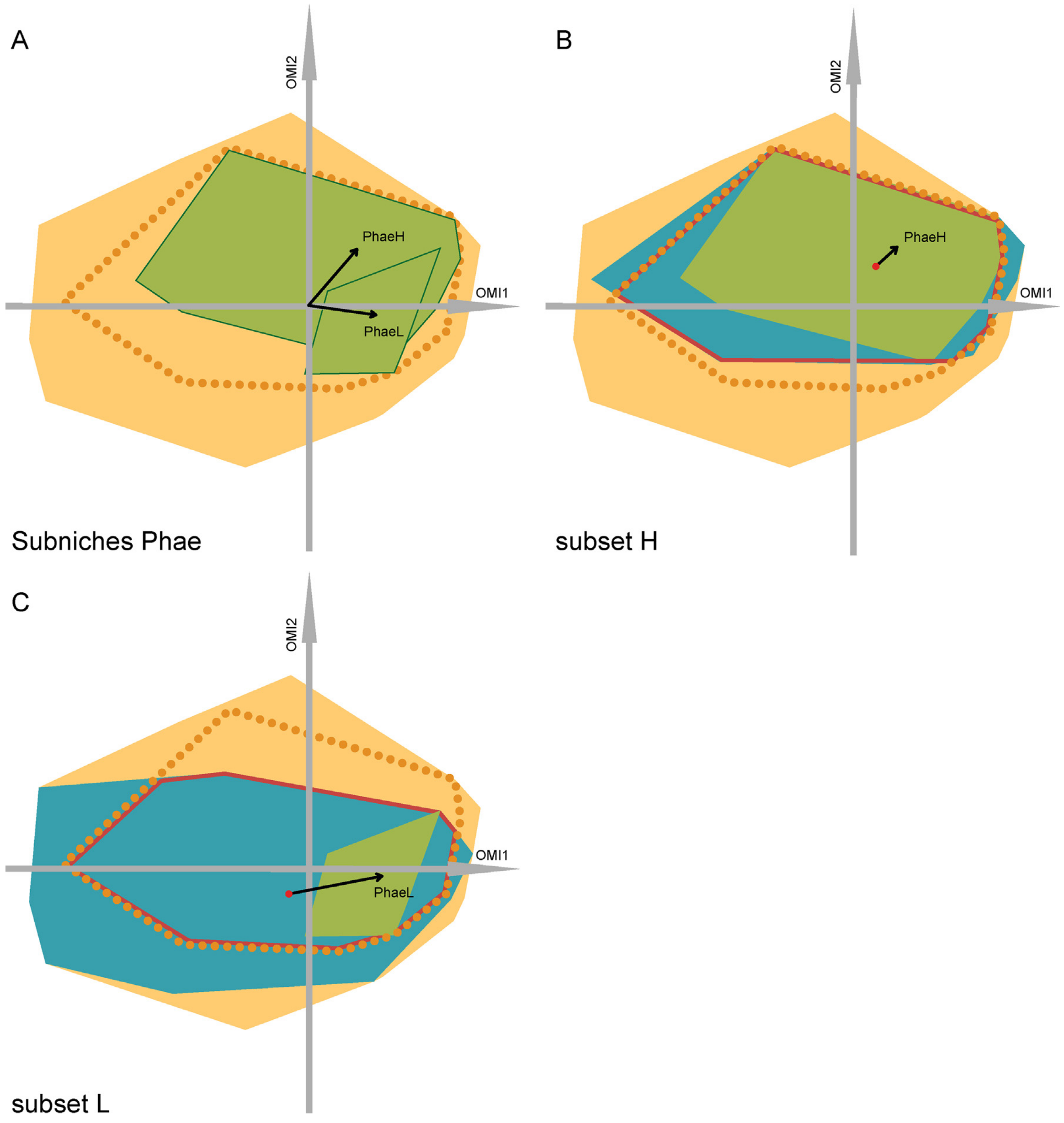

Fig. 6. *Phaeocystis* spp. subniches' dynamics. (A) The illustration of the *Phaeocystis* spp. subniches' dynamics found within the niche (the dotted orange contour). The green polygon represents *Phaeocystis* spp. subniches. The orange polygon represents the overall habitat environmental space. The labels represent the subniches' positions and the arrows represent the marginality. B and C are the graphical representations of *Phaeocystis* spp. subniches within the environmental subsets (blue polygons). The red contour represents the *Phaeocystis* spp. existing fundamental subniche. The red dots represent the mean environmental conditions found within each subset. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Hereafter, the robustness of actual hypotheses related to the *Phaeocystis* spp. niche in the literature are discussed followed by an examination of the possible biotic interaction explaining the fluctuating abundances.

4.1. Phaeocystis *spp. hypotheses*

The "silicate-*Phaeocystis* hypothesis" (Lancelot et al., 1987; Reid et al., 1990) has historically been a major explanation in the appearance of *Phaeocystis* spp. Environmental silicate concentration may determine the duration and stability of the diatom community. For instance, in both subsets, *Phaeocystis* spp. started to bloom when the silicate concentration dropped below 1.5 μmol L^{-1}. This threshold was reached later, in April, for subset L compared to March for subset H (see Fig. 4). The "silicate-*Phaeocystis* hypothesis" (Lancelot et al., 1987; Reid et al., 1990) was only partly verified since *Phaeocystis* spp. was already present in the subset H in January, but did not bloom until the silicate concentration dropped below the threshold. The lower inorganic P demand of *Phaeocystis* spp. compared to diatoms (Riegman et al., 1992) could explain the constant presence in subset H, characterized by low phosphate concentration from January to June. On the contrary, the "eutrophication hypothesis," which stipulates that *Phaeocystis* spp. abundance increases with higher N concentration,

Table 2
Subniche parameters of the 11 diatom species of interest and *Phaeocystis* spp. The marginality (WitOMI), tolerance (TOL) and mean abundance were calculated under the two subsets, L and H. The niche parameters were calculated from G and G_K. For code see Table 1. All subniches were significant ($P \leq 0.001$). – not applicable means that the species were absent in one of the two subsets, or not significant with the BV step analysis. For further details see Section 2.

Code origin	WitOMI				Tol				Mean abundance	
	G		G_K		G		G_K		(cells L^{-1})	
Data subset	L	H	L	H	L	H	L	H	L	H
Cha	–	1.34	–	0.31	–	0.56	–	1.95	–	111
Dit	–	1.93	–	0.58	–	0.45	–	1.26	–	100
Gud	0.6	1.26	0.2	0.16	0.62	1.28	2.97	1.97	295	298
Gus	1.09	2.07	1.3	0.65	1.43	0.91	2.05	1.49	226	222
Led	–	4.11	–	2.05	–	0.61	–	0.65	–	118
Nit	–	0.86	–	0.14	–	0.58	–	2.14	–	268
Par	1.48	0.63	0.52	0.16	1.73	0.45	1.68	2.85	138	284
Pss	0.83	–	0.28	–	0.6	–	1.69	–	173	–
Ske	3.17	2.88	1.71	3.85	3.83	2.14	3.86	2.45	206	126
Thn	6.61	0.77	4.36	0.63	2.17	1.19	2.22	3.03	163	197
Thg	2.02	–	0.78	–	3.83	–	4.13	–	139	–
Phae	2.64	2.11	3.24	0.59	0.59	0.64	0.67	0.46	29	237

was not validated in this study. Subset L was characterized by higher concentrations of nitrite, nitrate and ammonia than subset H, leading to a dominance of diatom species, but resulting in lower abundances of *Phaeocystis* spp. Furthermore, even though in subset L, leftover N from diatoms remained high, *Phaeocystis* did not bloom as much. *Phaeocystis* spp. might use the excess N leftover by the diatoms for growth, but this does not seem to determine the outbreaks of high abundance bloom events. The hypotheses linking *Phaeocystis* spp. appearances to N:Si (Tett et al., 1993; Tett and Walne, 1995) and N:P (Riegman et al., 1992) better at predicted the HAB timing. The maximum in N:Si or N:P corresponded to the start of *Phaeocystis* spp. bloom in both habitat subset conditions.

According to Borkman et al. (2016), higher salinity characterized the year of high *P. pouchetii* abundance and could also explain the years of high *Phaeocystis* spp. abundance. The higher salinity also reflected a lower precipitation flow rate from rivers and wind turbulence which can also take part in the turbidity level. Subset H was characterized by higher salinity and lower turbidity than subset L. Photosynthetically active radiation and temperature exhibited similar variations throughout the season. Temperature did not seem to impact *Phaeocystis* spp. appearance, because in subset H, *Phaeocystis* spp. was present in January, the coldest month (6.5 °C). The higher turbidity level in subset L suggested that the real amount of photosynthetically active radiation reaching the community was less than in subset H. Despite these conditions, *Phaeocystis* spp. still appeared under low PAR. This contradicts the hypothesis suggesting that *Phaeocystis* spp. dominates over diatoms when conditions resemble early summer along the Dutch coast (Peperzak, 1993).

4.2. Biotic interactions

The unused available conditions in the *Phaeocystis* spp. existing fundamental subniche is considered as the subset biotic reducing

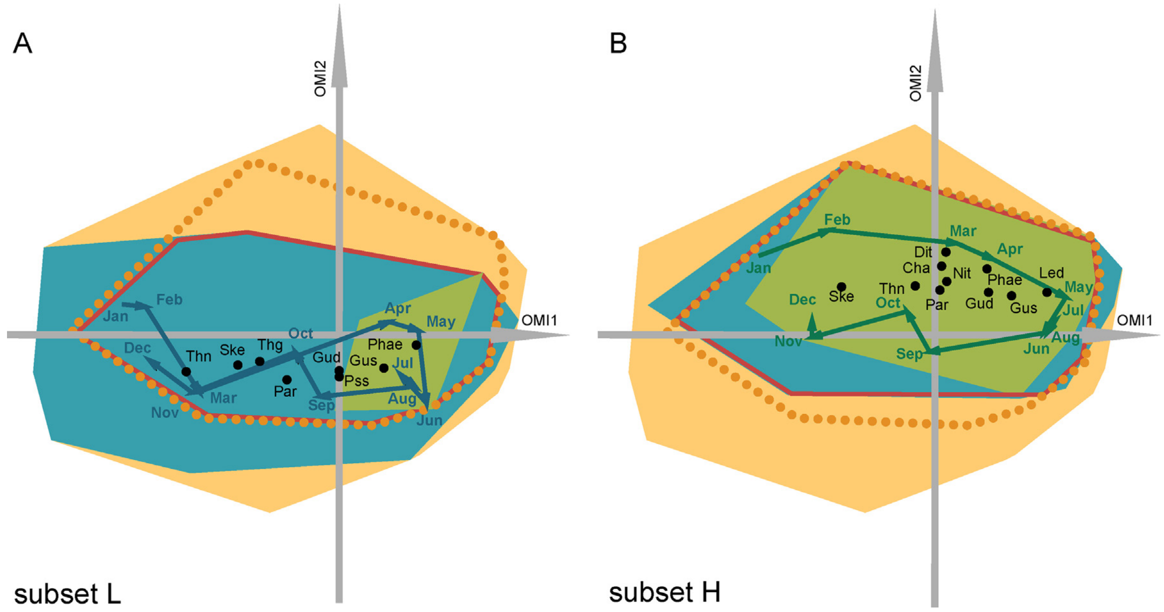

Fig. 7. *Phaeocystis* spp. subniches within the two subsets L and H. The green polygon represents the *Phaeocystis* spp. subniche. The orange polygon represents the habitat conditions space. The dotted orange contour represents the *Phaeocystis* spp. realized niche. The red contour represents the *Phaeocystis* spp. existing fundamental subniche. The labels represent the subniches' positions of the relevant species resulting from the BV-step analysis. The arrows represent the trajectory taken by the habitat conditions from January to December under their respective subsets. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

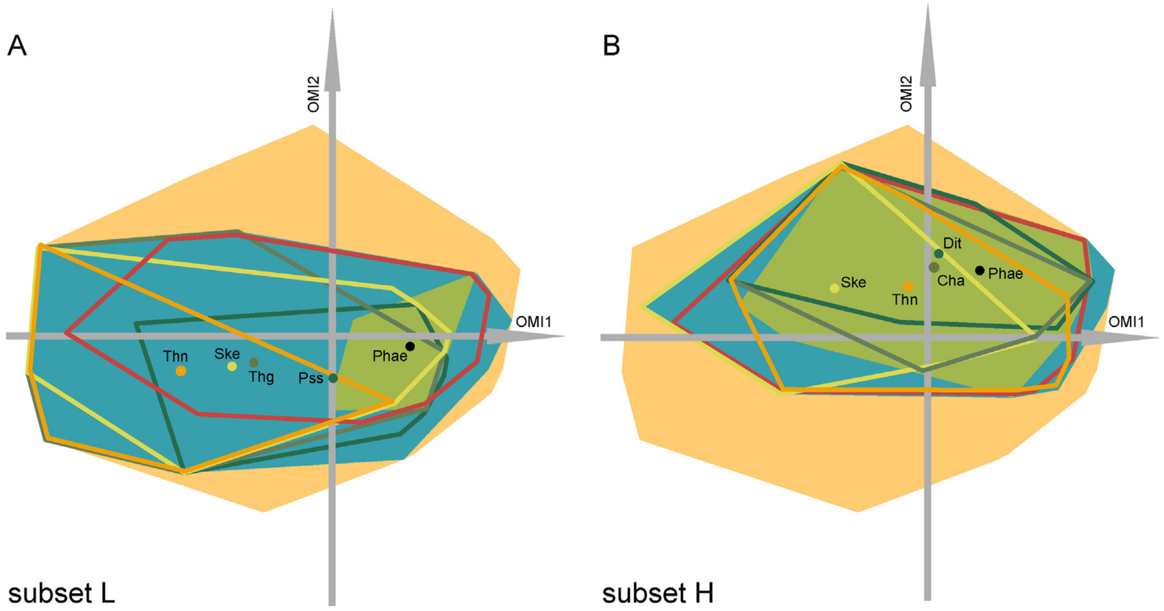

Fig. 8. *Phaeocystis* spp. and possible competitors' subniches within the two subsets L and H. The orange polygon represents the habitat conditions space. The blue polygon represents the subset habitat conditions space. The green polygon represents the *Phaeocystis* spp. subniche. The red contour represents the *Phaeocystis* spp. existing fundamental subniche. The colored dots and the corresponding polygon represent the subniche position and breadth respectively. Not all relevant species of each subset were represented for the sake of clarity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

factor. Infection by viruses can also cause the biological constraint. Experimental results showed that *P. pouchetii* cell mortality rates by virus infection can reach 0.8 d^{-1} (Brussaard et al., 2005) but viruses do not infect healthy colonies (Bratbak et al., 1998).

Predation is a possible biological interaction that can affect *Phaeocystis* spp. forms. The high plasticity of *Phaeocystis* spp. capacity to change life forms, single-cells and colonies in response to grazing is well known (Nejstgaard et al., 2007). Furthermore, it can respond to different chemical cues released by different consumer species (Wang et al., 2015). For instance, *Phaeocystis* spp. is capable of switching from single-cells to colonies when grazed by ciliates (Long et al., 2007). Oppositely, when confronted by grazing copepods, *Phaeocystis* spp. can significantly decrease its colony numbers by 60–90% (Long et al., 2007). Grazer abundances and diversity with different *Phaeocystis* spp. life forms should be considered in future studies, as they can directly impact HABs. The information on the different life-forms of *Phaeocystis* spp. and potential consumers were not available in the used dataset.

Another appropriate biological constraint in this study appeared to be competition, as the diatom community directly competes for resources with *Phaeocystis* spp. From late-winter to summer, the succession in blooms of the diatoms and their appearance depends on their preferences regarding environmental habitat conditions, further driving *Phaeocystis* spp. appearances and blooms. For instance, *Skeletonema* spp., *T. nitzschioides*, and *T. gravida* are known to be bloom forming species (Pratt, 1959; Smayda, 1958). They are considered as winter diatoms, according to their respective niche positions with preference for high nutrient concentrations and turbidity in association with low temperature, PAR and salinity. Their leading appearance, bloom magnitude and persistence determined the composition of the following community. The growth of *Skeletonema* spp. is known to be 25% faster when on sustained ammonia than on nitrate (Suksomjit et al., 2009; Tada et al., 2009). In addition, *T. nitzschioides* has also been shown to grow faster in ammonia and nitrate enriched conditions (Mochemadkar et al., 2013). In subset L, the high concentration of ammonia could have potentially helped *Skeletonema* spp., *T. nitzschioides* and *T. gravida*, which are pioneers, to grow faster and bloom, establishing their dominance in the community (Suksomjit et al., 2009; Tada et al., 2009) (Fig. 5B). Furthermore, the *P. seriata* complex occurrence is also known to be nitrogen-limited, and more than capable of using ammonia (Fehling et al., 2006). The growth of *Phaeocystis* spp. is faster on ammonia than on nitrate (Tungaraza et al., 2003), but seemed to be out-competed by the diatoms in these environmental habitat conditions. Other factors, such as silicate and phosphate were not limiting and favored the diatoms. The establishment of the diatom species, with a preference for ammonia, possibly out-competed *Phaeocystis* spp., until the concentration of silicate became limiting, succeeded by the *Phaeocystis* spp. bloom.

In subset H, *Phaeocystis* spp. managed to flourish despite the presence of the five same species (*Skeletonema* spp., *T. nitzschioides*, *Paralia sulcata*, *Guinardia delicatula* and *Guinardia striata*) and four other species (*Chaetoceros danicus*, *Ditylum brightwellii*, *Nitzschia longissima* and *Leptocylindrus danicus*). The lower concentration of phosphate favored *Phaeocystis* spp.'s presence over diatoms likely through *Phaeocystis* spp.'s capacity to store phosphate within its colony matrix (Schoemann et al., 2001; Veldhuis et al., 1991) coupled with its lower P demand (Riegman et al., 1992). Moreover, the strong competitive ability of *Phaeocystis* spp. to obtain nitrogen (Riegman, 1995), along with lower concentration of silicate, inhibited the diatom community from blooming as much as in subset L. Silicate limitation is thought to have resulted in an increase in magnitude and continuity *Phaeocystis* spp. blooms (Cadée and Hegeman, 1986; Lancelot, 1990; Lancelot et al., 1987). The silicate limitation dually selected diatom species which are less silicified, such as *Leptocylindrus danicus*, *Chaetoceros danicus* and *Nitzschia longissima* (Hasle et al., 1996). Furthermore, the N-source dependency of diatom silicate competitiveness, which determines the dominant species of the community (Ruth, 2012), reinforced the idea that *Skeletonema* spp., *T. nitzschioides*, *T. gravida* and *P. seriata* complex are decisive species for *Phaeocystis* spp. blooms.

The readjustment of nutrient concentrations rendered more than one resource limiting for the diatoms, resulting in a biodiversity increase (Hillebrand et al., 2014), as shown with the BV-step analysis (7–11 species from subset L to H). The niche expansion of *Phaeocystis* spp. (Tol: 0.59 and 0.64 for subset L and H respectively) can be partly explained by a relaxation in biological constraints (Table 2). The possible decrease in diatom competitive abilities resulted in the 25% of unused available environmental habitat conditions of the *Phaeocystis* spp. existing fundamental subniche.

4.3. Further perspectives

Further investigations on diatom competitive abilities can be done experimentally (Ruth, 2012), and with the trait-based approach (Litchman and Klausmeier, 2008). The major components of the trait-based approach are the species' traits, environmental gradients, species' interactions and performance currency, which determines the species' niche within the community (McGill et al., 2006). In this study, the niche and subniche dynamics within the overall environmental habitat and subset environmental habitat conditions were studied for the entire community. Furthermore, the quantification of the biological constraints exerted on *Phaeocystis* spp.'s subniches was made possible. The direct relationships between traits and the species' response to environmental conditions (Lavorel and Garnier, 2002) can give us clues on the mechanisms driving community composition. In parallel, the patterns of functional-trait distribution (Bello, 2009; Weiher et al., 1998) can help explain how the community functional-traits controls the following *Phaeocystis* spp. bloom. Some methods, which link niche analysis and trait-based approaches already exist. The OMI-GAM analysis (Kleyer et al., 2012) determines species' responses to environmental conditions using the OMI analysis (Dolédec et al., 2000), and additionally could explain these responses using generalized additive models (GAM) with the traits as explanatory variables (Kleyer et al., 2012). Such analyses can help solve the *Phaeocystis* spp. riddle and other HAB related issues. In future studies, more precise ecological dynamics models could be built as the diatoms can be split into different functional groups. Models, such as the MIRO model (Lancelot et al., 2014), which also studies the spring-diatom-*Phaeocystis* bloom, considers diatoms as a large pool responding homogeneously to nutrient concentrations and/or ratios. As shown in this study, the mechanism driving the bloom of *Phaeocystis* spp. is multifactorial, suggesting a greater consideration of diatom diversity, including their respective traits and competitive abilities. Trait-based understanding of plankton distribution started with the paradox of the plankton (Hutchinson, 1961). Margalef was the first to understand the balance between the physical and nutritional forces relating to different life forms of phytoplankton with the classical "mandala" (Margalef, 1978; Margalef et al., 1979). Since then, the concept of the "mandala" has found its way into predicting HABs (Smayda and Reynolds, 2001) and nowadays incorporates 12 dimensions (Glibert, 2016). Herein, the environmental trajectory can help predict the high abundance events of *Phaeocystis* spp. in future "mandala" like models, by using the WitOMI calculations.

5. Conclusion

The appearance of *Phaeocystis* spp. depends on multiple environmental factors, and moreover, on the preceding diatom community, which first appear in late winter. Within both habitat subsets, *Phaeocystis* spp. could have potentially realized a large subniche. The reduction and/or expansion of its subniche mostly depended on the winter environmental conditions and on the biological constraints. The competitive ability of diatoms appearing in late-winter are suspected to take part in the biological constraint of the *Phaeocystis* spp. subniche. The establishment of the leading species in the bloom succession, here *Skeletonema* spp., *Thalassionema nitzschioides* and *Thalassiosira gravida* seemed to be driven by nutrient concentration. Under non-limiting P environmental conditions, competition among diatoms for silicate will be N-source dependent. The high concentration of ammonia allowed a rapid growth and bloom of the later-winter diatoms (*i.e.*, *Skeletonema* spp.) (Fig. 3E), while Si limited their bloom magnitude. The effect of winter conditions on the *Phaeocystis* spp. bloom requires further investigation. The trait-based approach in relation with the community response to changing environmental conditions could be a promising field for studying the future of Harmful Algae Bloom.

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Package ‘subniche’

July 7, 2017

Title Within Outlying Mean Indexes: Refining the OMI Analysis

Version 0.9.7

Date 2017-07-07

Author Stephane Karasiewicz

Maintainer Stephane Karasiewicz `<stephane.karasiewicz@wanadoo.fr>`

Description Complementary indexes calculation to the Outlying Mean Index analysis to explore niche shift of a community and biological constraint within an Euclidean space, with graphical displays.

Suggests ade4TkGUI, adegraphics, ape, CircStats, deldir, lattice, maptools, MASS, pixmap, spdep, splancs, waveslim

Depends ade4

License GPL (>= 2)

RoxygenNote 6.0.1

NeedsCompilation no

LazyData true

Repository CRAN

Date/Publication 2017-07-07 10:16:59 UTC

R topics documented:

`ardecheinv` *Temporal data*

Description

The `ardecheinv` data are the temporal example used as an ecological application of the WitOMI calculations in Karasiewicz et al. (2017).

Usage

```
data(ardecheinv)
```

Format

The `ardecheinv` is a list of 3 components.

`env` is a dataframe of 67 rows with 5 environmental tables, collected in spring and autumn.

`Invertebrates` is a dataframe of 67 rows and 57 species of invertebrates.

`code` is a dataframe with 57 rows and 2 columns, the species scientific name and their respective code.

Source

Merigoux, S. and Doledec, S. (2004). Hydraulic requirements of stream communities: A case study on invertebrates. *Freshwater Biology*, **49**(5), 600-613.

References

Karasiewicz S.,Doledec S.and Lefebvre S. (2017). Within outlying mean indexes: refining the OMI analysis for the realized niche decomposition. *PeerJ* 5:e3364. `https://doi.org/10.7717/peerj.3364`.

`drome` *Spatial data*

Description

The `drome` data are the spatial example used as an ecological application of the WitOMI calculations in Karasiewicz et al. (2017).

Usage

```
data(drome)
```

Format

The `drome` is a list of 3 components.

`env` is a dataframe with 64 rows with 6 environmental tables, collected in 10 different rivers.

`fish` is a dataframe with 64 rows and 13 columns (12 fish species, including young and older trouts).

`code` is a dataframe with 13 rows and 2 columns, the species, common and scientific, name and their respective code.

Source

Doledec S., Chessel D. and Gimaret C. (2000). Niche separation in community analysis: a new method. *Ecology*,**81**(10), 2914-1927.

References

Karasiewicz S.,Doledec S.and Lefebvre S. (2017). Within outlying mean indexes: refining the OMI analysis for the realized niche decomposition. *PeerJ* 5:e3364. `https://doi.org/10.7717/peerj.3364`.

`sep.factor.row` *A function to seperate a matrix, by row, into submatrices.*

Description

separate matrix by rows into submatrices

Usage

```
sep.factor.row (x,factor)
```

Arguments

`x`	a matrix.
`factor`	a factor of the same length as the number of row in the matrix.

Value

list of submatrices

`subniche` *The Within Outlying Mean Indexes calculation*

Description

The indexes allows to divide the niche, estimated from the niche function in the ade4 package into subniches defined by a factor, which creates the subsets. See details for more information.

Usage

```
subniche(nic, factor)

## S3 method for class 'subkrandtest'
print(x, ...)

## S3 method for class 'subnikrandtest'
print(x, ...)

## S3 method for class 'subniche'
print(x, ...)

## S3 method for class 'subniche'
plot(x, xax = 1, yax = 2, ...)

margvect(x, xax = 1, yax = 2, colo = NULL, ...)

subplot(x, xax = 1, yax = 2, colo = NULL, ...)

## S3 method for class 'subniche'
summary(object, ...)

refparam(x)

## S3 method for class 'subniche'
rtest(xtest, nrepet = 99, ...)

subparam.refor(x)

rtestrefor(x, nrepet)

subparam.subor(x)

rtestsubor(x, nrepet)

subkrandtest(sim, obs, alter = "greater", call = match.call(),
  names = colnames(sim), p.adjust.method = "none")
```

```
subnikrandtest(sim, obs, alter = "greater", subpvalue, call = match.call(),
  names = colnames(sim), p.adjust.method = "none")
```

Arguments

`nic`	an object of class `niche`.
`factor`	a factor which will defined the subsets within which the subniches will be calculated (the same length of the number of sites)
`x`	an object of class `subniche`.
`...`	further arguments passed to or from other methods
`xax`	specify the x column in your matrix
`yax`	specify the y column in your matrix
`colo`	string of character specifying the subsets color. Default color is rezd.
`object`	an object of class `subniche`.
`xtest`	an object of class `subniche`.
`nrepet`	the number of permutations for the testing procedure
`sim`	a numeric vector of simulated values
`obs`	a numeric vector of an observed value
`alter`	a character string specifying the alternative hypothesis, must be one of "greater" (default), "less" or "two-sided".he length must be equal to the length of the vector obs, values are recycled if shorter.
`call`	a call order
`names`	a vector of names for tests
`p.adjust.method`	a string indicating a method for multiple adjustment, see p.adjust.methods for possible choices.
`subpvalue`	the subset pvalue resulting from `subkrandtest` function

Details

The Within Outlying Mean Index analysis is a statistical exploratory niche analysis which provides observation of niche shift and/or conservatism, of an entire community,at different subcales (temporal ,spatial and/or finer biological organisation level), and comparable under the same environmental gradients. This hindcasting multivariate analysis is based on the OMI analysis (Doledec *et al.* 2000) which is used as reference. The niches refinement is inspired by the K-select (Calenge *et al.* 2005) which emphasizes the limiting factors in habitat use in design II and III (Thomas and Taylor, 1990).The different estimations should help understand:

1. the environmental factors defining a species' reference niche, under on the full scale, within a community.

2. the environmental factors defining a species' subniches, under each subsets, within a community.

The subniches parameters can be calculated from both the reference origin,*G*, which corresponds to the reference plan origin, and from *G_k*, which corresponds to the suborigins. *G* is the graphical representation of the mean environmental conditions encountered over the full scale of the data.

G_k is the mean environmental conditions encountered at a subset defined by the factor. They are complementary has you can compare:

1. a single species' subniches to *G*.

2. the community' subniches to *G_k* at a specific subset.

The subniches of a single species can only be compared to *G* as it is the common origin to all subsets. Whereas *G_k* is only common to the species found within the subset. So comparing different subniches of one species, found within different subsets, is only relevant to *G*. The community's subniches can be compared to both *G* and *G_k*, but *G*, being the mean environmental conditions found within the full scale, will not express the specificity of the environmental conditions that the species encountered at the subset. *G_k*, being the mean environmental conditions of the subset, will reflect the atypical value of the environmental condition, making the comparison of the community's subniches parameters more relevant. More information on the ecological concept can be found in Karasiewicz *et al.* 2017.

For more details description on the package use:`https://github.com/KarasiewiczStephane/WitOMI`.

Value

Adds items in the niche list and changing the class into `subniche` containing:

`factor` the factor use to divide the environmental and species matrix into submatrices.

`G_k` a dataframe with the sub-origins, *G_k*.

`sub` a dataframe with the species subniche coordinates

Author(s)

Stephane Karasiewicz, `<stephane.karasiewicz@wanadoo.fr>`

References

Karasiewicz S.,Doledec S.and Lefebvre S. (2017). Within outlying mean indexes: refining the OMI analysis for the realized niche decomposition. *PeerJ* 5:e3364. `https://doi.org/10.7717/peerj.3364`.

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Doledec S., Chessel D. and Gimaret C. (2000). Niche separation in community analysis: a new method. *Ecology*,**81**, 2914-1927.

Thomas, D.L., Taylor, E.J. (1990). Study Designs and Tests for Comparing Resource Use and Availability II. *Natl. Widl.* **54**(2), 322-330.

See Also

niche niche.param

Examples

```
library(subniche)
data(doubs)
dudi1 <- dudi.pca(doubs$env, scale = TRUE, scan = FALSE, nf = 3)
nic1 <- niche(dudi1, doubs$fish, scann = FALSE)
# number of sites
N <- dim(nic1$ls)[1]
#Create a factor which defines the subsets
fact <- factor(c(rep(1,N/2),rep(2,N/2)))
# nic1 will be use as reference and fact will be use to define the subniches environment
subnic1 <- subniche(nic1, fact)
# the following two functions do the same display, plot.refniche is adapted to subniche objects
plot(nic1)
plot(subnic1)
#Display the marginality vector of the suborigins and the species subniche
margvect(subnic1)
#Display the subset's polygon, found within the overall environment's chull,
#and the corresponding species positions
subplot(subnic1)
# The following two functions do the same display, refparam is adapted to subniche objects
niche.param(nic1)
refparam(subnic1)
# The following two functions do the same display, rtest is adapted to subniche objects
rtest(nic1,10)
rtest(subnic1,10)
#Calculates the subniches' parameters from G with the corresponding rtest
subparam.refor(subnic1)
rtestrefor(subnic1,10)
#Calculates the subniches' parameters from G_k with the corresponding rtest
subparam.subor(subnic1)
rtestsubor(subnic1,10)
```

Index