Impact des changements environnementaux sur le phytoplancton : intégration des approches par niche écologique et traits fonctionnels à l'étude des communautés phytoplanctoniques en Baie de Seine

Angeline Lefran

▶ To cite this version:

Angeline Lefran. Impact des changements environnementaux sur le phytoplancton : intégration des approches par niche écologique et traits fonctionnels à l'étude des communautés phytoplanctoniques en Baie de Seine. Biologie végétale. Normandie Université, 2022. Français. NNT : 2022NORMC218 . tel-03827509

HAL Id: tel-03827509

https://tel.archives-ouvertes.fr/tel-03827509

Submitted on 24 Oct 2022

THÈSE

Pour obtenir le diplôme de doctorat

Spécialité PHYSIOLOGIE ET BIOLOGIE DES ORGANISMES - POPULATIONS - INTERACTIONS

Préparée au sein de l'Université de Caen Normandie

Impact des changements environnementaux sur le phytoplancton: intégration des approches par niche écologique et traits fonctionnels à l'étude des communautés phytoplanctoniques en Baie de Seine.

Présentée et soutenue par
ANGELINE LEFRAN

Thèse soutenue le 10/05/2022 devant le jury composé de		
MME VÉRONIQUE CRÉACH	Chercheur, Fisheries & Aquaculture Science	Rapporteur du jury
M. PHILIPPE PONDAVEN	Maître de conférences HDR, Université de Bretagne Occidentale	Rapporteur du jury
M. ERIC GOBERVILLE	Maître de conférences, Sorbonne Université	Membre du jury
MME TANIA HERNANDEZ-FARINAS	Chercheur, IFREMER	Membre du jury
M. RAFFAELE SIANO	Directeur de recherche, IFREMER de PLOUZANE	Membre du jury
MME HELENE HEGARET	Directeur de recherche au CNRS, Université de Bretagne Occidentale	Président du jury
M. PASCAL CLAQUIN	Professeur des universités, Université de Caen Normandie	Directeur de thèse
MME MARIE-PIERRE LEMEILLE	Maître de conférences HDR, Université de Caen Normandie	Co-directeur de thèse

Thèse dirigée par PASCAL CLAQUIN (Biologie des organismes et ecosystèmes aquatiques (Caen)) et MARIE-PIERRE LEMEILLE (Université de Caen Normandie)

UNIVERSITÉ
CAEN
NORMANDIE

497
NBISE
Normande de Biologie Intégrative, Santé, Environnement

BOREA
Biologie des organismes et écosystèmes aquatiques

Préambule

Ce doctorat a bénéficié d'un double financement ; provenant du projet européen Interreg S3-EUROHAB (2018-2022, `https://www.s3eurohab.eu/`) ainsi que de l'Institut Français de Recherche pour l'Exploitation de la Mer (IFREMER). Le projet s'articule autour de 3 objectifs : (i) créer un réseau de surveillance et un portail de données transfrontaliers afin d'évaluer le bon état écologique des eaux franco-anglaises communes de la Manche, (ii) produire un système d'alerte en ligne pour détecter la qualité de l'eau et les HABs en utilisant les données de l'agence spatiale Européenne et des satellites Copernicus les plus récents. (iii) mener une analyse socio-économique des impacts causés par les HAB dans la Manche.

Ce doctorat s'est entièrement déroulé à la station IFREMER de Port-en-Bessin, au sein du laboratoire environnement ressource de Normandie (IFREMER, Unité LITTORAL, LER/N). Il est rattaché à l'école doctorale de l'EDnBISE : Biologie Intégrative, Santé, Environnement (ED 497), de l'université de Caen. Les travaux furent encadrés par un chercheur du laboratoire de Biologie des Organismes et des Écosystèmes Aquatiques (BOREA)[1], ainsi que à des chercheurs des laboratoires DYNECO-PELAGOS (Brest) et LERN (Port-en-Bessin) de l'IFREMER.

---

[1] affilié au Muséum National d'Histoire Naturelle (MHNN), au Centre National de la Recherche Scientifique (CNRS 8067), à l'Université de Caen Normandie (UCN), à Sorbonne Université (SU), à l'Institut de Recherche pour le Développement (IRD-207) et à l'Université des Antilles (UA)

Affiliation des principaux collaborateurs cités dans les différents chapitres.

Angéline Lefran	• Unité Littoral Ifremer, LITTORAL, F-14520, Port-en-Bessin, France • Normandie Universités, Université de Caen Normandie, Caen, France
Anouska Panton	• School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, UK SO14 3ZH
Duncan Purdie	• School of Ocean and Earth Science, University of Southampton, National Oceanography Centre, European Way, Southampton, UK SO14 3ZH
Francis Gohin	• IFREMER, Département Dynamiques de l'Environnement Côtier, DYNECO/PELAGOS, Ifremer Brest, BP 70, 29280, Plouzané Brittany, France
Léon Serre-Fredj	• Normandie Universités, Université de Caen Normandie, Centre de Recherches en Environnement Côtier (CREC) - Station Marine, BP49, 54, rue du Docteur Charcot - 14530 Luc-sur-Mer, France
Nicolas Elie	• Normandie Université, UNICAEN, US EMERODE, CMABIO3, 14000 Caen, France.
Pascal Claquin	• Normandie Universités, Université de Caen Normandie, Centre de Recherches en Environnement Côtier (CREC) - Station Marine, BP49, 54, rue du Docteur Charcot - 14530 Luc-sur-Mer, France • Unité Biologie des ORganismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Sorbonne Universités, Muséum National d'Histoire Naturelle, CNRS, Université Pierre et Marie Curie, Université de Caen Normandie, IRD 207, Université des Antilles, Esplanade de la paix, F-14032, Caen, France
Stéphane Karasiewicz	• Unité Littoral Ifremer, LITTORAL, F-62200, Boulogne-sur-mer, France
Tania Hernández Fariñas	• Unité Littoral Ifremer, LITTORAL, F-14520, Port-en-Bessin, France

Remerciements

Vivre un doctorat ne figure pas dans les expériences que l'on renouvelle de multiple fois. C'est une suite d'épreuves, d'obstacles, de doutes, de challenges où l'on va toujours plus loin, on se surpasse, on se surprend aussi. Bref, ce sont un peu nos Jeux Olympiques à nous, étudiants universitaires. Et comme tout sport, c'est aussi le fruit d'un travail d'équipe où chacun joue un rôle de support, qu'il soit scientifique, technique ou moral. Je vais donc m'arrêter sur les membres de cette équipe qui ont fait de moi une doctorante accomplie et qui ont fait de ce travail ce qu'il est, tel qu'il est écrit dans les pages qui vont suivre.

Tout d'abord, je ne peux que commencer par remercier mes directeurs, directrice et encadrante de thèse. Merci Tania, pour ce sujet, pour ce que tu m'as laissé en faire, pour ta confiance et ton investissement dans chaque réflexion et chaque relecture que nous avons eu, et ce, malgré les haut et les bas. Merci Pascal, pour ta disponibilité, bien que l'agenda de ministre t'ait contraint de nombreuses fois, le résultat arrive toujours, avec toi le travail s'enrichit à chaque rencontre. Je m'excuse aussi pour mes envolées lyriques, la poésie que tu trouvais sans doute un peu "perchée" et que n'ai pas su me retenir d'écrire par-ci par-là.. Puis, je remercie Francis, pour ta direction les premières années, tes conseils et ta bonne humeur à chaque réunion. Puis un grand merci également à Marie-Pierre, tu as fait preuve d'écoute et d'investissement dans ce projet, tu as été un soutien moral de nombreuses fois, toujours quand j'en avais le plus besoin. Merci beaucoup !

Mes remerciements vont ensuite à l'équipe qui m'a entouré durant ces trois années et demi. Chacun des membres du labo a sa place dans ces travaux, Lotfi, Laure, Charlotte, Gaëlle, Benjamin, Franck, Frank, Florence, Bruno et Wilfried. Je remercie particulièrement Sylvaine, notre experte, motivée par chaque opportunité qui se présente, tu m'as beaucoup inspiré ces dernières années. Je remercie Camille, qui fut ma première stagiaire et qui a su apporter son aide précieuse durant cette expérience dans des conditions plus que particulières. Et je n'oublierai pas Julien, je te remercie du fond du coeur pour toutes les casquettes que tu as endossé. Tu as relu, revu, corrigé, dessiné, supporté et tu m'as surtout écouté et soutenu quand j'en avais besoin, tu es les épaules sur lesquelles je pouvais compter !

Ce travail n'aurait pas non plus été le même sans les RH, là-bas loin dans leur couloir. Je remercie tout particulièrement Jérôme, le premier à m'avoir ouvert les portes de sa maison pour une soirée détente et dont le départ brutal fut difficile pour moi comme pour chacun qui le connaissait. Merci aux filles ; Fanchon, Morgane, Carine et Camille (et Paddy) pour nos rencontres en dehors des heures et tous ces moments de détente ainsi que du soutien que vous m'avez apporté jusqu'au bout ! Les halieut' c'est aussi la bande de Laurent, désormais capitaine de navire, merci à toi d'avoir partagé ta science quand il me manquait un bout de connaissance et pour ta gentillesse infaillible, celle qui te caractérise et qui rassemble à des endroits et des heures improbables.

Merci à tous ceux qui sont là, au quotidien ou presque, ceux qui font l'environnement de travail et qui donnent le sourire le temps d'une pause thé/café (bière) si importante ; Andréa, Floriant, Erwann (et tes leçons de R sur mes jeux de données qui m'ont bien servi ;), Lorenzo, Clara, Clémentine, Anna.s, Valentine.s, Manon et Hippolyte. Je pense également à Léon, qui m'a grandement épaulé au CREC, merci pour ta patience et ta bienveillance. Et merci à ceux que j'oublie certainement. Puissiez-vous tous vous retrouvez dans le *Protoperidinium* sp. sacré !

J'adresse également mes remerciements aux membres du comité de suivi de thèse ; Nathalie Simon, Olivier Gauthier, Pauline Billard, Christelle Monteil. Je remercie fortement les membres du jury d'avoir accepté d'évaluer et de discuter ces travaux ; Philippe Pondaven et Véronique Créach ainsi que Hélène Hégaret, Raffaele Siano et Eric Goberville. De même, je remercie Gavin Tilstone d'avoir accepté d'être membre invité de ce jury.

Et enfin, merci à toi Thibault. Bientôt 6 ans que tu partages ma vie, et chaque jour tu me prouves que tout es possible. Si ces dernières années ont été intenses, elles nous montrent qu'ensemble nous pouvons tout affronter. Je suis tellement reconnaissante que nous ayons pu vivre nos thèses séparés par un simple couloir. Tu as ainsi été témoin des coulisses de cette expérience et, comme toujours, tu as su me soutenir, m'épauler et me guider de nombreuses fois dans mes choix. Ces dernières semaines ont été difficiles mais grâce à toi, ton calme, tes bouts de script et tes multiples talents, tu as tout rendu possible quand le temps m'oppressait. Tu es ma boussole, mon cap et j'ai hâte de découvrir l'avenir à tes côtés.

Pour finir, c'est avec grand plaisir que j'offre ce travail à tous les lecteurs, amateurs de science, de phytoplancton ou pas. Bonne lecture !

Table des matières

Liste des figures

Liste des tableaux

Table des abréviations

ASP	Amnesic Shellfish Poisoning
Chl-*a*	Chlorophyll-a
CoIA	Co-Inertia Analysis
COSTATIS	Co-inertia and organisation of three way tables in statistics
CTA	Community Trajectory Analysis
CTD	Conductivity Temperature Depth
DA, dDA, pDA	Domoic Acid, Disolved DA, particulate DA
DCE	Directive Cadre sur l'Eau
DCSMM	Directive Cadre Stratégie en Milieu Marin
DSP	Diarrhetic Shellfish Poisoning
DM	Dry Matter (of bivalves' tissues)
EG	Ecological Groups
ETR	Electron Transport Rate
FG	Functional Groups
FLC	Fluorescence Light Curve
GIEC	Groupe d'experts Intergouvernemental sur l'Evolution du Climat
GPA	General Procruste Analysis
HABs	Harmful Algal Blooms
HCPC	Hierarchical Clustering on Principal Components
HPLC	High Performance Liquid Chromatography
MCA,ACM	Multiple Correspondence Analysis
MLD	Mixed Layer Depth
NAO	Northern Atlantic Oscillation
NPP	Net Primary Production
OMI	Outlying Mean Index
PAM	Pulse Amplitude Modulated
PCA,ACP	Principal Component Analysis
PCR,qPCR	Polymerase Chain Reaction, quantitative PCR
PSP	Paralytic Shellfish Poisoning
REMI	REseau de contrôle MIcrobiologique
REPHY	Réseau d'Observation et de Surveillance du Phytoplancton et de l'Hydrologie dans les eaux littorales
REPHYTOX	Réseau de surveillance des phycotoxines dans les organismes marins
RHLN	Réseau Hydrologique Littoral Normand
ROCCH	Réseau d'Observation de la Contamination CHimique du littoral
S/V	Surface/Volume
TEP	Transparent Exoploymer Particles
WitOMI	Within OMI

Peinture acrylique réalisée par Julien Normand (2020)
à l'occasion de "Ma thèse en 180s".
Un grand merci !

" Looking at phytoplankton is like looking at the stars,
trying to guess the names of the constellations. "
A.L.

1

Introduction générale

1.1 Écosystèmes marins et phytoplancton, contexte et enjeux

1.1.1 Un environnement changeant à plusieurs échelles

Au cours des temps géologiques, des évènements climatiques divers se sont succédés, avec des augmentations et des baisses de température parfois abruptes, dont les derniers remontent à plusieurs dizaines de milliers d'années (Clement & Peterson, 2008). C'est pourtant bien récemment que la communauté scientifique a mis en avant des changements environnementaux à l'échelle planétaire. Ces derniers affectent les écosystèmes au travers de l'augmentation de la température (induisant entre autre stratification des masses d'eau et fonte des glaciers), de l'acidification des océans et de l'augmentation d'évènements extrêmes (vagues de chaleur, intempéries, crues, inondations, sécheresses, incendies parmi tant d'autres) (Décamps, 2007; Gruber, 2011). Ces événements représentent des co-stresseurs pour l'environnement, ce dernier étant déjà fragilisé directement par les activités anthropiques ; exploitation du milieu et de ses ressources (Swann et al., 2015; Gomes et al., 2019; Washburn et al., 2019; Yan et al., 2021), fragmentation de l'habitat (Püttker et al., 2020), eutrophisation (rejets excessifs de nutriments, de Raús Maúre et al. (2021)) et pollutions diverses (pesticides, métaux lourds, etc..., Van Ael et al. (2012)). Tout ceci est observable en de nombreux points du globe et fait l'objet d'une plus en plus grande préoccupation. Le GIEC (Groupe d'Experts Intergouvernemental sur l'Evolution du Climat) publiait, début 2021, un rapport illustrant les éléments scientifiques aujourd'hui à l'appui dans l'argumentaire autour de l'urgence climatique (Masson-Delmotte et al., 2021). S'il ne fait plus de doute que l'activité humaine depuis 1850 explique les changements environnementaux observés à l'échelle globale, ce rapport indique que, face aux augmentations généralisées des concentrations des gaz à effet de serre (dioxyde de carbone ; CO_2, méthane ; CH_4 et protoxyde d'azote ; N_2O), l'atténuation par les terres et les océans n'a elle pas bougé en six décennies (elle reste à hauteur de 56% par an, moyennant quelques variations régionales). Pourtant, cet emballement qui semble si récent ne l'est pas tant, le GIEC a été formé à la fin des années 80, amenant à un premier rapport en 1990 puis à la COP1 en Allemagne en 1995. Le terme "Global Warming", quant à lui, date de deux générations, Broecker (1975) prévenait alors que le *refroidissement* connu vers 1940 touchait à sa fin et que les émissions de dioxyde de carbone entraîneraient une augmentation de la température sans précédent à l'échelle du dernier millénaire. L'enjeu, aujourd'hui, réside dans la compréhension des effets de ces changements sur les individus, les populations et les écosystèmes aux échelles locales, régionales et mondiales.

Le milieu marin couvre plus de 70% de la surface terrestre et abrite une grande diversité d'écosystèmes (estuaires, mangroves, herbiers, récifs et tant d'autres). C'est un milieu en trois dimensions dont la riche biodiversité est encore sous-estimée et difficile à évaluer (on ne connaîtrait que 40 +/-30% des espèces marines selon Luypaert et al. (2020)). Il s'agit également d'un environnement au coeur des préoccupations au regard de ses rôles centraux dans la régulation du climat (Watson et al., 2020) mais également de ses fonctions et services qui sont grandement menacés par la perte de la biodiversité marine (Luypaert et al., 2020). En effet, le milieu marin est grandement influencé par les évènements climatiques qui affectent son hydrodynamisme (circulation et courants marins), son statut d'habitat, et le rôle qu'il joue dans les échanges gazeux avec l'atmosphère. En 2022, la température à la surface terrestre est prédit d'augmenter de 2.7 +/- 0.7°C d'ici la fin du siècle (considérant les réglementations en vigueur suite à l'accord de Paris (2015) ; `https://climateactiontracker.org/`). Si cela se confirme, la fréquence d'apparition des événements extrêmes augmenterait, modifiant le fonctionnement des écosystèmes (déplacements de populations marines, changements en abondances et phénologies, augmentation de la mortalité, Mills et al. (2013)). Concrètement, le 21$^{\text{ème}}$ siècle a vu naître des vagues de chaleur sans précédent amenant à des bouleversements au sein de la faune et de la flore marine ; comme ce fut le cas en 2012 sur les pêcheries d'Atlantique nord-ouest (Frölicher & Laufkötter, 2018). En 2016, la grande barrière de corail fut également victime d'un blanchiment massif de ses coraux sur 90% des zones surveillées suite à une augmentation brutale de la température (Hughes et al., 2017). De plus, l'augmentation du dioxyde de carbone (CO_2) atmosphérique se reflète désormais dans la composition océanique ; dans les zones extra-tropicales ; en 34 ans depuis 1982 l'écart hiver-été de la pression partielle en CO_2 (pCO_2) a augmenté en moyenne de 2.2 µatm (soit environ +10%, selon la latitude) par décennie (Landschützer et al., 2018). De tels changements conduisent déjà à une acidification progressive des masses d'eau impactant les organismes à tous les échelons, que ce soit les bactéries ou les organismes calcifiés jusqu'aux consommateurs primaires en changeant leur comportement et/ou la qualité de leurs proies (Feely et al., 2004; Hurd et al., 2018).

En milieu côtier, ces pressions environnementales sont d'autant plus importantes que les pressions anthropiques y sont beaucoup plus fortes (Halpern et al., 2007; He & Silliman, 2019). C'est notamment le cas avec les risques d'eutrophisation qui touchent de nombreux systèmes à l'échelle mondiale et qui nécessitent un suivi et des réglementations strictes (de Raús Maúre et al., 2021). L'eutrophisation correspond à l'apport excessif d'éléments nutritifs, notamment à base azotée ou phosphatée, pouvant entraîner un sur-enrichissement des milieux marins et aquatiques (de Raús Maúre et al., 2021). Les causes sont directement liées aux activités humaines ; les bassins versants hébergent de nombreuses zones dédiées à l'agriculture (apports d'engrais) et l'élevage intensif (rejets azotés) (Desmit et al., 2018), ainsi que des zones urbaines étant à l'origine de rejets multiples dont celui des détergents qui se retrouvent dans les fleuves avant de rejoindre le milieu marin. Ces produits furent l'objet d'une interdiction à l'échelle européenne dans les années 80, à moins qu'ils ne soient à 90% biodégradables[1] (Council Directives 73/404/EEC and 73/405/EEC, Romero et al. (2013)). Cela permit une réduction majeure des apports en phosphate et de ses effets néfastes sur le compartiment des producteurs primaires (Romero et al., 2013; Gohin et al., 2019). En effet, les conséquences de l'eutrophisation sont tout aussi nombreuses ; les marées vertes qui résultent des proliférations massives d'*Ulva* sp. (Gladyshev & Gubelit, 2019), les blooms algaux toxiques et nuisibles (HABs) y sont également plus fréquents et virulents. Ces derniers peuvent causer des épisodes d'hypoxies pouvant s'avérer fatales pour la faune alentour (Almroth-Rosell et al., 2021) voire directement libérer des toxines dans le milieu pouvant nuire à la vie marine (Hall & Frame, 2010; Lopes et al., 2018; Van Hemert et al., 2020), et atteindre l'homme

---

[1] Se dit d'une substance qui peut, sous l'action d'organismes vivants, se décomposer en éléments divers dépourvus d'effet dommageable sur le milieu naturel (selon le Journal officiel, https ://www.legifrance.gouv.fr/jorf/id/JORFTEXT000020506972)

par consommation des produits de la mer contaminés (Kouakou & Poder, 2019; Young et al., 2020). Les nombreuses réglementations nécessitent une période de mise en place et une certaine inertie existe aussi entre leur applications et les résultats visibles sur le milieu. Les effets des réglementations européennes sur le phosphate auraient ainsi permis une baisse de la biomasse des producteurs primaires (*via* chlorophylle-a), près d'une trentaine d'années après leur mise en place (Gohin et al., 2019).

Face à une perturbation majeure, un écosystème possède une certaine capacité de résilience, c'est à dire une capacité à retourner à l'état initial. Cependant, comme décrit précédemment, la multiplication des pressions issues du changement climatique s'ajoute aux pressions déjà exercées directement par les activités anthropiques amenant entre autre une baisse de la biodiversité affectant chaque échelon trophique, des organismes primaires aux top-prédateurs, dont dépend la capacité de résilience d'un écosystème (Bernhardt & Leslie, 2013). La synergie de l'acidification et d'une augmentation de la température est encore mal comprise, il est vraisemblable qu'elle permettra d'amortir certains risques et en amplifiera d'autres (Hurd et al., 2018). Néanmoins, la plupart des études préviennent que le changement climatique sera surtout catalyseur de phénomènes météorologiques et biologiques déjà connus, tels que ceux liés aux vagues de chaleur (Frölicher et al., 2018), aux précipitations extrêmes (Allan & Soden, 2008), à l'eutrophisation (Nazari-Sharabian et al., 2018), ou encore aux changements abruptes de communautés (Beaugrand et al., 2019).

1.1.2 Le phytoplancton ; rôles et réponses aux changements environnementaux

Dans un tel contexte, les organismes planctoniques ont un rôle central à jouer et comprendre leurs réponses à ces événements est essentiel afin de pouvoir prédire les changements écologiques attendus aux échelons supérieures. Tout d'abord, et traditionnellement, le plancton est divisé en deux ensembles d'organismes ; végétal (phyto-) ou animal (zoo-). Le phytoplancton se caractérise par une grande diversité d'organismes en terme de phylogénie que l'on regroupe sur des critères écologiques (organismes aquatiques qui "flottent") et sur un critère fonctionnel, la photosynthèse oxygénique. Ce compartiment est ainsi constitué d'eucaryotes unicellulaires photosynthétiques et de cyanobactéries (Belin & Soudant, 2018) (nous ne considérons pas les macroalgues pélagiques dans cette définition). Le phytoplancton constitue l'alimentation du zooplancton, lui-même constituant le pool de proies dont dépendent la majorité des chaînes trophiques marines pour se maintenir. Au delà de son rôle majeur dans les réseaux marins, le phytoplancton fait également partie intégrante des cycles biogéochimiques (exemple avec le cycle du carbone ; Figure 1.1). Effectivement, sa dégradation en fin de vie recycle la matière qui le compose soit directement à la surface, soit en retombant sous forme de neige marine sur les fonds marins, alimentant ainsi la boucle microbienne (Schlesinger & Bernhardt, 2013). De plus, via la photosynthèse, le phytoplancton transforme l'énergie lumineuse en énergie chimique qui sera transmise via le carbone organique aux niveaux trophiques supérieurs, c'est la production primaire nette (NPP). Via ce processus, le phytoplancton produit un déchet, l'O_2, dont il produit près de la moitié des molécules atmosphériques. Le phytoplancton marin contribue ainsi à plus de 45% de la NPP annuelle de la biosphère mondiale alors qu'il ne représente pas plus d'1% de la biomasse des producteurs primaires (Field et al., 1998). De manière générale, la capacité de renouvellement de la biomasse marine se fait sur quelques jours, contre une dizaine d'années pour le système terrestre, ce qui rend la NPP marine variable et dépendante de la biomasse photosynthétique disponible et des facteurs environnementaux (lumière, température, sels nutritifs) à un temps donné (Behrenfeld & Falkowski, 1997; Behrenfeld et al., 2006).

Le terme "plancton" définit clairement la particularité de ce compartiment. Il fut donné par Victor Hensen (1835-1924), d'après le grec ancien πλαγκτός, signifiant "errant" (D'Elbée, 2016). Ainsi, il s'agit d'organismes dépendants du mouvement des masses d'eau et surtout des fluctuations biotiques, abiotiques et hydrologiques de son environnement. Par conséquent, dans un contexte de changement environnemental, il est essentiel de s'interroger sur les réponses qu'auront des organismes dont dépendent les réseaux trophiques marins mais également les organismes vivants du dioxygène atmosphérique qu'ils produisent. Ainsi, des augmentations de la température vont être associées à une stratification plus intense

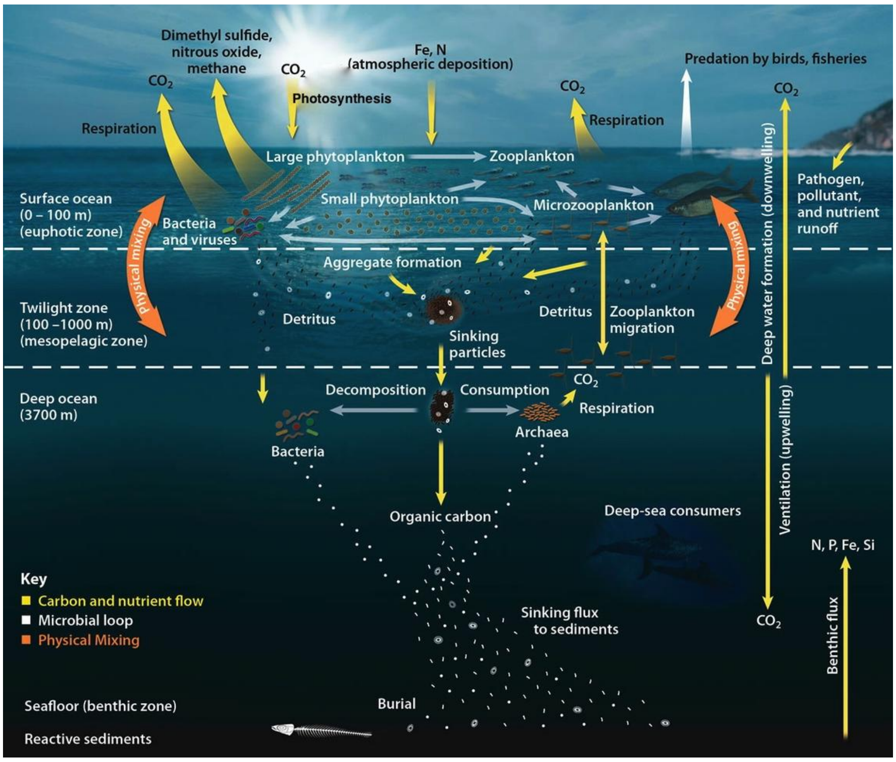


FIGURE 1.1 – Cycle du carbone dans les océans (crédit image : Oak Ridge National Laboratory.)

des masses d'eau (Hallegraeff, 2010; Yamaguchi & Suga, 2019; Gobler, 2020), ce qui entraînerait une diminution des nutriments en surface et une réorganisation de la communauté phytoplanctonique dans la colonne d'eau (Widdicombe et al., 2002). Des changements dans les intensités de précipitations et, plus largement, les apports et la disponibilité en nutriments s'ajoutent également aux pressions environnementales qui vont structurer et influencer la phénologie des organismes phytoplanctoniques ; c'est à dire la succession spécifique au sein des communautés et leur saisonnalité (Cavalcanti et al., 2018; Cibic et al., 2018). Des efforts de modélisation ont également pu projeter les restructurations significatives du phytoplancton au travers de déplacements de taxons vers les pôles, de changements de biomasses et de fonctionnalités des suites d'une acidification des océans (Dutkiewicz et al., 2015). Certaines études mettent en évidence des cas de "mismatches", c'est à dire d'incohérences temporelles entre les producteurs et les consommateurs primaires (zooplancton dont larves de poissons) causées par des modifications dans la phénologie des organismes primaires (Hallegraeff, 2010; Asch et al., 2019). Malgré tout, il est aussi important de noter qu'au regard d'un contexte temporel plus large, les valeurs de température et de teneurs atmosphériques en CO_2 mesurées ces dernières années ne sont pas supérieures à celles estimées sur des échelles géologiques ; certaines classes composant le phytoplancton du XXI$^{\text{ème}}$ siècle sont apparues à des concentrations près de 9 fois supérieures à celles actuels (cas des dinoflagellés) (Hallegraeff, 2010).

Des bouleversements au niveau de la production et des producteurs primaires ont déjà des répercussions sur la capacité des écosystèmes marins à fournir durablement des services à l'homme. Notamment, les pêcheries seront affectées alors qu'elles sont d'ores et déjà affaiblies par l'exploitation d'un environnement sujet aux pollutions et aux dégradations et dont les populations d'intérêt commercial ne se renouvellent plus assez vite (Sumaila et al., 2011). En parallèle, la qualité de l'eau fait l'objet de suivis dans le cadre de la Directive Cadre sur l'Eau (DCE) et de la Directive Cadre Stratégie en Milieu Marin (DCSMM), notamment face aux risques sanitaires relatifs aux proliférations alguales (HABs : Harmful Algal Blooms) (Fleming et al., 2006; Lassus et al., 2016; Anderson et al., 2017). Il est donc important de comprendre le rôle des facteurs biotiques et abiotiques qui vont influencer ce premier maillon de la chaîne trophique marine. Cela permettrait d'appréhender les répercussions que peuvent avoir les changements environnementaux sur les écosystèmes et, par conséquent, directement ou indirectement, sur l'Homme.

1.2 Description du compartiment phytoplanctonique

Les producteurs primaires en milieu marin rassemblent principalement des organismes autotrophes chlorophylliens utilisant la photosynthèse oxygénique pour transformer la lumière en énergie chimique. Parmi les organismes photosynthétiques, il y a les macroalgues marines (organismes pluricellulaires), les phanérogames marins (zoostères, posidonies etc. formant des herbiers), le phytoplancton (microalgues et cyanobactéries planctoniques), et le microphytobenthos (microalgues et cyanobactéries benthiques).

Le phytoplancton constitue un groupe polyphylétique premièrement différencié par plusieurs classes de taille (Table 1.1), la majorité des espèces ayant une taille comprise entre 0,4 et 200 µm (Simon et al., 2009). De part son besoin en lumière pour la photosynthèse, les cellules sont localisées à proximité de la surface, dans la zone euphotique du milieu marin (entre la surface et la limite de pénétration de la lumière (1%)). En milieu côtier, la lumière nécessaire à la survie des organismes photosynthétiques atteint le substrat et y permet le développement du microphytobenthos (Cahoon, 2019). Ces derniers ont la particularité de vivre associés à un substrat sableux, rocheux, vaseux ou artificiel (Vivier et al., 2021). Le microphytobenthos pourrait contribuer à près d'un quart de la production primaire annuelle dans certains milieux côtiers mais cela reste encore sous-estimé de part le faible nombre d'études sur ce compartiment (Ask et al., 2016).

TABLE 1.1 – Classement par taille du compartiment phytoplanctonique.

Dimensions	Classe de taille
< 2µm	pico-phytoplancton
2µm -20µm	nano-phytoplancton
20µm-200µm	micro-phytoplancton
200µm-2mm	méso-phytoplancton
> 2mm	macro-phytoplankton

La diversité phylogénique du compartiment primaire (marin et terrestre) s'explique par une théorie scientifique majeure de l'histoire des organismes eucaryotes ; l'origine des plastes (chloroplastes) par endosymbiose[2]. Il s'agit de l'intégration totale (cellulaire, génétique et biochimique) il y a au moins 900Ma d'une cyanobactérie dans un hôte eucaryote[3] hétérotrophe, puis qui a évolué en un organite permettant la photosynthèse (Sibbald & Archibald, 2020). Ce processus est à la base de l'évolution ayant conduit aux groupes des végétaux aquatiques et terrestres. Néanmoins, le transfert des plastes au sein des différentes branches

---

[2] Endosymbiose ; se dit d'une symbiose dans laquelle un organisme vit au sein d'un autre organisme

[3] Eucaryote : organismes dont la ou les cellule.s possèdent un noyau contenant l'ADN, opposé de procaryote

et lignées reste difficile à expliquer, les plastes s'étant déplacés au travers de multiples endosymbioses secondaires et tertiaires au cours du temps (Figure 1.2, Sibbald & Archibald (2020)). D'un point de vue taxonomique, le phytoplancton marin constitue un groupe polyphylétique extrêmement diversifié et se retrouve au sein de 2 domaines ; les bactéries et les eucaryotes. Chez les bactéries, seules les cyanobactéries appartiennent au phytoplancton.

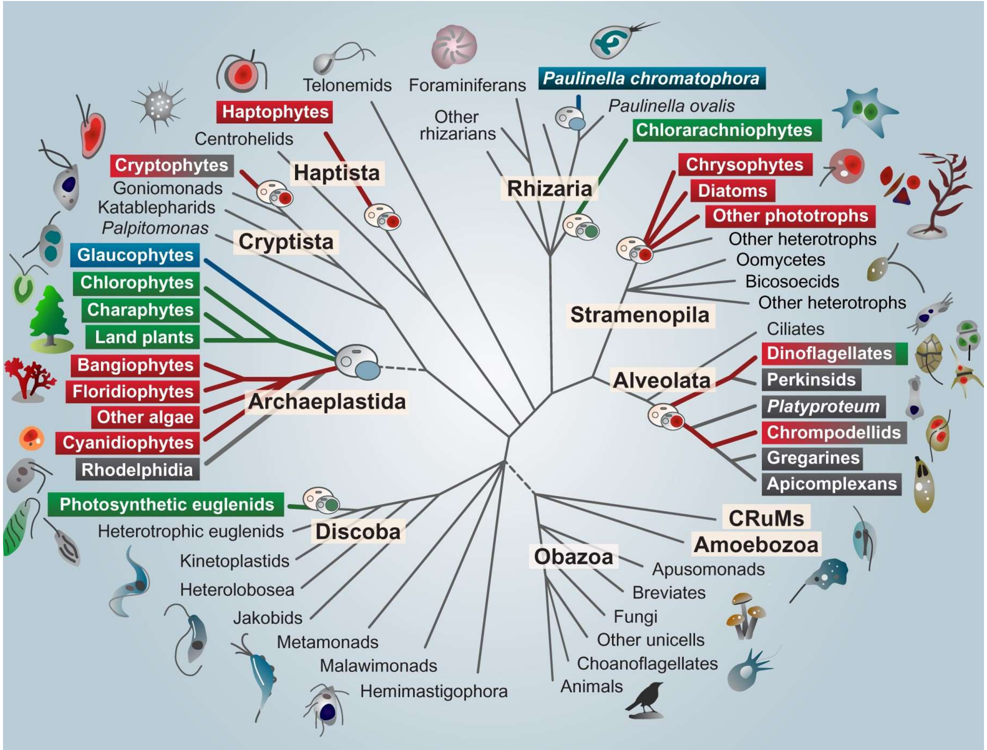


FIGURE 1.2 – Arbre schématique des lignées eucaryotes (organismes photosynthétiques colorés) (McGrath, 2020). Les membres des Archaeplastides ont des plastes primaires provenant directement de cyanobactéries. Les plastes primaires des algues rouges et vertes se sont propagés des Archaeplastides à d'autres branches de l'arbre, notamment celles des Rhizaires, Discoba et Stramenopiles. Les noms de taxons colorés dans ces lignées reflètent l'origine endosymbiotique secondaire ou tertiaire des algues vertes ou rouges de leurs plastes. Les noms de taxons surlignés en gris indiquent la présence d'un ou plusieurs membres secondairement non photosynthétiques.

Au sein du domaine des eucaryotes, les organismes phytoplanctoniques se retrouvent dans de nombreuses lignées. Cette phylogénie décrite brièvement ci-dessous est tirée de la review de Keeling & Burki (2019) et enrichie de divers apports scientifiques (Füssy & Oborník, 2018; Sibbald & Archibald, 2020).

- Les organismes possédant un "plaste primaire" à double membrane dérivant d'une endosymbiose avec les cyanobactéries sont appelés les "Archaeplastids". Ils contiennent les chlorophytes principalement représentés dans le pico- et nano- phytoplancton, mais également les macroalgues vertes (chlorophytes et charophytes) et rouges (rhodophytes). Les chlorophytes sont caractérisés par des chloroplastes contenant chlorophylle-b et chlorophylle-a ainsi que de l'amidon intraplastidial (Not et al., 2012).

- Les Haptophytes, sont une branche des Haptistes qui contiennent des taxons phytoplanctoniques aux plastes secondaires ayant pour origine une algue rhodophyte (voie dite "rouge", ex : *Phaeocystis* sp., prymnésiophycée connue pour causer des blooms nuisibles (Schoemann et al., 2005)). Certains sont capables de former des écailles de calcaire autour de la cellule (coccolithophores, ex : *Emiliania huxleyi* à l'origine des "eaux blanches" (Paasche, 2001; Tyrrell & Merico, 2004)), celles-ci sont à l'origine de dépôts de craies dans les sédiments et fossiles ; ils sont de couleurs dorées ou maronées (de part leurs pigments ; chlorophylle-a, -c et caroténoïdes, (Not et al., 2012)). Ces taxons sont caractérisés par l'haptomène, un organelle structurellement et fonctionnellement différent d'un flagelle. En effet, il peut, entre autre, être impliqué dans la fixation ou la capture de proies.

- Les Cryptista comprennent les cryptophytes, des algues reconnues pour leur plastes dérivés d'une algue rouge (voie dite "rouge") et contenant un noyau atrophié (relique de l'endosymbiose). Le complexe photosynthétique est armé de chlorophylle-a et -c_2, de xanthophylle et de phycobiliprotéines rouges ou bleues présentes dans le lumen des thylakoïdes (ex : *Rhodomonas* sp.). Les cellules ont des formes asymétriques et possèdent une invagination bordée d'éjectosomes (organites qui éjectent des contenus de la cellule) sensibles aux stress physiques et chimiques.

- Les chloroachniophytes et les eugléniales, appartiennent respectivement aux Rhizaria et Excavata, leurs plastes dérivent d'une chlorophyte (voie dite "verte"). Les Rhizaria sont principalement des protistes amibes, avec des pseudopodes utilisés pour l'alimentation. Excavata est un phylum controversé pour des raisons de phylogénie moléculaire. Il est majoritairement représenté en eau douce et possède un réservoir à carbohydrates dans lequel s'insère un flagelle (Not et al., 2012). Il est séparé en deux groupes, les Discobas, qui contiennent entre autre des euglenides photosynthétiques, et les Metamonades, qui sont des protistes anaérobiques.

• Les Straménopiles ou Hétérocontes sont reconnaissables à la présence de deux flagelles inégaux au cours de leur cycle. Ils sont représentés par la classe des bacillariophytes (diatomées), groupe ubiquiste représentant la majorité de la diversité et de la biomasse phytoplanctonique marine. Ces derniers possèdent des plastes dérivés d'une algue rouge (voie dite "rouge"). A noter que dans ce groupe des Straménopiles se trouvent également des macroalgues brunes (ex : laminaires).

• Les Alvéolés comprennent un des grands groupes phytoplanctoniques marins : les dinoflagellés, la plupart des phototrophes de cette classe sont caractérisés par des plastes à 3 membranes dérivés d'endosymbioses secondaires ou tertiaires essentiellement issus de la "voie rouge" bien que des espèces du genre *Lepidodinium* aient un plaste vert. De nombreuses endosymbioses ont eu lieu chez les dinoflagellés et leur capacité à acquérir et conserver les plastes au cours du temps fait la diversité de ces organismes (Zapata et al., 2012). Depuis, certains ont perdu leur capacité à faire la photosynthèse et sont devenus hétérotrophes mais auront pu maintenir la présence de leurs plastes, ou possèdent des plastes issus de kleptoplastie ou d'endosymbiose. Les alvéolés sont caractérisés par la présence de vésicules plates supportant la membrane cellulaire. On retrouve également dans ce phylum les apicomplexes (parasites) et les ciliés (prédateurs, parfois parasites, ex : *Mesodinium rubrum*).

Les deux dernières lignées regroupent les deux grandes classes caractérisant le microphytoplancton marin, les diatomées et les dinoflagellés, majoritairement étudiées et suivies dans les écosystèmes côtiers. A eux deux, ces organismes représentent une vaste majorité de la diversité taxonomique et fonctionnelle microphytoplanctonique (Wasmund et al., 2011; Guilloux et al., 2013). C'est pourquoi ils sont plus amplement évoqués ci-dessous.

1.2.1 Les diatomées, algues à la paroi de verre

Apparues au cours du Jurassique et du Crétacé, il y a près de 190 millions d'années, l'accumulation des cellules de diatomées dans les sédiments est à l'origine des diatomites, des roches sédimentaires siliceuses (Loir, 2004). Les scientifiques estiment leur diversité à plusieurs dizaine de milliers d'espèces, et seulement 10% de cette diversité (comme à l'échelle du microbiome) serait connue (Medlin, 2016, 2018). Leur présence est ubiquiste, elle se retrouve dans presque l'ensemble des milieux aquatiques ou humides (Medlin, 2016). Elles sont caractérisées par la présence des pigments de chlorophylle-a et -c, essentiels pour la photosynthèse, mais également de fucoxanthine, de β-carotène, de diatoxanthine et diadinoxanthine (Roy et al., 2011). Les diatomées assurent près de la moitié de la production primaire océanique et constituent un maillon clé des flux océaniques de carbone et des réseaux trophiques (Loir, 2004; Medlin, 2016).

Description

Les diatomées sont des algues unicellulaires à paroi de silice biogène. Ces frustules comportent de nombreuses ornementations qui se trouvent être les orifices permettant les échanges entre la cellule et le milieu (Loir, 2004). Certains frustules possèdent des pics ou épines (ex : *Asterionellopsis* sp.), d'autres développent des soies (ex : *Chaetoceros* sp.) (Medlin, 2016). Les cellules sont constituées de deux valves ; la première, l'épithèque, s'emboîte sur la seconde, plus petite, l'hypothèque (Figure 1.3). Elles présentent une grande diversité de formes ainsi qu'une capacité à refléter la lumière (Figure 1.4).

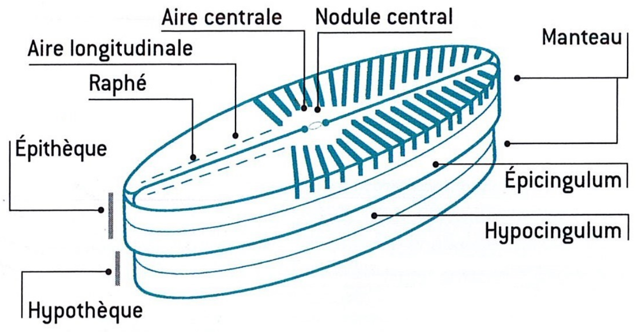


FIGURE 1.3 – Détails d'un frustule de diatomée (ici Naviculaceae) (Loir, 2004).

Pendant un temps, la classification des diatomées se basait naturellement sur leur description morphologique (centriques *vs* pennées). Medlin (2016) revoit les

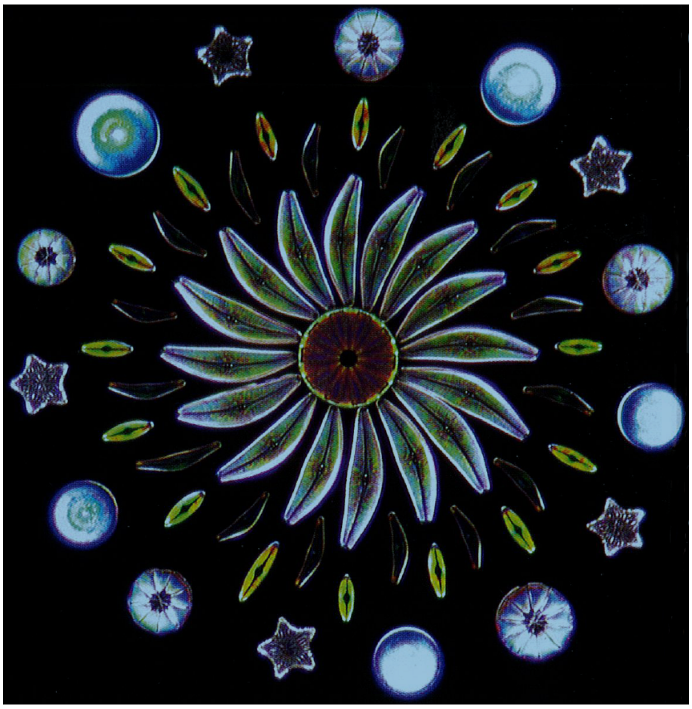


FIGURE 1.4 – Oeuvre du Docteur Osamu Oku, illustrant la diversité morphologique des diatomées (Société Japonaise de Plancton, 2011).

différentes classifications connues des diatomées (division des bacillariophytes) et les actualise en tenant compte des dernières avancées moléculaires et génétiques. Elle différencie 2 sub-divisions, et 3 classes :

- Coscinodiscophytina
  - ⊙ Coscinodiscophyceae (centriques à symétrie radiale)
- Bacillariophytina
  - ⊙ Mediophyceae (centriques multipolaires)
  - ⊙ Bacillariophyceae (pennées)
    - ⋆ Urneidophycidae (araphés basaux)
    - ⋆ Fragilariophycidae (araphés de core)
    - ⋆ Bacillariophycidae (présence de raphé)

Cyle de vie

Les cellules de diatomées se multiplient à la fois par division cellulaire végétative et par reproduction sexuée (Medlin, 2016). Dans le premier cas, au sein des deux structures de la cellule mère vont se développer deux nouvelles structures siliceuses plus petites, qui deviendront les "réceptacles" des cellules filles. A l'issue de cette division, la diatomée mère aura produit une cellule de taille comparable à la sienne et une cellule plus petite (Medlin, 2016) (Figure 1.5). Une cellule sur deux décroît ainsi de taille division après division. Lorsque qu'une taille limite est atteinte (variant selon l'espèce), la cellule devient fertile et apte à la reproduction sexuée. Behrenfeld et al. (2021) avancent par ailleurs que cette nécessité à la reproduction sexuée justifierait en partie la grande diversité des diatomées.

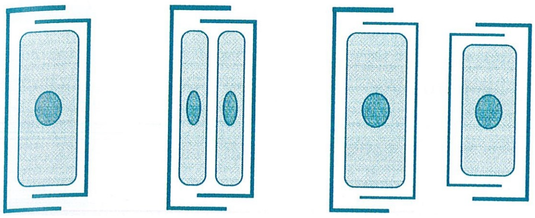


FIGURE 1.5 – Représentation schématique de la division cellulaire végétative d'une diatomée (Loir, 2004).

Formes de vie

La grande diversité des diatomées se reflète également dans les formes de vie de ces organismes. Les diatomées peuvent vivre isolées mais aussi fixées à un support ou en formant des colonies aux apparences très variées (Hasle & Syvertsen, 1997). Chez ces espèces coloniales, les cellules filles restent en lien avec la cellule mère, si bien que les colonies ont souvent une même signature génétique. Malgré ce lien, les cellules restent parfaitement autonomes si la chaîne se brise.

La classe des diatomées forme majoritairement le microphytobenthos dont les taxons vivent directement en lien avec le substrat (Morelle et al., 2020). Certaines diatomées peuvent également présenter des affinités benthiques et pélagiques au cours de leur cycle de vie. Il s'agit d'organismes tychopélagiques qui vont dépendre des courants et de la turbulence pour alterner leur localisation du milieu benthique (plus riche en nutriment) au milieu pélagique (plus lumineux), leur donnant une phénologie saisonnière (Safi, 2003).

De plus, lorsque les conditions environnementales ne sont pas favorables, certaines espèces peuvent former des hypnospores ; des spores de résistance pouvant avoir la même morphologie que la diatomée mère et qui permettent à l'espèce d'atteindre une phase de dormance (Medlin, 2016). Ces formes de dormance ont un frustule plus lourd et peuvent être caractérisées selon leur liaison avec la cellule mère (exogène ; structure à part, semi-endogène ; une valve du spore est enfermée dans la thèque de la cellule mère et endogène ; l'ensemble du frustule est enclavé dans la cellule mère)(Hasle & Syvertsen, 1997). La formation d'un tel spore va permettre à l'organisme d'atteindre plus facilement le sédiment et d'y survivre jusqu'à sa remise en suspension dans un milieu favorable à son développement, lors d'un épisode d'up-welling par exemple (Spilling et al., 2018). Ces remises en suspension peuvent conduire à des proliférations importantes en surface, elles vont "ensemencer" la colonne d'eau et influencer la composition spécifique du phytoplancton en favorisant la représentativité des taxons possédant des phases de dormance benthiques (Eilertsen et al., 1995; McQuoid & Godhe, 2004).

Les différentes caractéristiques développées ci-dessus permettent d'illustrer la grande diversité des diatomées. Il s'agit de traits reliés à des conditions environnementales et qui résultent de compromis en lien avec leur fitness ; c'est à dire limitant les effets de prédation tout en optimisant les processus métaboliques (Behrenfeld et al., 2021). L'écologie fonctionnelle de ces organismes sera développée plus amplement dans une section à part entière.

1.2.2 Les dinoflagellés, algues prédatrices

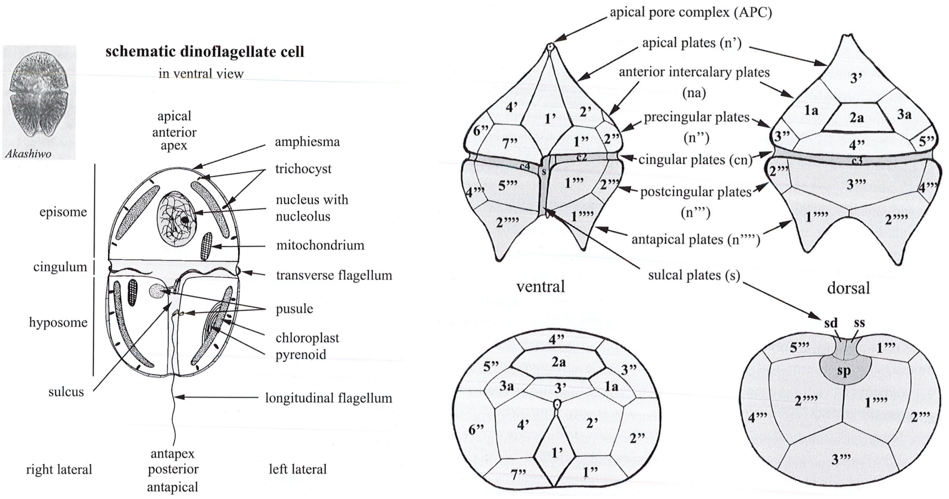
Après les diatomées, cette classe est des plus représentées au sein du phytoplancton marin, avec environ 2500 espèces décrites et une existence remontant à plus de 250 millions d'années, au milieu du Triasique, et ayant atteint un premier pic de diversité au Jurassique (MacRae et al., 1996; Hoppenrath et al., 2009).

Description

Les dinoflagellés font partie des alvéolés de part la présence de vésicules plates sous la membrane plasmique (Hoppenrath et al., 2009). Comme leur nom l'indique, la présence de flagelles caractérise cette classe. Ils permettent de distinguer deux types de morphologie, les desmoncontes ; qui possèdent deux flagelles distincts, tous deux sur la partie antérieure de la cellule, et les dinocontes ; qui possèdent également deux flagelles distincts, l'un est transversal au sein du cingulum et l'autre émerge du sulcus (voir figure 1.6a) (Steidinger & Tangen, 1997). Grâce à ces derniers, certaines cellules sont capables de se déplacer verticalement dans la colonne d'eau. Hoppenrath et al. (2009) décrivent ainsi la possibilité d'un déplacement d'une dizaine de mètres en quelques heures. D'un point de vue morphologique, la plupart des dinoflagellées sont caractérisés par la présence d'un cingulum, séparant l'épisome (partie supérieure) de l'hyposome (partie inférieure), ainsi qu'un sulcus sur la partie ventrale (Figure 1.6a). La couverture de la cellule est formée d'une membrane extérieure ; le plasmalème, recouvrant les alvéoles (ou vésicules corticales). Ces dernières peuvent contenir de la cellulose, ce qui forme alors une armure en plaques appelée thèque, ou peuvent être vides, on dit alors que les dinoflagellés sont nus, ou athéqués. Pour l'identification, des patrons de tabulation spécifiques existent et correspondent à l'agencement des plaques les unes par rapport aux autres. Le système Kofoidian (Fensome et al., 1993) est alors souvent utilisé comme référence (Figure 1.6b).

Modes de vie alternatifs

L'exploitation des ressources chez les dinoflagellés peut se faire au travers des stratégies alimentaires variées qui leur procurent un avantage écologique lorsque d'autres organismes sont limités par un stress environnemental (exposition à la lumière, apports en nutriments). Tout d'abord, il existe des dinoflagellés photosynthétiques strictes, chez qui les chloroplastes peuvent varier en structure et en composition pigmentaire (Zapata et al., 2012). La diversité de la signature pigmentaire des dinoflagellés illustre les différents modes de vie. On peut distinguer 6 types de composition pigmentaire dans les chloroplastes ; ceux contenant de la chlorophylle-b et de la péridinine descendent d'endosymbioses secondaires, les autres auraient été obtenus par endosymbioses tertiaires (Zapata et al., 2012). Ces derniers caractérisent les différentes lignées au sein des dinoflagellés (Figure 1.7). Parmi ces individus, certains ont besoin d'apports supplémentaires comme des



(a) (b)

FIGURE 1.6 – (a) Représentation schématique d'un dinoflagellé en vue ventrale. (b) Système Kofoidian pour la désignation des plaques qui forment la thèque des dinoflagellés. (Hoppenrath et al., 2009)

vitamines, ce sont les auxotrophes (Hoppenrath et al., 2009).

Sur l'ensemble des espèces de dinoflagellés décrites, seule la moitié serait photosynthétique (Taylor et al., 2008). L'hétérotrophie est une alternative répandue chez les dinoflagellés et réalisée par phagotrophie pour de nombreux protistes. Certaines espèces peuvent déployer un pédoncule leur permettant de percer leur proies et de les "aspirer", il s'agit de la myzocytose (Hoppenrath et al., 2009). Le "veil-feeding" est un autre mode de prédation qui se traduit par l'expulsion après contact du cytoplasme, le pallium, qui va entourer la proie et en permettre la digestion directement à l'extérieur de la cellule prédatrice (Hoppenrath et al., 2009). Certains dinoflagellés sont également parasites (Small et al., 2012) ou symbiotiques (Suggett et al., 2017).

La mixotrophie permet de combiner phototrophie et hétérotrophie simultanément ou consécutivement (Not et al., 2012). Il existe différents sous groupes (Stoecker et al., 2017). Le premier est photoautotrophe, ayant hérité initialement de chloroplastes et pouvant accéder à une ressource supplémentaire via la prédation de façon optionnelle. Certaines espèces dans cette catégorie peuvent notamment ne pas survivre dans des zones sans apport lumineux même en présence de proies, l'irradiance peut également fonctionner comme catalyseur du comportement de

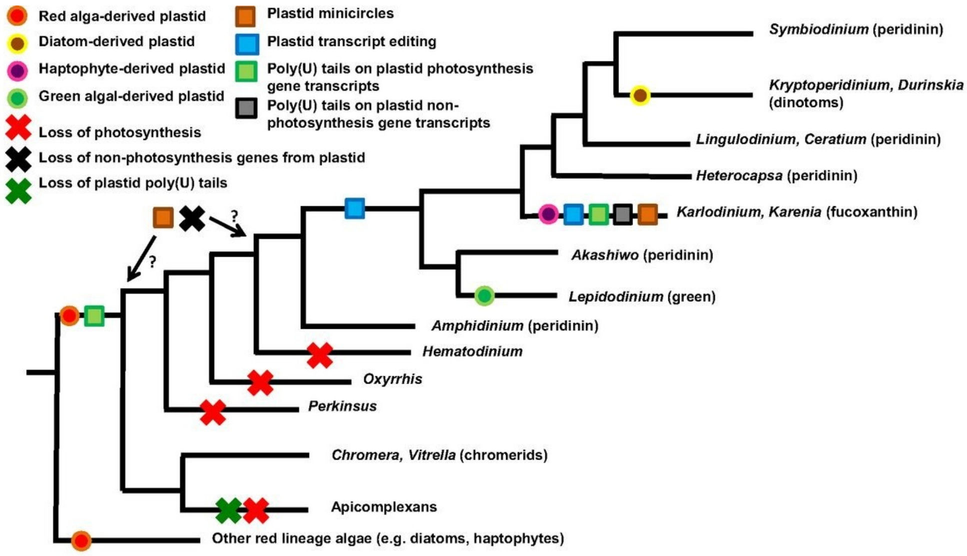


FIGURE 1.7 – Évolution des dinoflagellés et leurs plastes illustrée au travers de la représentation de quelques espèces et de leur proximité évolutive (extrait de Dorrell & Howe (2015)).

prédation. Ensuite, certaines espèces prédatrices ne possédant pas de chloroplastes vont bénéficier d'ecto- ou d'endosymbiontes photosynthétiques. D'autres sans chloroplastes propres vont exploiter les produits de la photosynthèse des chloroplastes prélevés à leurs proies, c'est notamment le cas du genre toxique *Dinophysis* sp. (Kim et al., 2012). Enfin, certains organismes peuvent absorber et garder intact leurs proies photosynthétiques et en exploiter la ressource de quelques heures à quelques semaines. La pratique des deux approches permet de garder un rythme de croissance malgré les potentielles limitations en nutriment du milieu. Ces organismes prédateurs ont des proies parmi les petites diatomées, les cryptophycées ou les ciliés (Stoecker et al., 2017).

Cycle de vie

Le cycle de vie des dinoflagellés est extrêmement complexe. Comme le dit très bien Elbrächter (2003) ; "If we accept this statement [You only know a species if you know its complete life cycle" H.A. von Stosch], and I do, then we only know about 1% of the 2500 recent dinoflagellate taxa —or do we know any dinoflagellate at all ?". Dans ce cycle de vie, on retrouve donc ainsi les deux modes de reproduction sexuée et asexuée (Steidinger & Tangen, 1997; Meier et al., 2007). Comme les auteurs ont pu l'observer au travers de cultures, le mode asexué permet l'obtention, par fission binaire, de deux à quatre cellules filles avec le même nombre de chromosomes. La plupart du temps, cette fission a lieu au niveau d'une zone prédéterminée. Quand au mode sexué, il est permis par la production et la fusion de deux gamètes qui donneront une nouvelle cellule, ou conduiront à la formation d'un kyste (une phase dormante) qui émergera ensuite en une nouvelle cellule lorsque les conditions le permettront. La présence de ces kystes est une facette évolutive qui s'ajoute aux nombreuses autres de cette classe et en améliore la *fitness*. L'enkystement peut être déclenché par un stress nutritif (azote ou phosphate), et peut perdurer de nombreux mois avant de se déclencher et de rejoindre le milieu pélagique (Anderson et al., 2012). Cet enkystement peut avoir un impact important puisqu'il permet d'entretenir certains blooms toxiques déjà très intenses (cas d'*Alexandrium minutum* qui produit une neurotoxine paralytique) (Anderson et al., 2012).

1.3 L'écologie du phytoplancton

Les études d'écologie de communautés montrent que dans un environnement à ressources limitées, les espèces partageant les mêmes besoins écologiques (donc occupant la même niche écologique), ne pourraient occuper le même espace. C'est le principe de l'exclusion compétitive (Hardin, 1960). En 1961, l'américain Hutchinson publiait le paradoxe du plancton. Comment est-il possible qu'un certain nombre d'espèces puissent coexister dans un environnent relativement isotrope et sujet à fortes variabilités ? (Hutchinson, 1961). L'explication pour une telle diversité pouvait résider, selon lui, principalement dans la forte variabilité des facteurs environnementaux dont dépendent les organismes photosynthétiques et dans la probable importante diversité de niches des espèces en présence. C'est un concept que l'on peut retrouver dans le livre de Harris (1986), suggérant que l'être humain est tenté d'aborder l'environnement à son échelle, anthropocentrée, alors que le phytoplancton devrait être considéré à une beaucoup plus petite échelle pour que l'on puisse appréhender le paradoxe qu'on lui associe. La variabilité à petite échelle reste sous explorée, malgré le potentiel lié à la compréhension des mécanismes régissant la variabilité phytoplanctonique, à son échelle, dans l'explication des phénomènes des échelles supérieures (Mandal et al., 2019).

1.3.1 La relation à l'environnement

Le phytoplancton est par définition dépendant de son environnement biotique et abiotique. Il peut proliférer très rapidement si les conditions sont réunies, notamment si les ressources en nutriments sont suffisantes (effet *bottom-up*). Il est également régulé par la prédation que ce soit par filtration ou broutage (effet *top-down*). La croissance et la productivité du phytoplancton dépendent des apports en lumière, en nutriments et de la température (Behrenfeld et al., 2008). De nombreuses études explorent les relations entre le phytoplancton et son environnement afin de comprendre les réponses de ce dernier aux divers changements environnementaux.

Dès la fin des années 70, des études sur l'eutrophisation (apports fluviaux de nutriments en sur-quantité) au sein de lacs (Vollenweider & Kerekes, 1980) ont permis d'établir une relation entre la concentration en chlorophylle-a et celle en phosphate. Depuis, cette relation a pu être vérifiée dans de nombreux cas d'étude et étendue à d'autres nutriments (et leurs ratios ; ex : azote/phosphate) (Zohary et al., 2010). Le phosphate est ainsi un élément limitant dans le milieu marin, tout comme l'azote, ainsi que la silice pour les diatomées et certains métaux traces tels que le fer, le cuivre ou le zinc en milieu océanique. Néanmoins, il ne s'agit pas des seuls paramètres pouvant influencer la prolifération des microalgues. Zohary et al. (2010) précisent qu'on ne peut résumer le phytoplancton à son proxy de biomasse (la chl-a), il s'agit en effet d'un groupe polyphylétique ayant développé diverses stratégies adaptées à la diversité des habitats, il est donc important de regarder l'assemblage des communautés pour comprendre la relation à l'environnement.

C'est dans cet objectif que Margalef (1978) compare le "végétal marin" au végétal terrestre, évoquant notamment l'importance de l'hydrodynamisme dans l'écosystème marin. La survie des cellules de phytoplancton repose donc sur un équilibre alliant flottaison et sédimentation. Dans cet article, Margalef reprend le concept de "formes de vie", concept encore peu étudié dans les années 1980, et le juxtapose à l'utilisation des nutriments, la croissance, la résistance au broutage et à la sédimentation (Figure 1.8). Il va ainsi relier la vitesse de sédimentation et donc l'accès aux nutriments à la forme de la cellule et des potentielles formes coloniales en justifiant qu'il s'agit des principaux facteurs ayant conduit aux formes actuelles des cellules au cours de l'évolution. Différentes études permettent de confirmer et d'approfondir ces relations. En effet, l'utilisation des nutriments augmente avec le biovolume des cellules (Edwards et al., 2012) notamment avec le ratio surface/volume (Friebele et al., 1978; Stanca et al., 2013), une forme élongée permet quant à elle d'optimiser l'acquisition de lumière en disposant les chloroplastes le long des parois (Stanca et al., 2013; Ryabov et al., 2021). De plus, pour résister à la pression de prédation les cellules possèdent des traits défensifs tels que la présence d'épines sur la cellule, la formation de longues chaînes pluri-cellulaires et/ou la production de toxines ou de mucus (Lürling, 2021). Ces mêmes caractéristiques (ou traits) décrivant les cellules selon leur morphologie, physiologie ou comportement sont ainsi favorisées par différentes conditions environnementales et leur cycle saisonnier (Loewen et al., 2021). Ainsi, on retrouve que les diatomées sont favorisées dans les systèmes à fortes concentrations en sels nutritifs et à fort degré de turbulence (homogénéité de la colonne d'eau), tandis que les dinoflagellés seront plus représentés dans les milieux moins turbulents voire stratifiés et également plus oligotrophes dans lesquels certains pourront opter pour un mode de nutrition alternatif, la mixotrophie (Figure 1.8).

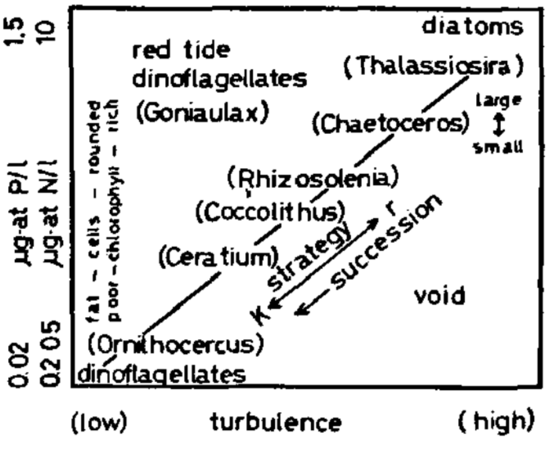


FIGURE 1.8 – Principales stratégies du phytoplancton, exemple des "formes de vie" replacées dans un espace écologique selon la concentration en nutriments et la turbulence (diffusion verticale) (issu de Margalef (1978)).

Si le Mandala de Margalef pose dès 1978 des bases écologiques certaines pour la compréhension du compartiment phytoplanctonique, il se repose sur une dualité de variables environnementales et la stratégie écologique r (croissance et productivité) *vs* K (maintenance et efficacité dans l'acquisition de ressources) dans un milieu qui en possède une multitude. Glibert (2016) reprend en effet le concept et y ajoute plusieurs dimensions directement en relation avec les traits fonctionnels du phytoplancton considérant un contexte de changement global et d'influence anthropique majeure sur le milieu marin (Figure 1.9). Ainsi, le nouveau Mandala inclut notamment la température (inversement corrélée à la turbulence) et précise l'impact des nutriments en incluant le rapport N/P puisque les apports anthropiques en azote sont plus importants que ceux en phosphates. En incluant également des traits fonctionnels (régime trophique, taille, taux de croissance, motilité, toxicité) dans le Mandala, Glibert (2016) retrouve une relation entre apports en nutriments inorganiques dissous, croissance et stratégie écologique. Dans celle-ci, P est un élément essentiel à la croissance relativement à N (faible N/P), favorisant la stratégie r alors qu'un haut ratio N/P serait plus caractéristique d'une stratégie K. Les nitrates favorisent les cellules de plus grandes tailles chez les diatomées (quelques exceptions chez les grandes dinoflagellés) comparativement à l'ammonium qui induirait par contre une plus forte production des toxines.

En milieu côtier, la variabilité à court-terme des paramètres physico-chimiques, associée aux changements d'irradiance et aux fluctuations des apports en nutriments, influence la communauté phytoplanctonique (Pannard et al., 2008). Litchman et al. (2012) précisent que les réponses du phytoplancton aux changements environnementaux s'approchent par l'étude des changements dans la composition de la communauté, la diversité des espèces, leur présence relative et abondance. Lorsqu'on regarde l'assemblage des organismes, les facteurs physiques (circulations des masses d'eau induites par les courants, la vitesse du vent ou encore la profondeur) et les stratifications saisonnières induites par la température jouent également un rôle clé sur le potentiel photosynthétique des microalgues (Zohary et al., 2010).

Récemment, Romero et al. (2019) ont publié un article sur le fonctionnement de l'écosystème au niveau de l'estuaire de Seine. Ils présentent notamment le réseau d'interaction complexe entre les organismes du milieu benthique (diatomées et zoo-benthos) et pélagique (phytoplancton et zooplancton), avec le recyclage des éléments nutritifs issus des sédiments, des faeces et des restes d'organismes composant la neige océanique (formes benthique, détritique, dissoute) (Figure 1.10).

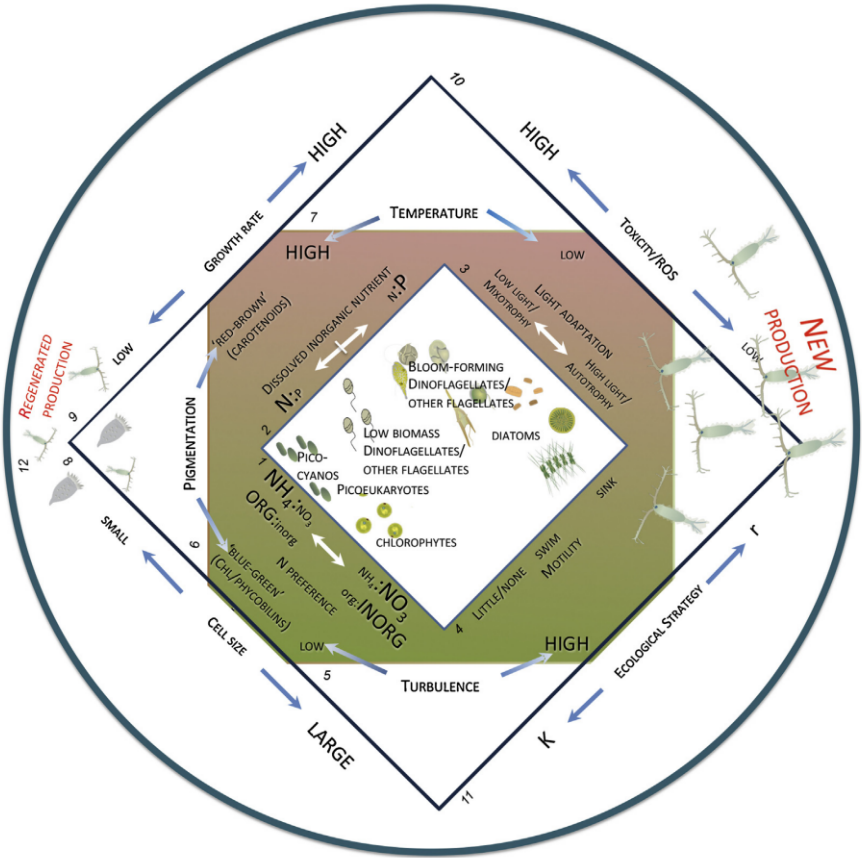


Figure 1.9 – Mandala de Margalef repris et actualisé par Glibert (2016)).

D'autre part, au niveau des zones conchilicoles, les parcs d'élevage de bivalves filtreurs ajoutent une pression de prédation qui n'équivaut pas à une pression naturellement présente dans le milieu. Dans ces zones, les bivalves produisent des éléments nutritifs nécessaires au développement du phytoplancton (effet bottom-up) mais représentent également une pression de filtration (effet top-down). En Baie des Veys (Normandie), l'effet bottom-up est effectif sur l'ensemble de la baie, quant à l'effet top-down, il est repéré de façon localisé (baisse de chlorophylle-a) au dessus des zones d'élevage (Grangeré et al., 2010).

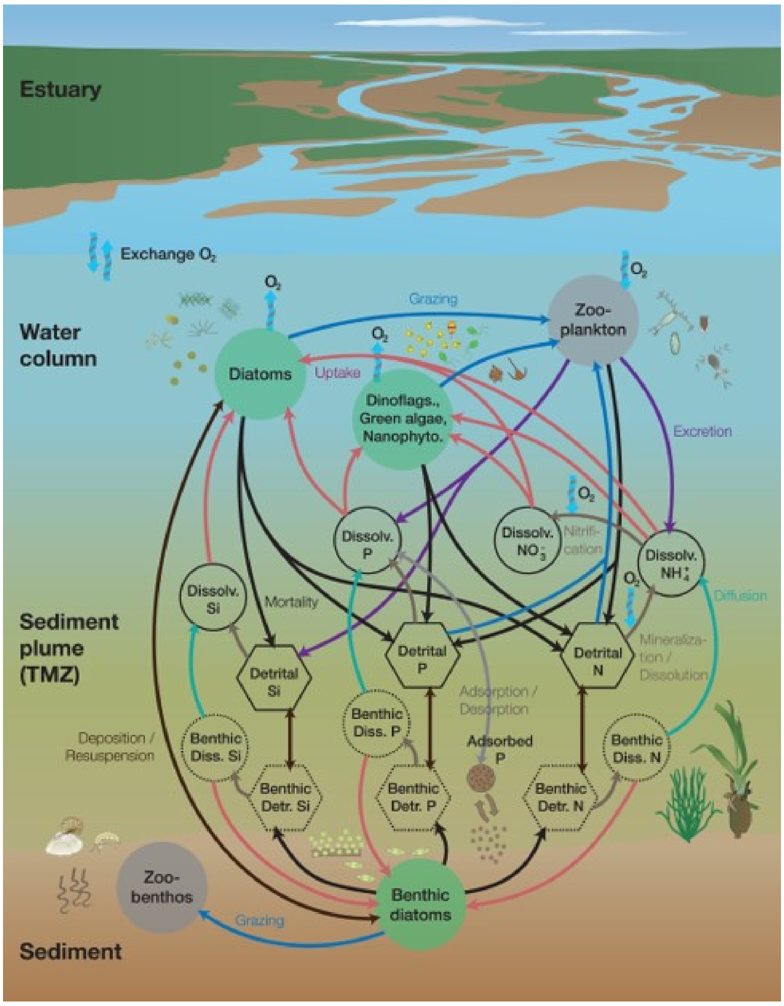


FIGURE 1.10 – Diagramme en flux du module écologique de MARS3D, présentant les compartiments de la colonne d'eau et du sédiment ainsi que les échanges entre eux (issu de Romero et al. (2019)).

1.3.2 Le cas des efflorescences algales nuisibles (HABs)

Les HABs se caractérisent par la prolifération rapide et soudaine d'une ou plusieurs espèces de micro-algue.s provoquant un bouleversement du milieu, soit directement par la production d'une substance toxique ou nuisible, soit indirectement au travers de sa présence et de l'anoxie que cela peut provoquer (Anderson, 2009, 2014).

Risques et impacts des efflorescences algales nuisibles

Bien que pouvant être fatal pour la faune environnante, c'est un phénomène naturel *stricto sensu* permettant de réduire la pression de prédation. Il devient néanmoins de plus en plus préoccupant au regard de la dernière décennie et du changement global (Lassus et al., 2016). Il s'agit d'une thématique de recherche importante puisque les effets néfastes de ces proliférations peuvent atteindre l'être humain, par inhalation ou ingestion des toxines lors de la consommation d'organismes marins (Kirkpatrick et al., 2004). La principale voie de transfert, la plus surveillée en Europe, concerne l'ingestion des toxines contenus dans les bivalves filtreurs prélevés en période à risque, notamment les moules, coques, coquilles St Jacques ou encore les huîtres. Ces organismes vont concentrer les toxines dans leurs tissus durant les efflorescences toxiques et se dépurer progressivement selon l'espèce une fois le bloom passé. Ces phycotoxines ingérées vont causer différents syndromes de contamination selon l'espèce productrice ; les trois principaux sont paralytiques (PSP ; ex : *Alexandrium minutum* ; Gessner & Middaugh (1995)), diarrhéiques (DSP ; ex : *Dinophysis* spp. ; Aune & Yndestad (1993)) ou amnésiques (ASP ; *Pseudo-nitzschia* spp. ; Kumar et al. (2009)). A l'échelle européenne mais également à l'international, des programmes de surveillance sanitaire et des réglementations permettent de suivre les niveaux de toxines contenues dans les organismes commercialisés (Table 1.2). En France, plusieurs réseaux majeurs ont été mis en place à partir des années 80 pour suivre les changements observables en milieu côtier, dont le réseau de contrôle microbiologique (REMI, 1989), le réseau d'observation et de surveillance du phytoplancton et des phycotoxines (REPHY/REPHYTOX, 1984) et le réseau d'observation de la contamination chimique du littoral (ROCCH, 1979). Cela permet de cibler les zones contaminées et de les fermer à la vente le temps de la dépuration des organismes.

Évolutions et relations environnementales

Depuis les années 60, un intérêt naissant pour les blooms algaux toxiques apparaît des suites d'une forte contamination des coquillages par une toxine paralysante (PSP) en Amérique du Nord puis en Europe (Lassus et al., 2016). Néanmoins, on pourrait se demander si les HABs sont de plus en plus fréquents et virulents ou si

Table 1.2 – Réglementations européennes et informations concernant contaminations dues aux efflorescences toxiques (EFSA, 2009; Hallegraeff, 2010; Grattan et al., 2016; Bhunia, 2018).

Syndrôme	Toxines	Code	Genre phytoplanctonique	Limite sanitaire (EU)
ASP	Acide domoïque	DA	*Pseudo-nitzscia* spp.	20 mg DA/kg DM
DSP	Acide okadaïque, Dinophysis toxines	OA, DTX	*Dinophysis* spp.	0,16 mg OA eq./kg DM
PSP	Saxitoxine	STX	*Alexandrium* spp., *Gymnodinium* spp., *Pyrodinium* spp.	0,8 mg STX eq. diHCl/kg DM
AZP	Azaspiracide	AZA	*Azadinium* spp.	0,16 mg AZA eq./kg DM
NSP	Brevetoxines	BTX	*Karenia* spp.	/
/	Yssotoxine	YTX	*Protoceratium* spp.	1 mg YTX/kg DM
CFP	Ciguatoxines	CTX	*Gambierdiscus* spp.	/
/	Palytoxines	PlTX	*Ostreopsis* spp.	/
/	Imine cyclique	CI	*Alexandrium* spp.	/

Note : ASP ; DSP ; PSP, respectivement pour Amnesic, Diarrhetic et Paralytic Shellfish Poisoning ; AZP, AZzaspiracide Poisoning ; NSP, Neurotoxic Shellfish Poisoning ; CFP, Ciguatera Food Poisoning et SM, Shellfish Meat ; EU, European Union.

l'intérêt qu'on leur porte s'accroît. Ainsi, Lassus et al. (2016) explorent différentes hypothèses pouvant expliquer ce phénomène. Ils évoquent effectivement l'effet de l'augmentation dans l'utilisation des zones côtières pour l'aquaculture (Guillen et al., 2019; Stiller et al., 2019) ainsi qu'une amélioration des préventions sanitaires (Belin & Soudant, 2018). Ces deux éléments vont de pairs et résultent d'une meilleure compréhension des conditions d'occurrences des blooms et des syndromes provoqués par les toxines. Pour autant, depuis quelques années, il est avéré que les incidents liés à certaines efflorescences toxiques augmentent sur de nombreuses zones côtières dans le monde entier et représentent une préoccupation majeure pour les politiques publiques (Van Dolah, 2000; Lassus et al., 2016).

Les effets de l'eutrophisation sur les HABs vont se traduire au travers non seulement de l'enrichissement du milieu mais également via la nature de cet enrichissement ; les changements dans les proportions et les formes organiques ou inorganiques des apports nutritifs vont avoir des répercussions sur les efflorescences algales (Heisler et al., 2008; Glibert et al., 2018). Plusieurs dinoflagellés s'avèrent être plus toxiques dans un milieu en large excès de N par rapport à P, c'est le cas d'*Alexandrium* spp. (Granéli & Flynn, 2006). Des études au niveau du Mississippi ont relié les efflorescences à *Pseudo-nitzschia* sp. et de hautes concentrations en acide domoïque à l'augmentation du niveau d'eutrophisation de l'estuaire (Dortch et al., 1997; Parsons & Dortch, 2002). D'autres paramètres vont influencer les effets de l'eutrophisation en favorisant ou pas la relation nutriments-HABs, c'est le cas du temps résidence et de l'hydrodynamisme du milieu (Glibert et al., 2018).

L'eutrophisation n'est pas le seul facteur pouvant expliquer une augmentation des risques liés aux HABs, il va agir en tant que co-stresseur avec le changement global (Nazari-Sharabian et al., 2018; Gobler, 2020). En effet, ce dernier se traduit par des augmentations de températures et de l'irradiance, des intempéries. Il est donc à prévoir une amplification des effets de l'eutrophisation par l'augmentation des afflux nutritifs issus des bassins versants souvent largement anthropisés (zones agricoles, d'élevages, zones urbaines) vers le milieu marin (Nazari-Sharabian et al., 2018). Les effets sur la température et l'irradiance se traduiraient par l'élargissement spatial et temporel des zones stratifiées, séparant avec une thermocline une zone appauvrie mais lumineuse en surface et une zone plus riche mais moins soumise aux radiations en profondeur. La thermocline représente une couche en subsurface à l'interface entre les deux et bénéficiant des avantages de la zone supérieure (luminosité) et de la zone inférieure (nutriments). Il a été observé que certains dinoflagellés toxiques se développent préférentiellement en milieu stratifié (Griffith & Gobler, 2020), c'est par exemple le cas de *Dinophysis* sp., prédit d'augmenter durant le siècle à venir (Boivin-Rioux et al., 2022).

Les activités anthropiques, qui ne cessent de se développer, peuvent également directement influencer les occurrences des efflorescences toxiques et nuisibles (Lassus et al., 2016). En effet, le transport de kystes par les eaux de ballastes des navires traversant les océans peut entraîner une augmentation des épisodes de HABs avec l'intensité du trafic maritime, et par conséquent amener à la prolifération de nouvelles espèces potentiellement à risque d'efflorescences nuisibles (Naik et al., 2019). Les effets de la sur-pêche, en impactant et en réduisant les populations des niveaux trophiques supérieurs, entraînent quant à eux une augmentation des petits pélagiques prédateurs du zooplancton qui verront à leur tour leur effet de régulation (top-down) sur les microalgues potentiellement toxiques réduit (Figure

1.11).

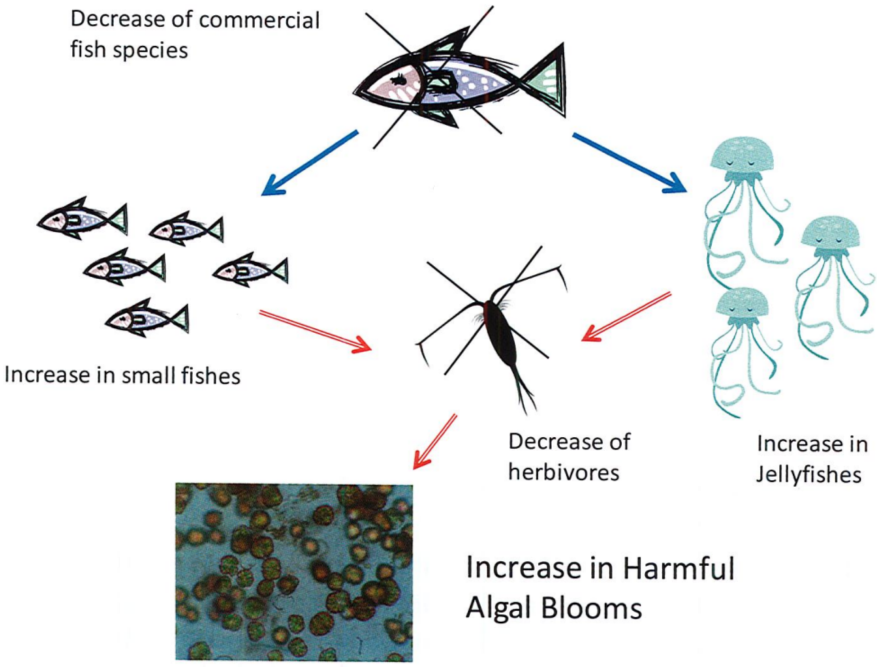


Figure 1.11 – Explication possible de l'effet de pêche sur la formation de blooms algaux toxiques, la modification du contrôle 'top-down' des herbivores (repris de Lassus et al. (2016)).

Le projet S3-EuroHAB

Dans ce contexte des efflorescences algales toxiques ou nuisibles et de l'augmentation des risques associés, que ce soit par l'augmentation des occurrences des HABs directement et/ou par l'augmentation des zones conchilicoles le long du littoral, il est nécessaire de renforcer les méthodes de détection et de prévention des risques.

Au cours du projet Interreg S3-EUROHAB, dans lequel s'insère ce projet doctoral, des suivis ont montré que l'impact des HABs est encore mal connu des professionnels de la mer et les réglementations sont économiquement contraignantes pour leurs activités (fermetures de zones d'élevage ou de pêche, destructions des produits contaminés). Ce projet a donc pour objectif de mettre en place un portail en ligne (`https://www.s3eurohab.eu/portal/`) permettant l'utilisation des données satellites dans le suivi des conditions environnementales en temps quasi réel et des risques d'efflorescences de certaines espèces phares de la Manche ; c'est déjà le cas pour *Karenia* sp., *Phaeocystis* sp., *Pseudo-nitzschia* sp. et en cours pour *Dinophysis* sp. (illustration de l'outil Figure 1.12). A partir des observations de terrain et des études relatives à l'écologie des algues toxiques et des communautés phytoplanctoniques, ces algorithmes satellites sont développés avec un maximum de précision, prenant notamment en compte les relations espèce-environnement régissant les dynamiques des blooms.

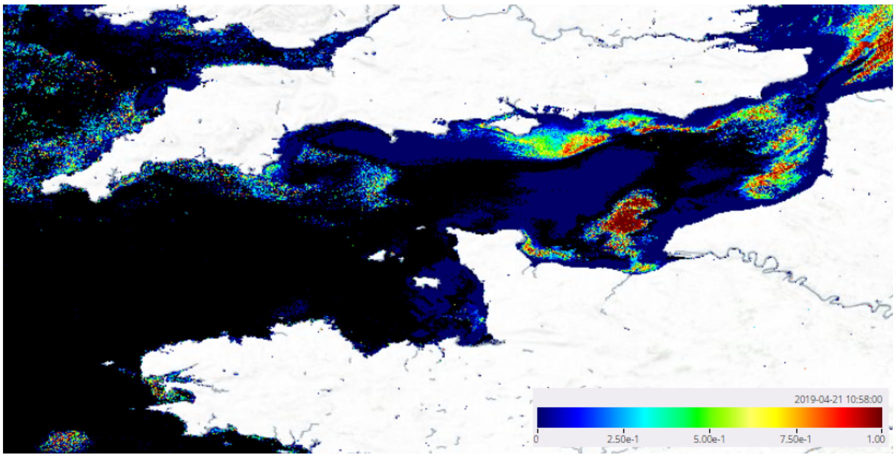


FIGURE 1.12 – Illustration de la probabilité de blooms de *Pseudo-nitzschia* sp. en Manche le 21 avril 2019. Note importante, le niveau de couleur donne une notion de probabilité (entre 0 et 1) de présence du genre et non de sa présence factuelle ou de son abondance (`https://www.s3eurohab.eu/portal/`).

L'accès à un tel outil servirait de repère pour les professionnels de la mer, notamment dans le choix de la zone à exploiter en vue d'une commercialisation. Il s'agirait également d'un outil de suivi pour les scientifiques étudiant ces phénomènes ; il permet d'accéder aux informations relatives à la dispersion des blooms, jusque là difficilement accessibles par les études régulières de terrain sur points fixes.

1.4 La Manche : étendue aux environnements contrastés

1.4.1 Géographie et influences anthropiques

Située entre l'Angleterre au Nord et la France au Sud, la Manche est une mer épicontinentale en milieu tempéré. Elle constitue un passage amenant les eaux de l'Océan Atlantique vers la mer du Nord. Elle couvre une aire de 77 000km^2 et décroît en profondeur d'ouest en est (Dauvin, 2012; Ménesguen et al., 2019). La Manche est sous forte influence des marées avec un courant central allant d'ouest en est et présentant de nombreux gyres autour des îles anglo-normandes et près des côtes anglaises, en prolongation de la pointe du Cotentin (Ménesguen & Gohin, 2006).

De part ses caractéristiques hydrologiques, océanographiques et biogéographiques bien différenciées, la Manche peut être subdivisée en deux eco-régions distinctes ; avec une division spatiale au niveau de la péninsule du Cotentin (Spalding et al., 2007; Dauvin, 2012; Louchart et al., 2020) (Figure 1.13). Dauvin (2012, 2019) décrit ainsi un bassin occidental aux fortes influences Atlantiques et marines, une zone également plus profonde et sujette à l'apparition estivale d'une thermocline (Lewis & Allen, 2009; Smyth et al., 2010), et un bassin oriental, moins profond, plus influencé par les débits fluviaux et notamment celui de la Seine. Le long des côtes françaises, l'influence de la Seine remonte jusqu'en Picardie entraînée principalement par les vents du Sud-Ouest, ce qui lui vaut l'appellation courante de *fleuve côtier* (Brylinski et al., 1991).

La Manche est un espace grandement exploité par les activités humaines. De part sa position géographique, la Manche est une voie privilégiée pour les divers flux maritimes. Ainsi, le détroit du Pas de Calais est un carrefour de circulation majeur, avec près de 400 navires commerciaux et touristiques qui l'empruntent chaque jour (`https://www.defense.gouv.fr/`). Une telle circulation entraîne de nombreuses nuisances et pollutions qui font l'objet de suivis à l'échelle européenne (Johansson et al., 2013). Ils se concentrent également au niveau de grandes zones portuaires telles que Le Havre, Cherbourg, Dunkerque ou encore Southampton et

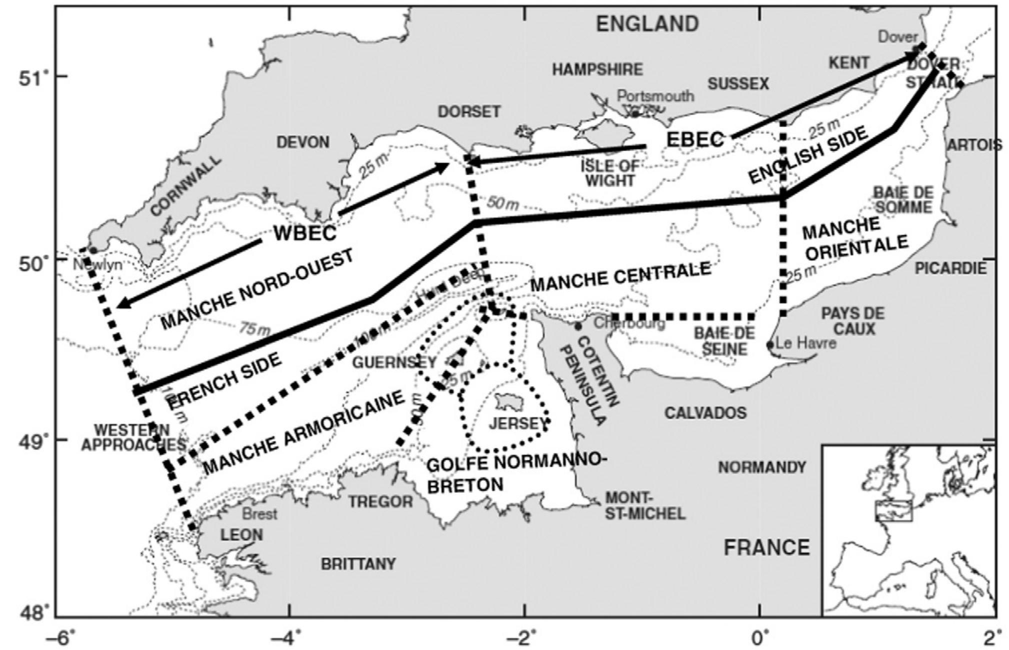


Figure 1.13 – Carte de la Manche représentant les différentes sous-division géographiques, notamment les bassins ouest (WEBEC) et est (EBEC) (extrait de Dauvin (2012)).

Douvre. Le Havre a notamment connu une expansion majeure de son port dans les années 2000, réduisant l'espace alloué à l'estuaire de Seine (Cariou et al., 2021). Depuis quelques années, le développement de parcs éoliens en mer s'accélère et de nombreux projets se mettent en place le long des côtes françaises (Raoux et al., 2019; Pezy et al., 2020). Ces zones de perturbation du milieu marin, notamment le temps des travaux pour les mettre en place s'ajoutent aux perturbations liées aux extractions des granulats siliceux ou calcaires (Dauvin, 2019).

Toutes ces activités représentent des pollutions physiques, chimiques et biologiques des eaux de la Manche induites par l'homme (Garnier et al., 2019). L'anthropisation de la Manche se retrouve également au travers de l'étendue de ses bassins versants (Figure 1.14, Millward et al. (2015)). La Seine est un des plus grands fleuves français, elle contribue à 50% des apports en eaux douces de la Manche (Dubois, 2012). Du point de vue des afflux nutritifs, l'estuaire de Seine est comparable à l'estuaire de la Neuse en Caroline du Nord ou la Baie de Chesapeake en Virginie (Cloern & Jassby, 2008). De son bassin versant sont transportés pesticides, engrais, rejets de stations de traitements des eaux usées et des zones urbaines dont celle de la capitale française, Paris. En 2011, ce bassin versant hébergeait un quart de la population française (Dubois, 2012). D'un point de vue biologique néanmoins, une baisse de la chlorophylle-*a* sur l'ensemble de la Manche a été constatée au travers des données satellites et confirmée sur le terrain (Gohin et al., 2019). Les auteurs précisent que ces observations seraient dues à une baisse des apports fluviaux, notamment une réduction significative des apports en phosphate des suites de réglementations européennes (Romero et al., 2016; Aissa-Grouz et al., 2018).

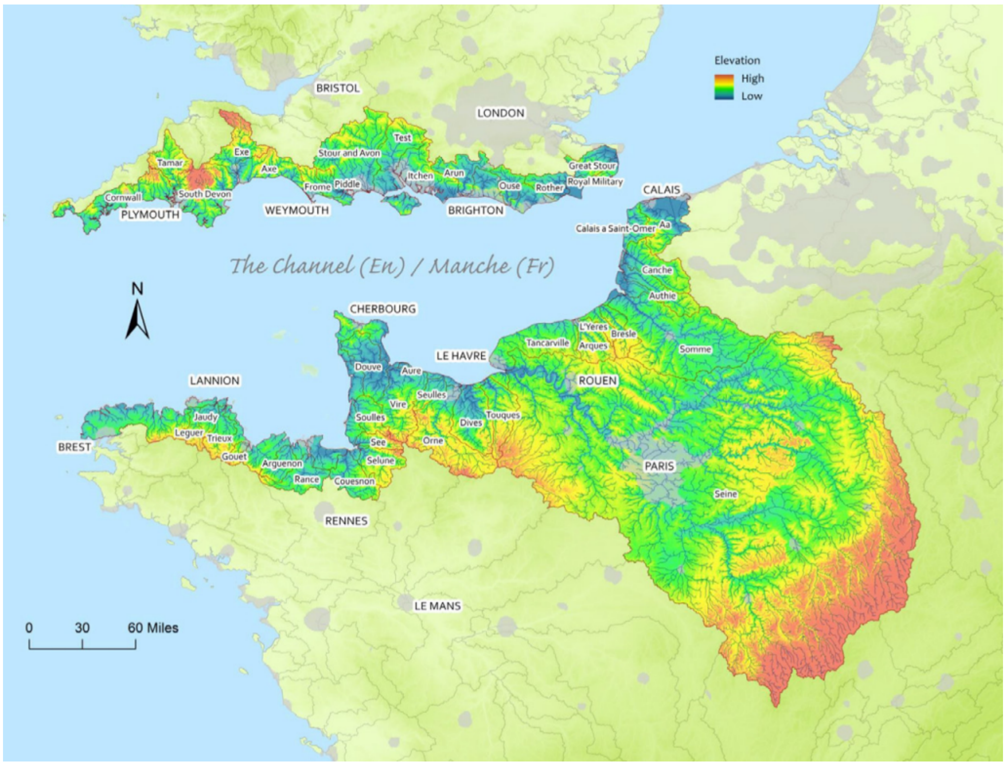


FIGURE 1.14 – Carte des différents bassins versants anglais et français se déversant dans la Manche (extrait de Millward et al. (2015)).

1.4.2 Contrastes et enjeux régionaux

Les côtes de la Manche sont ponctuées de différentes baies et estuaires qui lui procurent une grande diversité d'écosystèmes côtiers. Ces écosystèmes sont autant de sites d'études pour les communautés phytoplanctoniques. En Manche orientale, les zones côtières françaises sont plus influencées par la mer du Nord et les apports de la Seine qui longent les côtes françaises transportés par le *fleuve côtier* (Brylinski et al., 1991). Des blooms nuisibles à *Phaeocystis* sp. et *Pseudo-nitzschia* sp. y sont régulièrement observés au printemps (Bonato et al., 2015; Karasiewicz et al., 2018; Lefebvre & Dezécache, 2020). C'est une zone sous eutrophisation de part les apports d'azote. Il est ainsi estimé que la qualité de l'eau, bien qu'en amélioration, ne devrait pas permettre la résilience de la communauté phytoplanctonique de la zone (Lefebvre & Dezécache, 2020). Entre 1992 et 2011, Hernandez-Farinas et al. (2013) montraient un changement des communautés dont la composition avait évolué sur le long terme, précisant que la proportion des dinoflagellés par rapport au diatomées avait augmenté.

Au centre de cet espace géographique, la Baie de Seine représente une zone sous l'influence d'un grand estuaire dans lequel les risques d'eutrophisation sont élevés, malgré une baisse notable des apports en phosphate depuis 2001 (Romero et al., 2013). La Baie de Seine est connue pour son importance économique, contribuant à 50-70% de la production nationale de coquilles St Jacques (Husson et al., 2016). On retrouve également une production importante de palourdes, moules et huîtres, ce qui en fait une zone d'enjeux économiques importante mais également une zone où les interactions biotiques entre échelons et notamment la pression des zones conchilicoles sont conséquentes (Grangeré et al., 2010). La Baie de Seine est affectée par des blooms toxiques de deux espèces particulières, *Pseudo-nitzschia* spp. et *Dinophysis* spp.. Le premier est notamment présent tout au long de l'année avec des blooms de mai à septembre (Husson et al., 2016) et serait la cause de nombreuses contaminations de coquilles St Jacques sur la période 2011-2014 (Belin & Soudant, 2018). En 2012, une paralysie presque totale de la pêche et donc de l'économie autour de la coquille St Jacques a eu lieu suite à une prolifération du genre *Pseudo-nitzschia* spp. (HABs) (Schapira et al., 2017). Le deuxième genre, *Dinophysis* spp., est particulièrement présent sur la fin de l'été. Il a la particularité d'être à l'origine de toxines entraînant des fermetures sanitaires bien que le genre ne soit présent qu'à très faible concentration cellulaire.

La Manche occidentale est une zone ouverte à l'Atlantique, l'influence fluviale y est moindre. Le long des zones côtières, c'est le régime de marée qui va rythmer l'hydrodynamisme locale, la Baie du Mont St Michel connaît en effet un des plus haut niveau de marnage, causant l'érosion de ses lignes de côte, ce qui en fait un système privilégié dans les études morpho-sédimentaires (Bonnot-Courtois et al., 2014). La côte Nord de la Bretagne est également une zone conchilicole active, hébergeant certains organismes invasifs (*Crepidula fornicata*), formant un système qui fonctionne comme régulateur de la biomasse phytoplanctonique (Cugier et al., 2010). D'un point de vue biologique, la côte bretonne est connue pour subir les effets d'élevages intensifs au travers des apports azotés des rivières vers les milieux côtiers. Ces derniers causent de nombreux problèmes de proliférations d'algues nuisibles, les "marées vertes" (*Ulva* sp.) dont l'intensité ne semble pas réduire malgré la réduction des apports azotés de certains systèmes (Perrot et al., 2014; Schreyers et al., 2021). Les blooms algaux toxiques en revanche sont peu présents le long de ces côtes françaises. Ce sont les côtes Anglaises du Sud-Ouest, notamment au large de Plymouth, qui rencontrent des efflorescences toxiques, comme celles à *Karenia* spp. dont la présence est associée à des facteurs fluviaux et de fortes précipitations estivales (Barnes et al., 2015). Également, des blooms de plus en plus fréquents de *Dinophysis* spp. (Ross Brown et al., 2022; Panton & Purdie, 2022) sont également observés dans cette zone, principalement associés à de fortes stratifications et un maintien, voire transport des cellules du large vers les côtes permis par des vents du sud dominants (Ross Brown et al., 2022; Panton & Purdie, 2022).

1.5 Objectifs et déroulé de la thèse

Dans le cadre d'un projet d'étude des impacts des efflorescences toxiques et nuisibles au sein du système large et contrasté qu'est la Manche, cette thèse vise à approfondir notre compréhension des dynamiques phytoplanctoniques en milieux côtiers et estuariens. Pour ce faire, elle repose principalement sur des données de suivis de ces communautés ainsi que de l'environnement qui l'entoure grâce aux apports des réseaux régionaux et nationaux (REPHY, RHLN, SRN). Afin d'approfondir les connaissances associées à la variabilité des organismes phytoplanctoniques dans le milieu marin, elle s'appuie également sur des résultats de terrain et de laboratoire issus de protocoles originaux adaptés. Notre zone d'étude s'articule autour de la Baie de Seine avec des points de suivis en Baie de Somme et dans le golfe Normano-Breton.

Dans le **Chapitre 3**, le compartiment microphytoplanctonique est exploré sur la période 2008-2019 sur 6 stations d'observation du REPHY. L'objectif est d'utiliser les données biotiques et abiotiques existantes pour retracer les trajectoires et dynamiques temporelles et saisonnières passées des communautés. Cette étude permet également de caractériser spatialement les zones d'études selon l'assemblage microphytoplanctonique qu'il possède. Ce chapitre a fait l'objet d'une publication en mai 2021.

Dans le **Chapitre 4**, une approche par traits fonctionnels est décrite à partir des informations taxonomiques issues des identifications REPHY et d'une base de traits fonctionnels adaptée aux taxons de nos zones d'études (utilisation et développement d'une base existante à partir des données bibliographiques disponibles). Ces données permettront de mettre en place des groupes fonctionnels au travers d'analyses de correspondances et de clusterisation. Ces groupes enrichiront l'approche communautaire du chapitre 3, cette fois dans le contexte de la baisse de chlorophylle-a observée à l'échelle de la Manche vers 2008.

Dans le **Chapitre 5**, une approche par niche écologique est effectuée pour caractériser l'espace écologique dans lequel évoluent les groupes fonctionnels établis au chapitre 4. Il a pour objectif de répondre au questionnement implicite chez les organismes phytoplanctoniques suivant ; le partage de traits fonctionnels conduit-t-il au partage d'une même niche écologique ? En reprenant la même diversité taxonomique, une ordination par niche permet de classer les taxons selon leur affinité environnementale et d'établir des clusters par niche. Une analyse des dendrogrammes fonctionnels et écologiques est donc permise afin de déterminer les similitudes et de répondre à la problématique.

Dans le **Chapitre 6**, cette approche a pour ambition d'explorer une des limites de l'approche par traits fonctionnels que l'on a pu rencontrer au chapitre 4 ; la prise en compte de la plasticité cellulaire. Elle vise donc à étudier la variabilité spatiale et temporelle de l'information fonctionnelle. Ainsi, les teneurs en chlorophylle-a et en lipide des cellules phytoplanctoniques sont obtenues par microscopie confocale au CMABio3 de Caen. Un protocole de prélèvement chaque mois pendant 1 an permet l'acquisition de données sur trois sites contrastés, c'est à dire à influence marine, estuarienne ou intermédiaire comme déterminés au chapitre 3.

Dans les **Chapitre 7 & 8**, nous explorons la thématique des algues toxiques. Dans un premier temps, les résultats d'une collaboration avec le laboratoire de Plymouth dans le cadre du projet S3-EUROHAB sont mis en avant. Il s'agit d'une étude comparée des efflorescences de *Dinophysis* spp. et des facteurs environnementaux qui les conditionnent. Dans un second temps, les résultats d'une campagne menée en estuaire de Seine fin avril et fin mai 2019 sont présentés. Il s'agit d'une étude sur la dispersion spatiale d'une efflorescence de *Pseudo-nitzschia* sp. et de l'influence d'un panache fluviale sur cette dispersion. Cette dernière est approfondie au travers de l'analyse de données historiques autour de *Pseudo-nitzschia* sp. et de ses influences environnementales, dans ce même environnement estuarien.

Dans le cadre du projet doctoral, l'exploration de la diversité génétique de *Pseudo-nitzschia* sp. par qPCR dans l'étude de la succession spécifique du genre avait été initiée en collaboration avec le Marine Institute de Galway (Irlande). Il s'agissait de comparer la succession spécifique et le timing d'apparition de certaines espèces clés (*P. australis, P. pungens, P. delicatissima, P.fraudulenta, P. seriata* *et P. multiseries*) au cours d'une année. Si les financements pour deux mois de mobilité, les prélèvements et le protocole étaient prêts, la mobilité n'a pu être réalisée. La crise sanitaire de Covid19 a éprouvé la communauté scientifique durant près de deux ans, et le laboratoire d'accueil n'a pas été épargné. Le Marine Institute s'est donc malheureusement retrouvé incapable d'accueillir une étudiante étrangère dans ses locaux des suites des difficultés qu'a pu rencontrer le pays irlandais au cours de cette crise.

2

Données et Choix méthodologiques

Si le format de ce manuscrit permet d'accéder aux divers développements méthodologiques au sein de chaque chapitre à l'instar de la construction d'un article scientifique, ce chapitre a pour objectif d'exposer les coulisses des enrichissements matériels et méthodologiques rencontrés durant les travaux de ce doctorat.

Cette partie est divisée en plusieurs sections qui reviennent sur les choix et les partis pris pour répondre aux problématiques. La première fait un retour sur le jeu de données qui aura permis d'explorer un grand nombre de points écologiques durant ce doctorat. La deuxième explore l'aspect fonctionnel ; une partie très riche qui a suscité beaucoup de questions et d'aller-retours entre bases de données et analyses. Une troisième partie développe l'approche par niche écologique. Enfin, la dernière revient sur les études expérimentales, de terrain ou de laboratoire.

2.1 Les cellules de suivi, acquisition de données

2.1.1 Les besoins en données pour répondre aux problématiques écologiques

La recherche s'articule autour de quelques axes simples : hypothèses, méthodologies, acquisitions de données, traitements et résultats, discussions et valorisations. La première étape, la donnée, est la plus importante. Beaucoup de chercheurs se rendent compte qu'il est difficile voire impossible d'exploiter un jeu de données sans en connaître les méthodes d'acquisition. C'est à dire, de la théorie protocolaire à la réalité de terrain, et les difficultés et imprévus associés. Néanmoins, un manque d'homogénéisation et de comparabilité des protocoles à une échelle nationale ou internationale risque d'amener à une perte de pertinence des observations et des conclusions car celles-ci deviennent discutables vis-à-vis d'autres études aux questionnements similaires mais aux protocoles différents.

Aujourd'hui, il existe des réseaux de suivis dont l'ancienneté permet d'accéder à un haut niveau d'information, celui des séries temporelles. Pour le compartiment phytoplanctonique, l'Europe possède des réseaux de rare qualité que ce soit par leur résolution ou leur étendue géographique et temporelle ; le Continuous Plankton Recorder survey [1] (CPR) en mer du Nord qui fut créé en 1931 et la série journalière d'Helgoland [2] (île au Nord de l'Allemagne) qui a débuté en 1962.

En France, l'Ifremer (l'Institut Français de Recherche pour l'Exploitation de la Mer) a déployé en 1984 un réseau national d'observation appelé REPHY (Réseau de surveillance du phytoplancton et de l'hydrologie dans les eaux littorales). Ce réseau, ainsi que de nombreux autres (suivis des contaminants - ROCCH, suivis microbiologiques - REMI, de la faune et flore benthiques - REBENT, etc...), s'insèrent dans le cadre d'une volonté de surveillance de l'environnement

---

[1] www.cprsurvey.org

[2] www.awi.de/en/science/biosciences/shelf-sea-system-ecology/working-groups/long-term-observations-lto/helgoland-roads-phytoplankton.html

littoral[3] (Envlit) et furent particulièrement motivés par la présence de risques sanitaires suite à la consommation de mollusques contaminés par des blooms algaux toxiques (réseau REPHYTOX). Le REPHY permet la coordination des prélèvements mensuels à l'échelle nationale selon un protocole standardisé et rigoureux de prélèvements et d'analyses des flores phytoplanctoniques mais également des paramètres hydrologiques associés (température, salinité, turbidité et concentration en oxygène dissous) (Neaud-Masson, 2016). Dans ce programme, il existe 3 stratégies de lecture des flores selon les besoins : flores totales (FLORTOT) ; identification et dénombrement complète de la communauté microphytoplanctonique qui est faite régulièrement (sous réserve de conditions météorologiques adéquates), flores indicatrices (FLORIND) ; ciblées sur les taxons dont l'abondance dépasse 100 000 cellules.L^{-1} ou qui sont avérés toxiques et flores partielles (FLORPAR) ; des taxons toxiques, fréquemment mis en place en période à risque. L'identification est faite de sorte à avoir la plus haute précision connue pour l'observation ; l'espèce. La base de données regroupe néanmoins différents rangs taxonomiques (Tableau 2.1). Le suivi du REPHY s'est vu perfectionné en 2016 par l'arrivée des IPI (Intercomparison of Phytoplankton Identification), des tests d'identifications multi-laboratoires, coordonnés par le Marine Institute de Galway (Irlande). Ce type de test permet d'évaluer la stabilité de l'identification à l'échelle internationale et de permettre une homogénéisation et comparabilité des résultats.

2.1.2 Perfectionnement du jeu de données de la Manche

C'est sur ces données REPHY que ce travail base la majorité de ses résultats. C'est pourquoi il est essentiel d'expliciter les différents traitements et ajustements qu'il a été nécessaire d'appliquer avant leur utilisation. En effet, afin de mieux comprendre la diversité spatiale de la Manche et de la particularité de la Baie de Seine, la zone d'étude a été élargie le long des côtes françaises de la Manche, du Golfe Normano-Breton à la Baie de Somme (Figure 2.1). Les stations de suivis proches (même baie, même estuaire) de St Cast et Les Hébihens ont été

---

[3] wwz.ifremer.fr/envlit/Surveillance-du-littoral

TABLE 2.1 – Rangs taxonomiques initialement identifiés dans la base de données REPHY pour la période 2002-2018. L'appellation *e-* correspond au terme *ensemble de* et désigne des groupements d'espèces ou de genres

Rang	Nombre de taxons	%
Genre	**67**	**38,5**
Espèce	**50**	**29**
e-espèces	**18**	**10,3**
Famille	13	7,5
e-genre	12	7
Classe	6	3,5
Ordre	3	1,8
Autre	3	1,8
Phylum	1	0,7
Sous-classe	1	0,7

rassemblés sous un même libellé (STCA), la série temporelle régulière s'étant arrêtée sur l'un en 2003 et ayant repris sur l'autre en 2007. Les six stations de suivi sur cette zone d'étude ont été déterminées de part leur pertinence en terme de qualité de données et de régularité d'acquisition également. Ainsi, de 2008 à 2019, chacun des sites a été échantillonné a minima mensuellement (7.3). Pour les sites de Baie de Seine uniquement, on peut remonter la série régulière à 2002. Les périodes temporelles ainsi que le niveau de résolution (bi-mensuel, saisonnier à annuel) qui sont présentés tout au long de cette thèse ont été sélectionnés pour répondre aux exigences méthodologiques ainsi qu'à la problématique du chapitre dans lequel elles s'articulent (le détail de la fréquence d'échantillonnage est donné Figure 7.3).

Les données de flores phytoplanctoniques utilisées ont été acquises et traitées par trois Laboratoires Environnement-Ressources Ifremer (LER) différents ; Dinard, Port-en-Bessin et Boulogne-sur-mer. Dans le cadre d'une analyse de communauté, l'information associée à l'appellation d'un taxon est importante. Chaque laboratoire a donc été contacté concernant la dénomination utilisé pour chaque taxon. Des vérifications ont également été faites quant aux cohérences temporelles ;

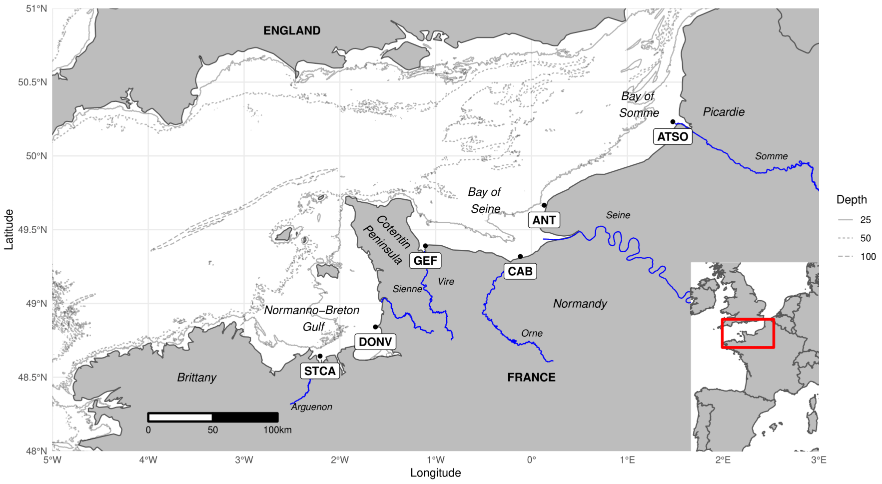


FIGURE 2.1 – Zone d'étude française, les étiquettes indiquent la position des 6 sites étudiés au cours du projet.

suivi des changements de regroupements taxonomiques (dites "e-species" ou "e-genus"), acquisition de données à un plus haut ou plus bas niveau d'identification, ainsi que le suivi des actualisations conformément aux nouvelles appellations accessibles grâce la plateforme World Register of Marine Species (WoRMS)[4]. Cet effort d'homogénéisation sur initialement près de 200 taxons, a été une tache nécessaire qui fut souvent reprise et corrigée au cours des différents traitements de données. Une base valide a finalement été développée en vue d'être publiée sur la plateforme Zenodo en parallèle des articles scientifiques.

---

[4] www.marinespecies.org

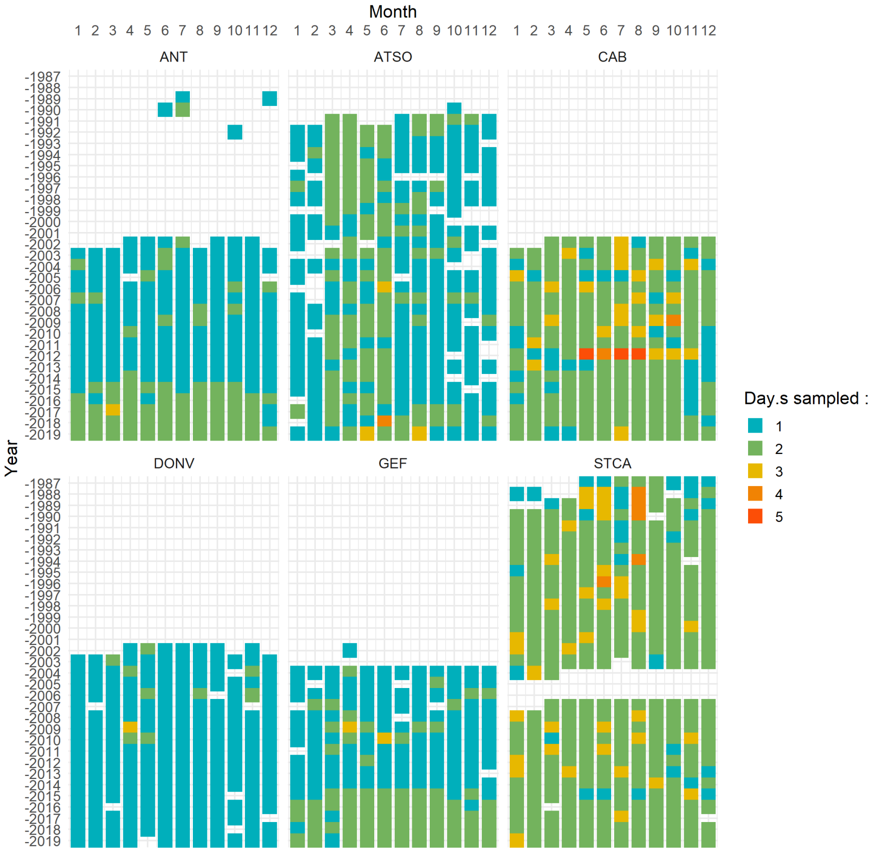


FIGURE 2.2 – Évolution des résolutions de prélèvements REPHY & RHLN d'eau de mer aux six stations d'intérêts (Antifer, At So, Cabourg, Donville, Géfosse, et St Cast) depuis 1987. En couleur est indiqué le nombre de prélèvement.s effectué.s durant le mois (colonne) et l'année (ligne) concernés.

2.2 Approche fonctionnelle

2.2.1 Une approche au coeur de la relation organisme-environnement

L'approche par traits fonctionnels est de plus en plus utilisée en écologie. Elle permet de renseigner sur le ou les rôle.s d'un organisme au sein d'une communauté, voire d'un écosystème. Cette approche détient notamment un fort potentiel pour expliquer la structuration d'une communauté, et elle peut apporter des éléments de réponse pour comprendre les réorganisations qui découleraient d'un changement global, tel que celui prédit pour les quelques dizaines d'années à venir (Litchman & Klausmeier, 2008).

McGill et al. (2006) définissent un *trait* comme étant une caractéristique bien définie et mesurable d'un organisme. Un trait dit *fonctionnel*, est par définition un trait qui va influencer les performances de l'organisme dans son écosystème. Certaines approches de regroupements fonctionnels ont pu être mises en place par le passé, elles sont notamment plus largement utilisées en milieu aquatique. Pour le milieu marin, Margalef (1978) aborde cette thématique en démontrant que le phytoplancton est structuré selon deux axes principaux que sont la concentration en nutriments et la turbulence. Il s'agit d'un principe connu sous le nom de "Mandala de Margalef", séparant les organismes à stratégie r (diatomées en eaux mixes et riches) et à stratégie K (dinoflagellés au sein d'eaux oligotrophiques et stratifiées). Cette classification suit ainsi la division taxonomique des deux principales classes de phytoplancton. En parallèle, principalement en milieu aquatique, Reynolds (1984) et Kruk et al. (2021) vont développer une classification selon un schéma nommé "CSR" différenciant les espèces coloniales, tolérantes au stress, et rudérales[5]. La difficulté dans ces approches réside dans le partitionnement des taxons dans l'un ou l'autre des groupes. Contrairement à la théorie, ces taxons n'ont pas une limite stricte, ils possèdent en revanche une certaine plasticité sur la plupart des traits. Le choix de regrouper un taxon dans un groupe particulier revient donc à l'observateur ou l'analyste. C'est une approche "manuelle" qu'il a été choisi d'éviter dans nos études. C'est pourquoi, la construction d'une base de traits complète et une approche mathématique ont été préférées dans l'approche fonctionnelle explorée.

2.2.2 Contraintes et choix dans la création d'une base fonctionnelle adaptée

A l'échelle phytoplanctonique un grand nombre de traits peuvent être considérés, certains plus accessibles que d'autres. Afin de pouvoir travailler sur une table de traits complète pour un grand nombre de taxons phytoplanctoniques, il a été choisi d'utiliser des traits couvrant à la fois l'aspect morphologique,

---

[5] Terme botanique désignant des plantes vivant sur des décombres ou des rejets, en milieu anthropisé et eutrophe.

physiologique et comportemental tels que décrit par Litchman & Klausmeier (2008) (Figure 2.3). Cependant, leur étude préconise également l'utilisation de traits relatifs à l'acquisition de nutriments ou à l'utilisation de la lumière. Ces traits n'ont pas été définis dans l'approche présentée aux chapitres 4 et 5 puisque les modalités associées à ces traits ne sont pas connues pour chacun des 87 taxons étudiés et leur variabilité à l'échelle individuelle est telle que cela aurait augmenté le niveau de complexité et d'incertitudes des résultats et des conclusions. La plupart des traits morphologiques sont en effet déjà soumis à une forte plasticité.

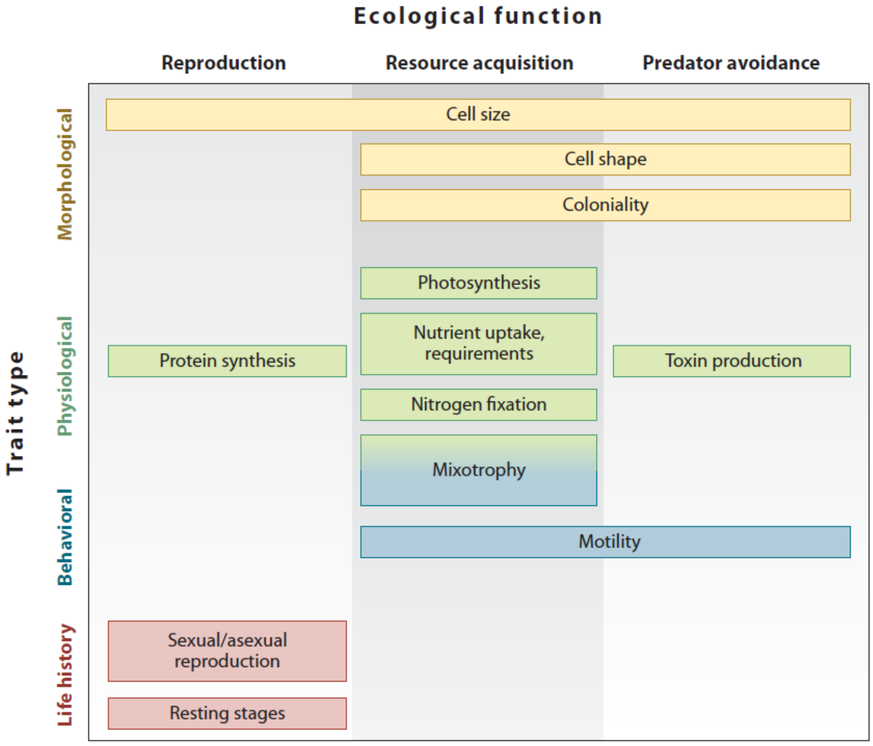


FIGURE 2.3 – Typologie des traits fonctionnels phytoplanctoniques (extrait de Litchman & Klausmeier (2008))

Entre avril et mai 2020, l'encadrement de Camille Durant (stage de M1) durant cette thèse a permis une première approche à la fonctionnalité. Son stage avait pour objectif de rassembler les informations relatives à la construction d'une base de traits adaptée à la zone d'étude de la Manche et à la communauté phytoplanctonique associée. Les travaux issus de la littérature permettent d'accéder à un grand nombre de ces informations et, afin d'éviter toute redondance avec des travaux passés publiés, le travail de stage s'est concentré d'abord sur les travaux de Ramond et al. (2018). Leur base reprend un grand nombre de genres de protistes marins et est complète pour de nombreux traits morphologiques, physiologiques et comportementaux. Néanmoins, certains traits importants (régime trophique, mobilité, habitat) étaient parfois peu renseignés ou manquants une fois notre sélection taxonomique effectuée. Des recherches bibliographiques supplémentaires ont été faites par taxon, par trait pour répondre à des besoins supplémentaires :

- Avoir une base de trait respectant la distinction de rang à l'espèce, voire parfois au genre.
- Compléter les informations manquantes pour certains traits majeurs ; rapport surface/volume, présence de soies ou d'épines, forme géométrique (finalement pas retenue car redondante avec d'autres traits morphologiques comme la taille et le rapport S/V), régime trophique, habitat préférentiel, production de substances nuisibles ou toxiques, capacité à former un stade de dormance.
- Faire en sorte que la modalité des traits soit adéquate vis-à-vis de la zone d'étude (Atlantique Nord-Est). Ainsi, l'ensemble des traits relatifs à la taille (tailles mininmum et maximum, biovolumes, surface volumique et ratio S/V) sont issus ou calculés à partir des données du site Nordic Microalgae (`http://nordicmicroalgae.org/`) dont l'origine des données provient d'organismes de Mer du Nord.

Ces différents traitements de données ont abouti à la sélection de 10 traits couvrant un total de 36 modalités et décrivant 87 unités taxonomiques (espèces, genres ou ensembles de l'un ou de l'autre)(Tableau 2.2). A chaque trait choisi pour décrire l'aspect fonctionnel de chaque taxon est associée une signification écologique qui va de la facilitation dans l'acquisition des nutriments (ex : pour les organismes à fort rapport Surface/Volume), au captage de la lumière (ex : forme élongée, capacité à rester en surface), en passant par l'évitement de la prédation (ex : présence d'épines ou de soies, formations de colonies, production de substances bio-chimiques).

Parmi les traits utilisés, la description de l'habitat préférentiel permet de mettre en évidence des taxons dont la présence est plutôt associée au fond marin, bien que le protocole de prélèvement soit réalisé en surface. Principalement distingués chez Hernández Fariñas et al. (2017), les taxons sont distribués selon leur critère *planctonique* ; libre dans la colonne d'eau, dispersion strictement planctonique, *benthique* ; sur le fond, *épiphytique* ; accroché à un autre organisme, sur une particule, un algue ou un résidu, souvent pour faciliter le déplacement dans la colonne d'eau, ou encore *tychoplanctonique* ; c'est à dire présentant un cycle bentho-pélagique relié au niveau de turbulence.

Certains taxons peuvent produire des substances toxiques ou nuisibles. Le caractère toxique est donné lorsque la molécule produite induit des contaminations et intoxications chez d'autres organismes, c'est le cas des toxines à ASP, DSP et PSP (Amnesic, Diarhetic, Paralytic Shellfish Poisonning). La substance est nuisible si par sa présence, il y la production de mousses ou mucus (ex : *Phaeocystis globosa*, *Lepidodinium chlorophorum*), ou si, via une prolifération importante, elle va entraîner des phénomènes d'hypoxie ou de gênes pour les autres organismes présents sur la zone concernée (Gladyshev & Gubelit, 2019).

TABLE 2.2 – Traits fonctionnels et leurs modalités (* : trait utilisé pour distinguer les organismes siliceux (eq. diatomées) des autres organismes, ils seront analysés séparément).

Traits	**Modalité**	**Type**	**Fonction écologique**
Taille max (µm)	0-25 / 25-50 / 50-100 / 100-200 / 200-500 / 500-1500	Morphologique	Acquisition de ressources Évitement de la prédation Vitesse de sédimentation
Ratio Surface / Volume	0-1 / 1-10 / 10-30 / 30-60	Morphologique	Assimilation de nutriments
Épines ou soies ?	Épines / Soies / Absence	Morphologique	Évitement de la prédation
Forme	Ronde / Élongée	Morphologique	Acquisition de ressources Évitement de la prédation
Mobilité	Flotteur / Glisseur / Nageur	Comportemental	Déplacement dans la colonne d'eau Relation à la lumière
Forme coloniale	Courbée / Droite / Absente	Comportemental	Facilitation de sédimentation Évitement de la prédation
Régime trophique	Autotrophe/ Hétérotrophe / Mixotrophe	Comportemental	Gestion de la pression nutritive
Habitat préférentiel	Planctonique / Épiphytique / Benthique / Tychoplanctonique	Comportemental	Relation à la lumière Relation à la pression de filtration
Phase de dormance	1 (oui) / 0 (non)	Physiologique	Fitness
Production de substance	Toxique / Nuisible / Absente	Physiologique	Évitement de la prédation Intéraction biotique
Couverture*	Siliceuse / Nue / Organique	Physiologique	Acquisition de ressources, Division de classe

2.3 Approche par niches écologiques

2.3.1 Une illustration de la place d'une espèce dans son environnement

La relation espèce-environnement est au coeur du fonctionnement des écosystèmes marins, aquatiques et terrestres. C'est sur cette relation que se jouent les grands cycles de la vie que l'on suit chaque saison sans plus tellement y porter attention ; c'est le froid qui fait tomber les feuilles en automne, et le manque de nourriture qui amène certaines espèces à hiberner durant toute une saison. Si ces exemples font partis de nos connaissances générales et sont acquises, il reste néanmoins de multiples cas d'études méconnus du grand publique, où cette relation est au coeur du fonctionnement de l'écosystème. C'est notamment le cas dans la saisonnalité phytoplanctonique. La succession d'espèces selon les conditions environnementales va amener des taxons plus adaptés, plus compétitifs à proliférer dans un environnement qui leur est idéal. Cet environnement, l'ensemble des conditions dans lesquels ils font pouvoir croître et se reproduire, caractérise leur niche écologique. Ce terme date du début du XX$^{\text{ème}}$ siècle, et a été utilisé pour la première fois dans un article de recherche ornithologique sur le Moqueur de Californie (*Toxostoma redivivum*) par Grinnell (1917). La niche est propre à chaque taxon et peut être amenée à évoluer dans le temps, et comme Grinnel l'indique déjà en 1917, elle est telle que deux espèces ne peuvent posséder une exacte même niche écologique.

Vers le milieu du XX$^{\text{ème}}$ siècle, Hutchinson (1957) développe un concept qui est depuis utilisé comme référence dans la plupart des approches par niche. Il définit une niche dite *fondamentale* qui se présente comme un hypervolume théorique de n-dimensions dont chaque extrémité correspond aux limites des n facteurs pour garantir la présence *ad vitam aeternam* de l'espèce. A côté de cette théorie est définie la niche *réalisée* (inclue dans la niche fondamentale) qui rassemble les circonstances dans lesquelles l'espèce est réellement présente considérant les interactions avec les autres espèces et co-stresseurs environnementaux qui vont influencer sa survie.

2.3.2 Les approches méthodologiques, l'OMI expliquée

Dans les études de niches écologiques, l'utilisation de modèles, notamment des modèles de distributions des espèces (EDMs ; distribution réalisée) et des modélisations de niches écologiques (ENMs, distribution potentielle, par exemple dans le cas des espèces invasives) permet de comprendre les phénomènes ayant conduit à des distributions, des croissances particulières chez certaines espèces (Melo-Merino et al., 2020). Majoritairement utilisées, les méthodes d'ordinations permettent d'estimer et de visualiser la niche écologique d'un organisme. Ce sont des approches corrélatives où la relation entre la distribution (intégration de l'abondance et non la simple présence) et les variables explicatives choisies est exploitée en vue d'établir une représentation en 2 ou 3 dimensions de cette distribution. Les travaux présentés ici exploitent une approche d'ordination particulière pour explorer les niches écologiques ; l'OMI (Outlying Mean Index), qui permet de comparer l'habitat d'une espèce à une moyenne correspondant à la zone échantillonnée (Dolédec et al., 2000).

La méthode OMI prend en compte l'ensemble des niches écologiques de chacune des espèces d'une communauté et aspire à maximiser la *marginalité* des espèces en combinant les variables environnementales. Il s'agit de la distance entre l'habitat moyen utilisé par le taxon et l'habitat moyen de l'ensemble des prélèvements, tous taxons confondus. Un espèce dite marginale (valeur élevée) sera caractérisée par une présence dans un habitat atypique de la région, une espèce non marginale (valeur faible) sera au contraire dans un habitat typique de la région. L'analyse permet également d'accéder à l'étendue de la niche, c'est la *tolérance*, qui permet de différencier des espèces généralistes (grande tolérance) vis-à-vis des pressions environnementales, et les espèces spécialistes (faible tolérance), dont la présence nécessite des conditions environnementales particulières.

En 2017, Karasiewicz et al. (2017), reprend et adapte la méthode OMI pour pouvoir intégrer les notions de différences spatiales et temporelles, c'est la WitOMI (Within OMI, Figure 2.4). Ainsi, le long de deux axes représentant les gradients environnementaux issus de l'ordination, il est possible de représenter plusieurs informations autour de la niche écologique d'une espèce phytoplanctonique :

- L'ensemble des informations relatives à l'environnement permet de définir l'espace globale **E**.
- L'espace réellement occupé par l'espèce d'intérêt est donc la niche réalisée $\mathbf{N}_R$ ($N_R \bigcap E$).

A titre d'exemple, au cours de notre approche au chapitre 7, c'est le critère spatiale qui va guider la division en sous-ensembles (eq. sous-niches), c'est à dire que notre jeu de données couvre plusieurs sites et l'information sera graphiquement représentée pour illustrer la position de l'espèce dans chacun d'entre eux. Au chapitre 8, 3 périodes temporelles (3 sous-niches) seront comparées de la même manière. Ainsi :

- Pour le sous-espace choisi, un sous-espace environnemental **K** peut être représenté, celui-ci appartient à E ($K \bigcap E$).
- Au sein de la niche réalisée N_R, on peut définir la niche potentielle $\mathbf{S}_p$ qui est à l'intersection entre la niche réalisée N_R et l'environnement considéré K ($\mathbf{S}_p = N_R \bigcap K$).
- La présence réelle de l'espèce dans l'environnement K est donnée par la surface S_R.
- La place de la contrainte biotique S_B, d'après Jackson & Overpeck (2000), pour les organismes végétaux, correspond à l'espace qui pourrait être potentiellement occupée par l'espèce mais dans les faits ne l'est pas . En effet, il existe 3 axes contraignant la niche d'une espèce, c'est le diagramme dit BAM ; pour biotique (compétitions, prédations, interactions diverses), abiotique (tolérances à l'environnement, température, salinité, etc...), mouvement (capacité à se mouvoir rapidement ou pas du tout dans son environnement) (Soberón & Peterson, 2005). Cependant, l'aspect mouvement n'est pas déterminant pour le plancton dont le déplacement par définition n'est pas maîtrisé.

Dans leur approche Litchman et al. (2012) argumentent le besoin de l'intégration des processus physiologiques d'une espèce en fonction des gradients

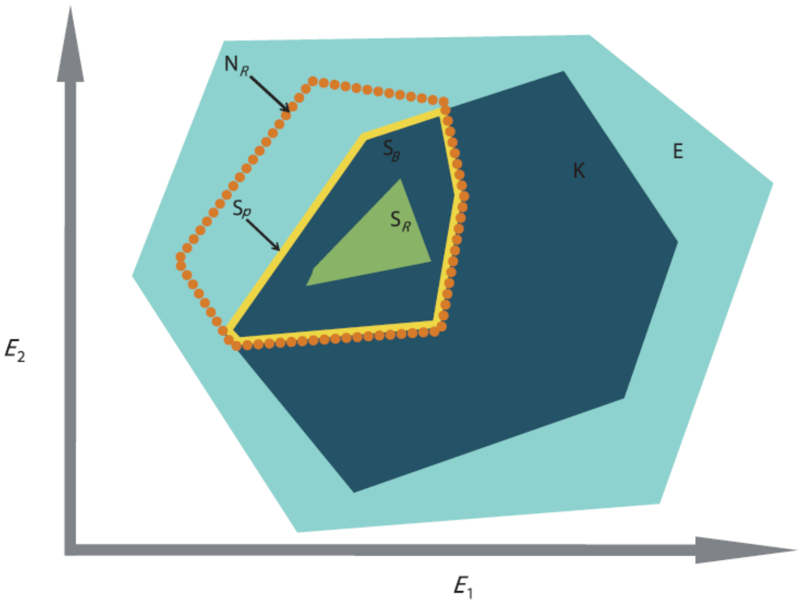


FIGURE 2.4 – Concept de la niche fondamentale, de la niche réalisée, de la place relative aux interactions biotiques amenant à la localisation de la sous-niche (extrait de Karasiewicz et al. (2017)). E1 et E2 caractérisent l'espace environnementale des suites d'une ordination. **E** (bleu pâle) = environnement réalisé. $\mathbf{N}_R$ (orange) = niche réalisée. **K** (bleu foncé) = sous-environnement selon le critère de sélection choisi. $\mathbf{S}_p$ (jaune) = niche potentielle = $\mathrm{S}_B + \mathrm{S}_R$. $\mathbf{S}_B$ = contrainte biologique. $\mathbf{S}_R$ (vert) = sous-niche réalisée

environnementaux afin de pouvoir estimer et prédire sa distribution à partir de modélisation de niches. Ainsi, utiliser des traits tels que l'utilisation de ressources ou des courbes de tolérance vis-à-vis de certaines variables environnementales permettraient la construction de niches capables d'évoluer selon les changements environnementaux. Si, compte tenu du contexte actuel de changement global, il serait effectivement pertinent de pouvoir établir des modélisations de niches évolutives, cela demande des connaissances complètes et précises de l'espèce étudiée, notamment des connaissances adaptées à la vie en milieu naturel (notion de plasticité). La plupart des résultats obtenus dans cet optique sont pour le moment principalement issus de cultures mono-spécifiques en laboratoire, par conséquent ils restent principalement indicatifs du potentiel de résistance ou du fonctionnement cellulaire en milieu contrôlé.

2.4 Approche de terrain et de laboratoire

L'utilisation et l'exploration du milieu naturel sont inhérentes au projet de recherche, et cela se fait dans les limites des possibilités techniques et matériels. Les combinaisons de nombreuses méthodes : prélèvements pour le suivi de communautés, campagnes ponctuelles visant à comprendre des phénomènes soudains, utilisation de bouées hautes fréquences et exploitation des images satellites, permettent d'accéder aux informations de terrains et de les confronter aux théories et hypothèses scientifiques issues de modélisation ou de milieux de cultures.

Au sein du projet, la part initialement prévue des travaux de terrain et de laboratoire était minoritaire et concentrée autour d'une sortie en mer visant à explorer la relation entre *Pseudo-nitzschia* sp. et le panache de la Seine. Cette dernière s'est déroulée au printemps 2019. Dans un second temps, les travaux du doctorat furent enrichis avec un axe expérimentale supplémentaire. En effet, la variabilité des traits caractérisant le phytoplancton a été approchée par un suivi de 12 mois de la teneur en chlorophylle-a et en lipides des cellules du milieu marin aux points habituels du programme REPHY.

2.4.1 Une campagne en embouchure de Seine pour suivre une efflorescence de *Pseudo-nitzchia* sp.

Afin de mieux comprendre la dispersion des cellules de *Pseudo-nitzschia* sp. et de la toxine potentiellement associée ; l'acide domoïque, un des premiers enjeux du doctorat fut de concevoir deux sorties en mer afin de caractériser au mieux un bloom du genre dans une zone ciblée de l'estuaire de Seine. Ainsi, une première approche d'analyse numérique a permis de localiser les apparitions des HABs du genre *Pseudo-nitzschia* à proximité de l'embouchure de Seine et du panache fluviale de celle-ci. Dans la partie qui suit, le raisonnement et le protocole sont expliqués, des détails techniques sont également développés au chapitre correspondant (chapitre 8).

Un bloom de *Pseudo-nitzschia* sp. se caractérise en deux phases ; la prolifération et le déclin, qui se succèdent sur un interval de temps de quelques semaines. L'exploration des données historiques sur la zone a mis en évidence qu'une densité de *Pseudo-nizschia* sp. de plus de 10^4 cellules par litre annonce soit le début de la phase exponentielle d'un bloom soit son pic de densité maximale (selon l'intensité du bloom et l'année donnée) avant son déclin. En 2020, les données issues des suivis REPHY et RHLN ont permis de cibler la période de prolifération du bloom fin avril, donnant lieu à une première sortie le 25 avril. Trois semaines plus tard, le déclin a été enregistré et a déclenché une deuxième sortie le 21 mai.

Considérant que le phytoplancton en milieu marin est suivi uniquement en surface, le prélèvement devait pouvoir renseigner sur la distribution verticale du genre potentiellement toxique. Cela était d'autant plus important que le panache fluvial en estuaire peut entraîner une stratification haline, créant une couche de maximum de chlorophylle-*a* à quelques mètres sous la surface (MLD ; mixed layer depth), dans une eau sondée en moyenne à 10m de profondeur. Il était donc probable d'identifier une répartition verticale des cellules de *Pseudo-nitzschia* sp. comme observée par Velo-Suárez et al. (2008) en milieu estuarien de Galice.

Ensuite, les données satellites de dispersion du panache (Figure 2.5) mettaient en évidence que ce dernier était majoritairement influencé par les vents du sud-ouest, et par conséquent se dirigeait vers le nord, formant un fleuve côtier le long des côtes jusqu'à atteindre la Baie de Somme (Brylinski et al., 1991). Un protocole de prélèvement théorique en 3-dimensions a donc été mis en place avec les équipes du LERN de Port-en-Bessin, pour un échantillonnage de 3 transects, chacun divisé en 4 points de prélèvements, à 4 niveaux de profondeurs (surface, 3m, 6m et fond) . Ce protocole a pu être réalisé sur une période de quelques heures autour de l'horaire de marée haute, dans les limites des conditions météorologiques et de temps de sortie permis par les horaires d'ouvertures du port (Figure 2.6). Trois embarcations ont été nécessaires pour réaliser cette campagne, chacune commençait au point le plus proche de l'estuaire et prélevait simultanément, au possible, chacun des points dont il avait les coordonnées GPS.

Une sonde CTD était fixée sur le bout des bouteilles Niskin de sorte à as-

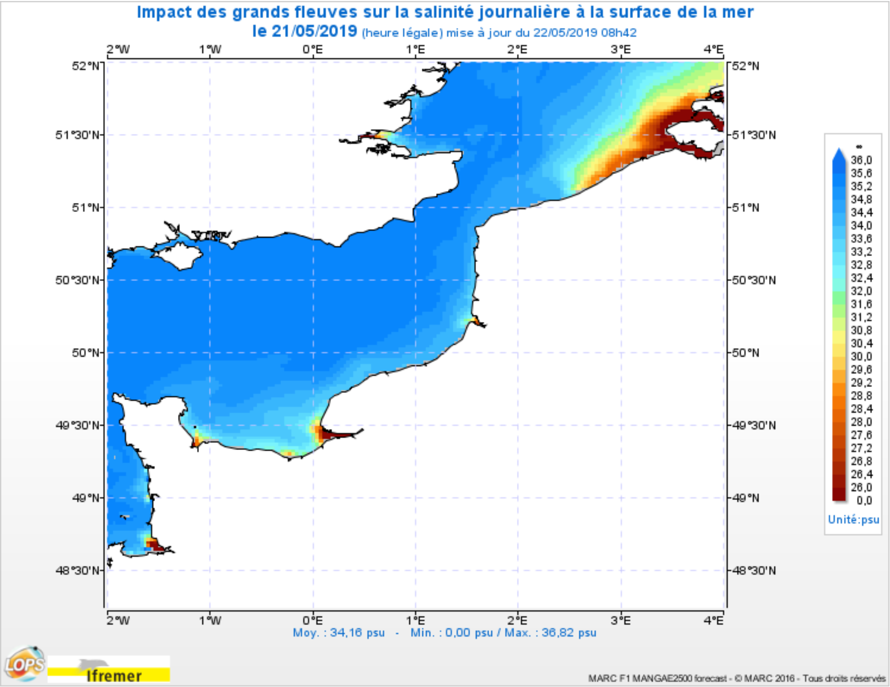


FIGURE 2.5 – Distribution de la salinité en embouchure de Seine le 25 avril 2020 (extrait de `https://marc.ifremer.fr/`)

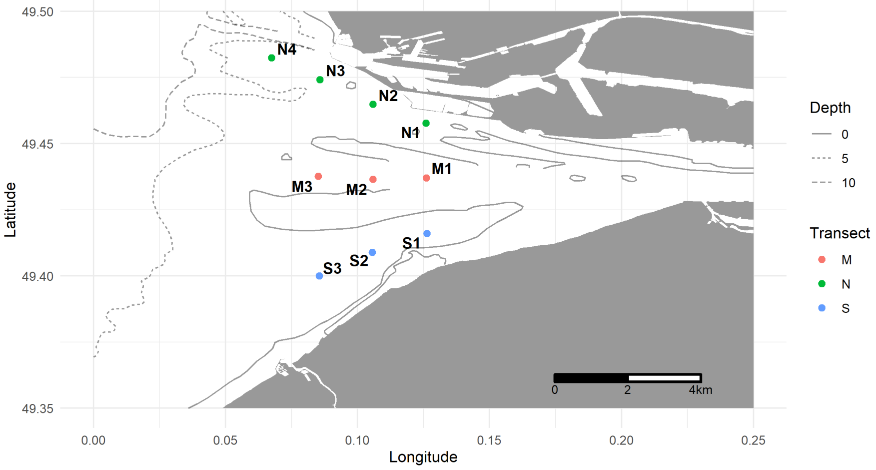


FIGURE 2.6 – Plan d'échantillonnage réalisé en estuaire de Seine. A l'exception du transect Nord (N), aux 2 premiers points 4 profondeurs ont pu être prélevées, au 3ème point seules 3 profondeurs ont pu être executées (surface, mi-profondeur, fond).

surer la profondeur du prélèvement et de permettre l'acquisition des données de température, de salinité et d'oxygène dissous. A chaque remontée de bouteille, des flacons étaient nettoyés et remplis en vue d'être analysés en laboratoire. A chaque prélèvement, les informations concernant les concentrations en nutriments (ammonium, nitrate, nitrite, phosphate et silicate), la turbidité, l'acide domoïque dissous et particulaire ainsi que les abondances de *Pseudo-nitzschia* sp. et l'état physiologique de la communauté (mesure au PAM) étaient obtenues. Additionnellement, des analyses par cytométrie au CREC (Centre de Recherche en Environnement Côtier) de Luc sur Mer, ont permis d'acquérir les densités de pico et nano-phytoplancton pour chaque prélèvement.

2.4.2 Une expérimentation par microscopie confocale inédite

A l'issue de l'approche fonctionnelle, la notion de plasticité des traits par espèce voire par individu n'avait pas pu être explorée et restait au coeur des interrogations. Quelle est la capacité du phytoplancton à s'adapter aux conditions environnementales ? Les plantes sont des organismes fixes, à mobilité théoriquement négligeable, pourtant elles adoptent des mécanismes leur permettant de gérer au mieux les flux lumineux et la disponibilité de la ressource. De la même manière que les tournesols s'orientent face aux soleil, que les oxalis s'ouvrent le jour et se ferment la nuit, il est tout naturel d'associer le phytoplancton à de tels mécanismes. On connaît déjà sa capacité à adapter la flottabilité de ses cellules pour se repositionner dans la colonne d'eau et exploiter au mieux la luminosité de la zone euphotique et l'environnement nutritif (Gemmell et al., 2016). C'est pourquoi, en voulant approcher cette variabilité et des suites d'une initiation à la microscopie confocale, l'idée est venue de tester cette variabilité au niveau intracellulaire et à partir d'organismes prélevés en milieu naturel. Dans la partie qui suit, le raisonnement et le protocole sont expliqués, des détails techniques sont disponibles au chapitre correspondant (Chapitre 6).

Le microscope confocale est un outil dont dispose le CMABio3 de l'US EMERODE de l'Université de Caen, basé sur l'utilisation de lasers. Lorsqu'une cellule d'intérêt est repérée au microscope, il est possible d'obtenir les niveaux de hauteurs minimales et maximales entre lesquels elle se situe et de définir un plan de découpe. A partir de ces informations, l'appareil va scanner des plans à hauteurs régulières, en faisant varier la visse micrométrique selon le pas pré-défini. Sur le logiciel de traitement d'images *ImageJ*, l'ensemble des plans permet de reconstituer l'organisme en 3-dimensions, en extrapolant à chaque fois l'information contenue entre deux plans.

Après quelques tests et réglages à partir de cellules phytoplanctoniques incubées en bouteilles, il a été possible de définir un protocole de suivi de ces teneurs sur 12 mois. Cependant, nous avons mis en évidence que dans un échantillon fixé au lugol acide, la chlorophylle-a répondait à l'ensemble du spectre laser et ne permettait plus de distinguer la fluorescence liée à la teneur en lipide seule. Afin d'observer les deux éléments dans le même individu, il était donc nécessaire d'étudier des organismes vivants, prélevés le jour même.

Dans le cadre de notre étude sur le phytoplancton issu de prélèvements d'eau de mer, la chlorophylle-a va émettre naturellement une fluorescence lorsqu'elle est excitée par une longueur d'onde $\lambda = 633$nm. En revanche, l'utilisation d'une coloration par rouge de Nile (diluée dans du DMSO-Diméthylsulfoxyde pour faciliter l'accès à l'espace intracellulaire), est nécessaire pour obtenir une réponse par fluorescence des composés lipidiques. Ces derniers répondent alors à une excitation laser à $\lambda = 488$nm (Figure 2.7). Le processus d'acquisition utilise un pas de découpe de 0.56µm, défini de sorte à ce que l'extrapolation des informations à l'ensemble de la cellule soit cohérent.

Une fois les images acquises, le fichier correspondant à 1 prise contient l'ensemble des plans et se sous-divise en trois champs superposables, (i) l'acquisition en lumière blanche ; pour l'observation de la cellule via une observation par microscopie classique, (ii) un champs présentant uniquement en sur-brillance (ici vert sur noir) les surfaces associées à la chlorophylle-a répondant à une excitation laser de $\lambda = 633$nm, puis (iii) un champs présentant uniquement en sur-brillance (ici rouge sur noir) les surfaces associées aux contenus lipidiques ayant répondu à une excitation de $\lambda = 488$ nm. Sur le logiciel ImageJ, en suivant les consignes d'un script adapté à cette approche (développé par Nicolas Elie du CMABio3), l'utilisateur détermine sur plusieurs plans issus du champs "lumière

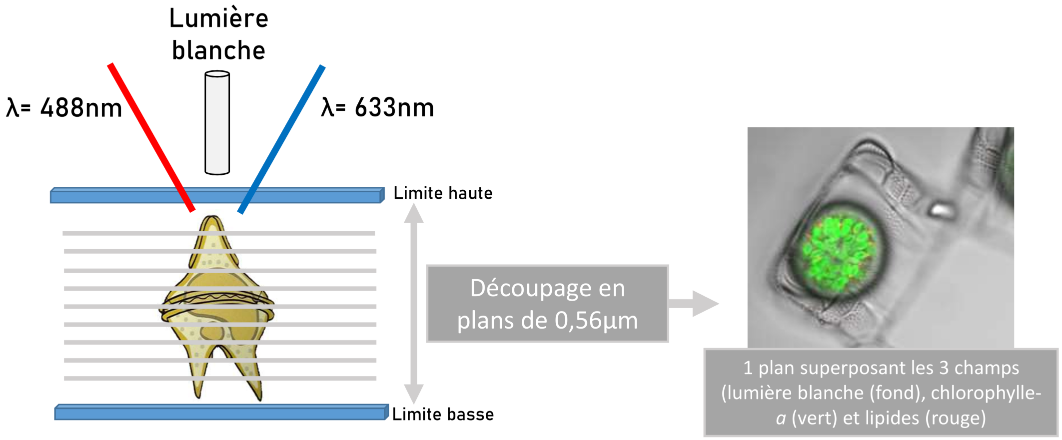


FIGURE 2.7 – Illustration du processus d'acquisition des images par microscopie confocale (gauche) et du résultat obtenue sur un plan (le dessin de *Protoperidinium* sp. est extraite de la Société Japonaise de Plancton (2011), l'image de *Trigonium alternans* est issue de l'analyse.)

blanche" les limites de la cellule cible afin d'estimer son biovolume. À partir de ces informations, le déroulement automatisé du script permet le calcule des teneurs intra-cellulaires souhaitées. L'observation des évolutions des teneurs par microscopie confocale s'est donc avérée une approche originale et précise à l'étude de la plasticité intra-cellulaire des cellules de phytoplancton.

Le temps d'analyse, une fois les limites hautes et basses de la ou les cellule.s d'intérêts déterminées, est relativement lent ; de l'ordre de 7 minutes pour numériser un volume d'intérêt sur toute sa hauteur. Ainsi, une moyenne de 10 fichiers d'images numériques étaient obtenus par échantillon. C'est pourquoi le protocole vise des échantillons issus de 3 sites chaque mois ; STCA, GEF et CAB. Ces derniers avaient déjà été caractérisés comme contrastés du point de vue de l'assemblage de la communauté phytoplanctonique durant une première approche (Chapitre 3) et permettaient de caractériser à nouveau les systèmes estuarien, intermédiaire et marin, ajoutant ainsi une dimension spatiale à l'étude.

3

Decadal trajectories of phytoplankton communities in contrasted estuarine systems in an epicontinental sea.

Angéline Lefran, Tania Hernández Fariñas, Francis Gohin, Pascal Claquin

Ce chapitre revient sur la dernière décennie et explore la variabilité spatio-temporelle du phytoplancton en Manche. Dans un contexte d'environnement changeant, que ce soit climatique ou via une variabilité saisonnière, il est important de connaître les réponses du phytoplancton des milieux côtiers, notamment à l'échelle communautaire. La composition spécifique permet en effet de mettre en évidence différents systèmes, contrastés selon leurs influences fluviales ou marines. D'un point de vu temporelle, les communautés phytoplanctoniques gardent un assemblage stable sur la période étudiée. Sur période estivale, les communautés entre-elles présentent le plus haut taux de similarité inter-annuelle.

Ce chapitre a fait l'objet d'une première publication dans le journal Estuarine, Coastal and Shelf Science (Lefran et al., 2021).

Highlights

- Decadal stability was found in phytoplankton communities in several estuarine systems.
- Average of 30–40% of similarity observed between pair of samples over the decadal period.
- Co-inertia analysis highlighted four separate systems according to their major drivers.
- Community Trajectory Analysis shows greater spatial heterogeneity during summer.
- The dominance of few species explains phytoplankton's estuarine site's specificity.

3.1 Abstract

In coastal areas, global changes are known to affect estuaries and their plume leading to water temperature increase and river discharge variations, which are two of the main drivers controlling phytoplankton dynamics. This paper aims at understanding the past 10 years' variations in term of communities' stability and trajectories along with their relationship with the environment. Considering the high environmental variability along coastal areas, we focused our study on six contrasted estuarine systems from the eastern English Channel. Using monthly monitoring from 2008 to 2019, the response of the micro-phytoplankton compartment was investigated through the abundances of a hundred taxa and several abiotic parameters' records. The results indicate an overall stability in community composition with an average of 30–40% similarity between pairs of samples over the study period. The phytoplankton assemblages also display greater spatial heterogeneity during summer in comparison with other seasons. The co-inertia analysis highlighted four separate systems linked to major drivers ; a system under strong river and nutrient flows influence, a well-mixed and oxygenized estuary, a system challenged by offshore marine waters, and finally a system under shellfish farms pressure. This structuration is built from the dominance of a handful of species that differs from one place to another, which explains why phytoplankton is mostly site specific. Additionally, the low variations led a by few species'

dominance also explains the inter-annual stability noticed during summer at each area, in spite of the high diversity observed.

3.2 Introduction

Phytoplankton, as primary producers, are at the base of the marine trophic network and heterotrophic biomass in coastal ecosystems. Understanding phytoplankton dynamics is crucial for explaining variations encountered at higher levels, and eventually leading to changes on an ecosystemic scale (Sumaila et al., 2011). However, there is a high diversity within the phytoplankton compartment, with thousands of species within the world's oceans (Dutkiewicz et al., 2020; Sournia et al., 1991; Tett & Barton, 1995). Physico-chemical environment and biotic pressures (grazers and parasites) are frequently highlighted as major drivers for these communities (Litchman et al., 2010). At the interface between the river's mouth and the sea, estuarine systems are particularly affected by parameters variability and seasonal patterns. River inputs as well as weather events (rainfall, upwelling, heatwaves and turbulences) trigger saline or thermal stratifications of the water column and affect the assemblage of the phytoplankton communities (Cloern & Jassby, 2008; Mallin et al., 1993). These factors vary through temporal and spatial scales, thus defining the seasonal patterns of phytoplankton structure from one ecosystem to another. Therefore, the primary producers' community assemblage, being dependant of long and short-term physical and chemical factors, is also the reflection of the ecosystem's dynamic.

Chlorophyll *a* (chl-*a* - phytoplankton biomass indicator) in estuarine-coastal ecosystems are mainly due to micro-phytoplankton (cell size > 20 µm) (Carstensen et al., 2015; Wollschläger et al., 2015). Pattern variations within this compartment, such as the decrease of diatoms and the increase of dinoflagellates, have been recorded over the last 40 years with climate oscillations on a global scale (Xiao et al., 2018; Wasmund et al., 2011; Bode et al., 2009; Leterme et al., 2005). Moreover, changes in species seasonal assemblage with a higher homogeneity or even the increase of harmful algal blooms (HABs), have been documented for the past few decades in the North Sea (Nohe et al., 2020). The ongoing climate change is an environmental pressure playing a substantial role in the ecosystem's functioning and could lead to triggering changes within the primary producers. However, climate change can also induce mismatches between primary producers and consumers when differentially impacted (Hallegraeff, 2010). With eutrophication, primary producers may increase in numbers, the degradation that follows of such amounts of organic matter then causes low oxygen levels and water quality deterioration (Rabalais et al., 2014; Kimor, 1992). The combination of both global changes and eutrophication will likely intensify these symptoms (Rabalais et al., 2009). Indeed, with projections of rising temperatures, phytoplankton would be more efficient in nutrient use, causing mismatches with the upper trophic levels, which would alter the ecosystem's functioning (De Senerpont Domis et al., 2014).

Identifying temporal changes within the phytoplankton community's structure is made possible thanks to the study of time-series, which is also a mean to retrace and identify events like harmful algal blooms occurrences (Hernandez-Farinas et al., 2013; Wasmund et al., 2011). Long-term series at Helgoland Roads highlighted both a zooplankton species-specific response to an increasing temperature, as well as a close relation between these populations and phytoplankton cycling (Greve et al., 2004; Radach et al., 1990). This relation coupled with light penetration was seen as a major controlling factor of phytoplankton communities (Wiltshire et al., 2015). However, after a 30-year long time series study, Wiltshire et al. (2008) could not conclude any changes in spring bloom dynamics, or in their timing. This would indicate a persistent resiliency of the phytoplankton community over time. Amongst other analyses, namely on spring blooms and recurrent community structures, a 12-month periodicity was revealed through chl-a monthly time series from temperate and sub-tropical zones, explaining most of the variance encountered between 1967 and 1979 (Winder & Cloern, 2010). However, more recent results within the English Channel, including satellite and *in situ* data, demonstrate a decline in chl-a concentration over 1998 and 2017 (Gohin et al., 2019).

This study's objective is to target contrasted coastal ecosystems in order to cover a range of estuaries, within an epicontinental sea in a temperate area (Fig. 3.1). There are two separate areas along the French coast of the Channel. The western basin is mostly affected by oceanic and megatidal hydrologic features from the Atlantic Ocean (Dauvin, 2012; Gohin et al., 2019; Liénart et al., 2017). The eastern basin is mainly affected by the Seine Estuary with macrotidal environment and a coastal hydrodynamic system that drifts from the Seine estuary to the Northern parts of the Somme Estuary (Brunet et al., 1996; Brylinski et al., 1991). Such spatial diversity enquires about the relationship between an estuary and its local micro-phytoplankton community composition over time. Therefore, the aim of this study is to look at the decadal stability and reconstruct seasonal trajectories of phytoplankton communities in contrasted coastal areas. Moreover, it should highlights how the known different ecosystem's dynamics affect the community composition. Indeed, we could expect a binary differentiation between systems dominated by high fluvial influence and more marine systems with a tidal influence.

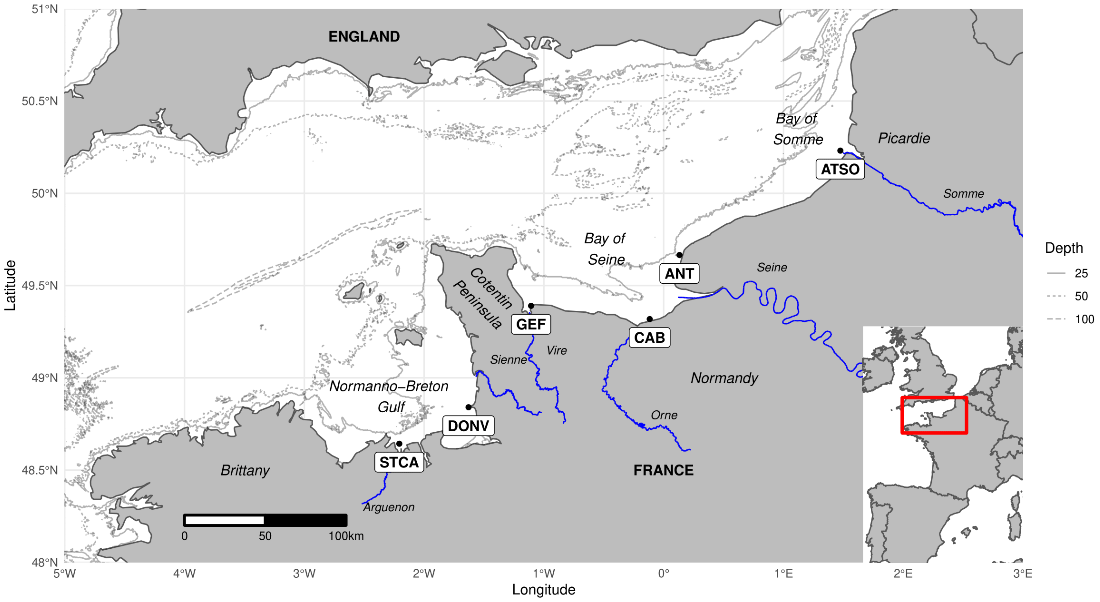


FIGURE 3.1 – Study area : The Eastern English Channel. (R package : rnaturalearthhires (South, 2020)).

3.3 Material & methods

3.3.1 Study area

The study was conducted in the Eastern Channel, on France's coast, at the western Europe. Three coastal points located within the Bay of Seine (ANT – CAB – GEF), one point northward (ATSO), and two points in the Normanno-Breton Gulf (DONV – STCA) were selected (Fig. 3.1). The sites could be dissociated into two categories ; ANT, CAB, GEF and ATSO that have high estuarine influence, mainly from the Seine river ; whereas DONV and STCA are under marine influence. In addition, ANT is located southward of an artificial seawall, and within a restricted area where fuel cargo are unloaded. Finally, GEF is located in the small Bay of Veys, known for hosting several oyster farms.

3.3.2 Datasets compilations

Most of the data collected are from the French Research Institute for Marine Exploitation's (IFREMER) REPHY (Monitoring network for phytoplankton and phycotoxins), RHLN (Hydrologic Network for the Normandy Littoral) and SRN (Regional Nutrient Monitoring) programs. The flora dataset gathers information on phytoplankton abundance and diversity on the sub-surface level at a bi-monthly or monthly resolution for the time period of 2008–2019 (Neaud-Masson, 2016). The abiotic dataset either is from field sampling, or has been extracted from local weather networks (Météo France, Hydrological bank) on a daily resolution.

3.3.3 Phytoplankton datasets

The flora dataset was initially composed of 131 taxa (60% diatoms, 29% dinoflagellates) most of which were identified to the species or genus level or regrouped as sets of species or genus (85% of the taxa). In order to ensure robust analyses, taxa that represented more than 99% of the total abundance over the studied period and areas were selected. Moreover, only the abundances above 100 cells.L^{-1} were considered since this concentration is the detection limit with microscopy observations (Neaud-Masson, 2016). Special attention was put towards the naming convention so as to ensure temporal coherence. The final list for the 108 considered taxa is given in supplementary data.

3.3.4 Environmental variables

Abiotic parameters were obtained through the monitoring programs' quality protocols (Neaud-Masson, 2016). Hydroclimatic parameters were taken from the Météo France database from the closest meteorological station and the Hydrologic Bank (Table 5.1). Wind direction was transformed into a percentage of similarity from the local major wind (270°) (Table 5.1).

TABLE 3.1 – Summary of the abiotic variables (with their unit) used for the numerical analyses and their measuring or calculation methods.

Parameter	Method		
Temperature (°C)	*In situ* temperature sensor		
Salinity (PSU)	*In situ* conductivity sensor		
Dissolved oxygen (mg.L^{-1})	*In situ* oxygen sensor		
Turbidity (FNU)	Optical turbidimeter		
N/P ratio	Spectrophotometry flows for the ammonium, nitrate, nitrite and phosphate nutrient $N/P = ([NH_4^+] + [NO_3^-] + [NO_2^-])/[H_3PO_4]$		
Rainfall (mm)	Amount of rainfall gathered between 06H00 UTC Day D and 06H00 UTC Day D+1 (1 mm = 1 L.m^{-2})		
Wind Speed (m.s^{-1})	Average of the maximum speeds recorded over 10 min		
Wind direction (% of a West wind)	Similarity of the wind direction (realWD) with a West wind (270°). $NewWD = abs(100 - abs(realWD - 270)/180 * 100)$		
Daylight duration (min)	Duration of light (intensity over 120 W m^{-2}, enough to create distinct shades) over a period of 24h (from 00H00 UTC)		
Inflow (m^3.s^{-1})	River	Average	Basin
	Seine (at Paris, Austerlitz)	315	78650km^2
	Somme (at Bray sur Somme)	8.5	6650km^2
	Vire (at Malloué)	7	1969km^2
	Sienne (at St Cécile)	2	794km^2
	Arguenon (at Jugon Les Lacs)	0.8	534km^2

3.3.5 Numerical analyses

Data analyses were managed through R, version 3.5.1 (R Core Team, 2018), with the use of "ggplot2" package (Wickham, 2016) for the majority of the graphical outputs. Datasets and scripts are available on a GitHub repository (`https://github.com/AngieLef/PhytoComm_Channel21`). All phytoplankton cell counts were transformed to a logarithm base-10, with two decimals. Seasons are defined as three successive months with winter being the combination of the 12^{th} month of year Y and the 1^{st} and 2^{nd} months of year Y+1.

Environmental exploration

For each station, parameter and year, every seasonal mean value was compared to the overall mean (μ_s) of the same season (s) over the 2008–2019 period, and the difference (μ_s - s) plotted. Due to important flow differences between rivers, the percentage to the mean of the difference (μ_s/s × 100) per station was plotted for this abiotic parameter only.

Phytoplankton stability approach

To investigate the stability over time of the communities found at each site, the Bray Curtis dissimilarity index (Bray & Curtis, 1957) was calculated for every pair of samples (not only consecutive) using the “vegan” package (Oksanen et al., 2018). The sampling protocol being bimonthly, all time intervals were rounded to be proportionate to 15 days, so as to allow the calculation of the average, Q1 and Q3 similarity between samples of same time intervals.

Seasonal temporal trajectories of phytoplankton

Trajectory analysis is an ordination that aims at comparing the behaviour of each community (trajectories) according to two main criteria; the resistance and resilience of communities, and the convergence or divergence for each year. For this, a recent Community Trajectory Analysis (CTA) was applied using the dissimilarity matrix described above (De Cáceres et al., 2019). It displays, through annual arrows, the temporal evolution of the community assemblage over the study period. The function is part of the “vegclust” package (De Caceres et al., 2010) and the analysis was made independently for each season (ie : all years included).

Phytoplankton-environment relationship

Community and environment variables both varies in time and thus, there is a great interest to capture how their variations are related. COSTATIS (Co-inertia and organization of three way tables in statistics) is a method for the study of the relationship and structure of three way tables (referred as k-tables), that is to say the combination of community compositions, environment variations and time, altogether (Slimani et al., 2017; Thioulouse, 2011). Detailed in Thioulouse (2011), COSTATIS is the CO-Inertia Analysis (COIA) of 2 submatrices called 'compromises', obtained by 2 separate Partial Triadic Analysis (PTA) on each of the community and environment matrices. It was preferred to the similar STATICO analysis because of the relationship between environment and species that is strong and of main interest, and the chronological structure is not of primary importance in this case as it has been covered by the trajectory analysis described before (as advised in Thioulouse (2011)). Linking environmental and community datasets can draw out the structuration of each stations' community, depending on the main abiotic influences. For this analysis, both data tables needed to be scaled to the same temporal index, namely for the sites and years without any gaps. This is why only the seasonal scale was considered. However, STCA station was missing a value for the N/P variable during Winter of 2019 ; therefore, the mean value of all past winters' N/P ratio was used to complete the dataset.

3.4 Results

3.4.1 Environmental historical context

To better understand the temporal variations in phytoplankton community composition, it is important to know about past environmental events that occurred over the studied period (Fig. 3.2). Even when considering all sampled sites, two parameters indicated strong changes during the period of 2008–2019. The period from 2012 to mid 2013 displayed colder water temperatures, with successive negative anomalies values. The N/P ratio was at its highest in 2013, followed by lower values for the next two consecutive years, 2014 and 2015. Afterwards, a shift for both the water temperature and the N/P ratio occurred. Indeed, since 2014, the temperature variable indicated successive positives anomalies (except summers of 2015 and 2016). Also, the occurrences of positive anomalies concerning the N/P ratio are higher after 2013 compared to the 2008–2013 time period, due to lower phosphate concentrations. This ratio is influenced by the

ANT and CAB stations, and follows the flow input pulses from the Seine river. During 2018, and at the beginning of 2019, the conditions were exceptional with a longer light duration, low rainfall and less windy conditions. One can also notice that the GEF station was less affected by a wind speed changes and ATSO was the most affected by turbidity variations. The sampled sites' distributions allows different degrees of salinity influence, which is an important characteristic of each estuary's hydrodynamic situation.

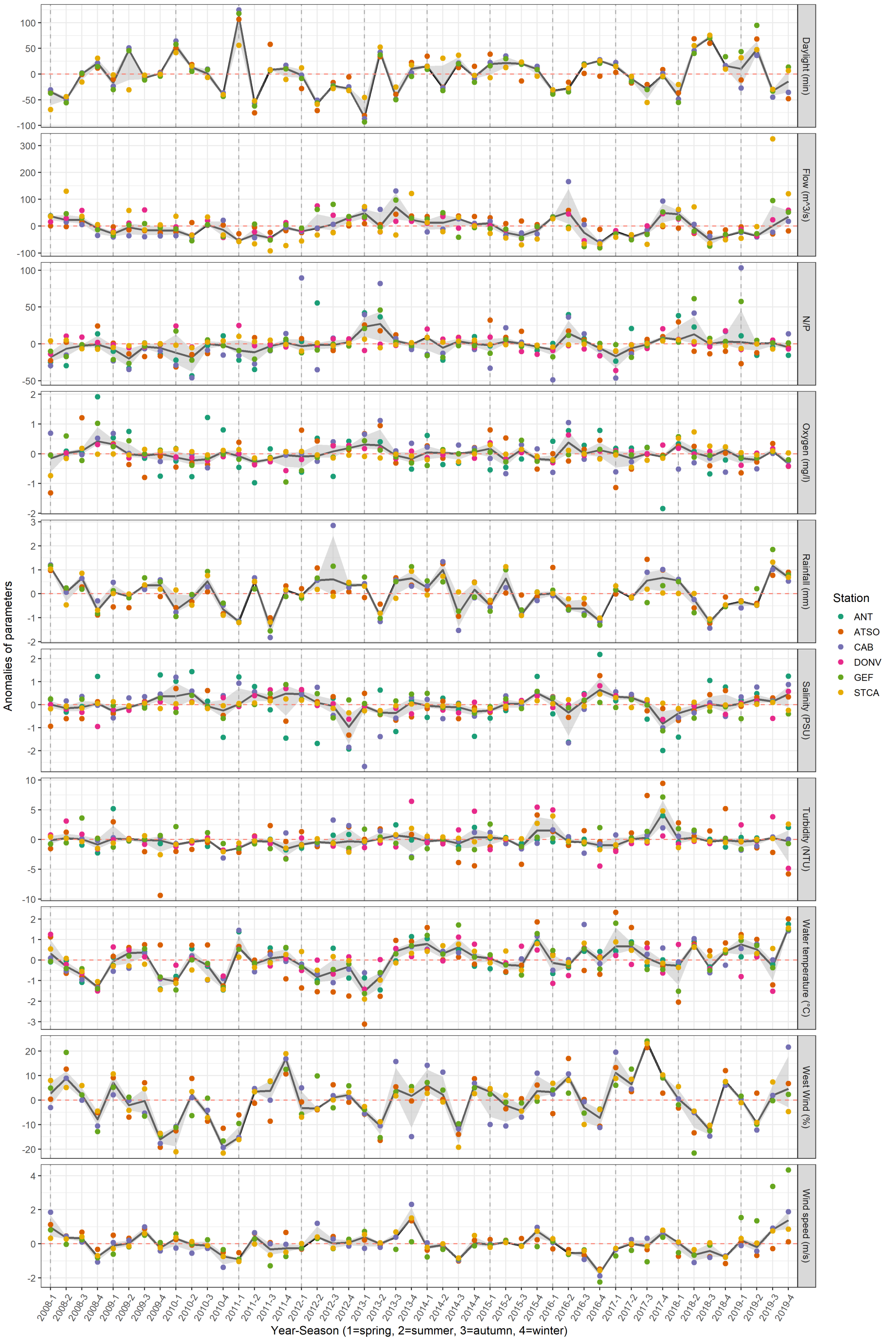


FIGURE 3.2 – Seasonal anomalies of environmental variables over the period of 2008–2019 (black line : median value between all stations ; grey ribbon : Q1 and Q3 limits).

3.4.2 Community temporal stability along the French channel coastline

The Bray Curtis index indicates a mean similarity of 0.35 for ANT, CAB, DONV and GEF, while the index is around 0.45 for ATSO and STCA (Fig. 3.3). This shows a stability between samples separated by nearly 11 years for most sites, and only ANT and GEF display a change of stability around the six years mark. Indeed, the mean similarity index decrease between samples separated by 15 days and those separated by 11 years is around 0.1 for ANT and GEF, and is below 0.05 for the other stations. The amplitude in similarity is stable and below 0.20 for STCA and CAB. Additionally, GEF displays the smallest amplitude.

One can notice that the oscillations present peaks of higher similarities for samples separated by a lapse period proportionate to 12 months. Whereas, the lowest similarities, indicated by a rounded end, occur between samples separated by a period proportionate to 6 months (but not to 12 months).

Kendall's index indicates a significant downward trend on the mean similarity for five over six stations (STCA is stable). Even though the trends of the mean level (μ) are not straight lines, the estimated slopes are very low for all sites, between -$5e10^{-4}$ and $8e10^{-8}$ per two weeks.

3.4.3 Community seasonal trajectories contrasts

Community Trajectory Analysis (CTA) displays the annual variation undertaken by communities in term of species assemblage. Like in common ordination plots, the first two axes explain most of the variance ; from 20% (spring and winter facets) to 27% (summer facet), which is correct considering it describes 12 years trajectories of 6 phytoplankton communities (Fig. 3.4). The seasonal display of the community trajectories undertaken by each site's community indicates that summer is hosting the most site-specific communities. ANT and CAB, have overlapping trajectories due to their closeness with the Seine river's mouth. Summer is known as the season during which major blooms occur and when diversity is at its highest (Table S4). It is also the season during which the communities at each station show the least temporal variations but the most geographical distinctions.

Three types of patterns can be distinguished. (1) Bay of Seine sites follow simi-

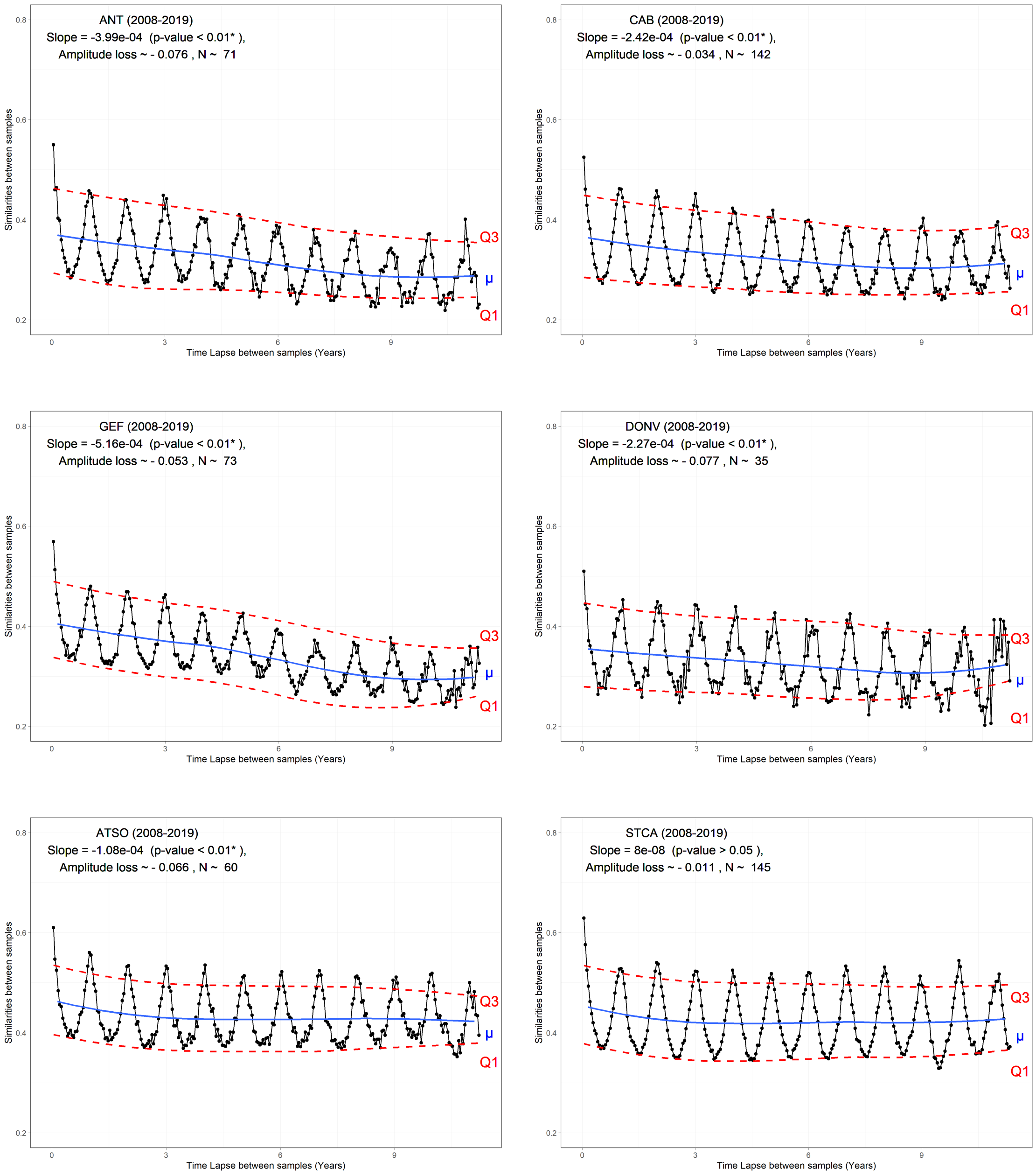


Figure 3.3 – Bray-Curtis similarity between samples sharing a same time lapse between sampling dates, per station. The slope is according to Sen's test and the associated p-value is part of Kendall's trend test (McLeod, 2011), (*) indicates significant downward trend of the blue line (mean similarity). The amplitude is estimated through the difference between Q3 and Q1 (third and first quantile). N is the average number of samples considered for the calculation of each similarity point (black dots).

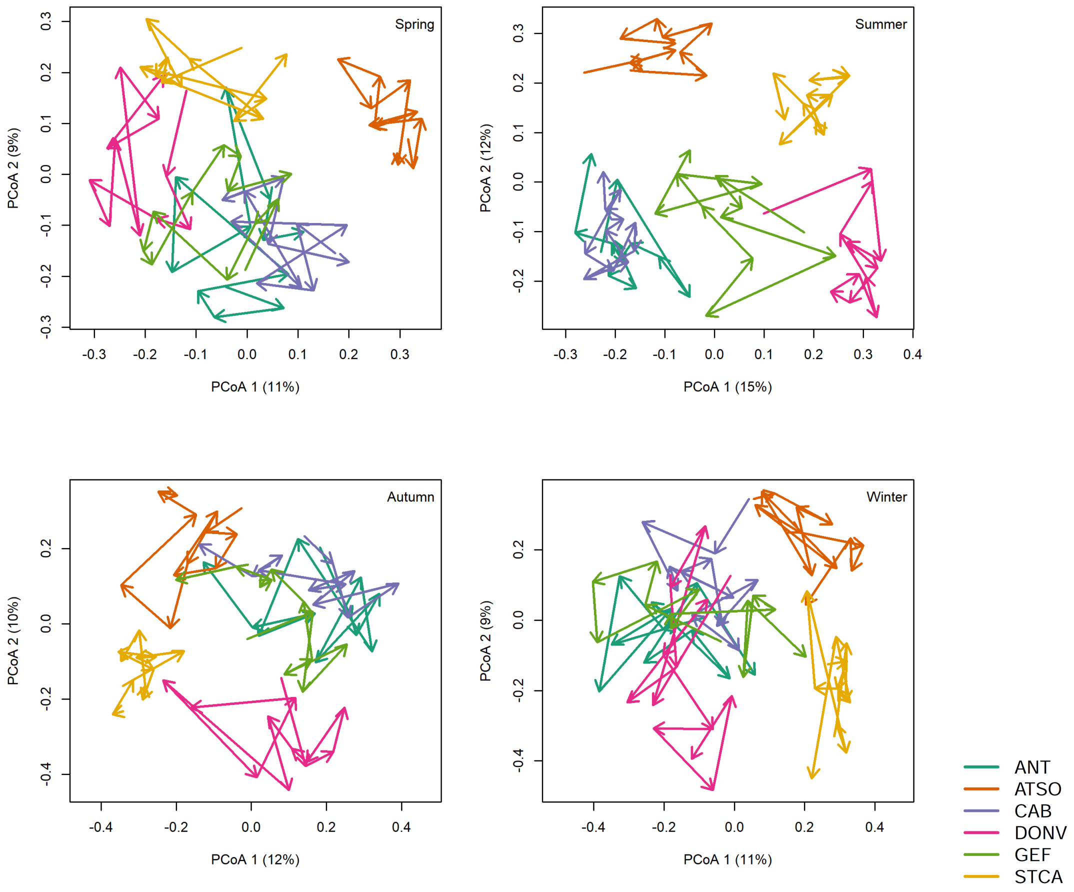


FIGURE 3.4 – Seasonal Community Trajectories Analysis (CTA) at 6 stations. The arrows drawing the trajectories represent the annual assemblage variations, from 2008 to 2019.

lar global direction, taking similar paths and displaying the longest trajectories. (2) STCA displays a tight node of shorter trajectories every season as if all the years trigger very similar phytoplankton assemblages. (3) ATSO, always isolated from other trajectories, only differs in length from STCA during autumnal trajectory, which varies from one year to another (Table 3.2). DONV has a different temporal behaviour as it displays the longest trajectories like the Bay of Seine sites but also displays a path closer to STCA's communities' (Table 3.2, Table S5).

Two groups of sites can be identified. The first, composed of ANT and CAB, displays very close trajectories that sometimes overlap. The second group, with GEF, DONV and STCA show similar scores on axis 1 for spring and summer and

Table 3.2 – Trajectories' length calculated from the CTA (Fig. 3.4) giving the community temporal evolution between 2008 and 2019, per season and station.

	Spring	**Summer**	**Autumn**	**Winter**	**Total**
DONV	1.728	1.180	2.303	3.283	**8.493**
ANT	1.830	1.169	2.262	2.690	**7.952**
GEF	1.165	1.790	1.475	2.282	**6.713**
CAB	1.659	0.870	1.592	1.985	**6.106**
ATSO	1.035	0.935	1.572	2.164	**5.706**
STCA	1.531	0.925	1.040	2.128	**5.625**

axis 2 for autumn and winter (Table 3.2). Finally, on the axis scores, ATSO is closer to ANT and CAB sites compared to the three others.

Additionally, CTA scores indicate changes in trajectories' directions between 2013 and 2014 on the first axis (for winter and autumn) and second axis (for spring and summer but also autumn for GEF), mainly within the Bay of Seine (details in Table S5).

3.4.4 Estuarine influence on phytoplankton community structure

To better understand the community behaviour, we need to investigate the environment associated to each area, this is the purpose of the co-inertia analysis COSTATIS (Fig. 3.5). It gives two results ; one displays the station's affinities to environmental parameters and the other indicates the most representative taxa found at the stations. The vectorial correlation coefficient (RV) between the environment and community k-tables is 0.809, which indicates a strong correlation displayed through this analysis.

On first hand, the axes display two major meanings ; close to the x-axis there is a marine-freshwater gradient running from flow to salinity arrows and close to the y-axis there is another gradient from oxygen and turbidity to water temperature arrows (Fig. 3.5a). There are four communities influenced by different parameters.

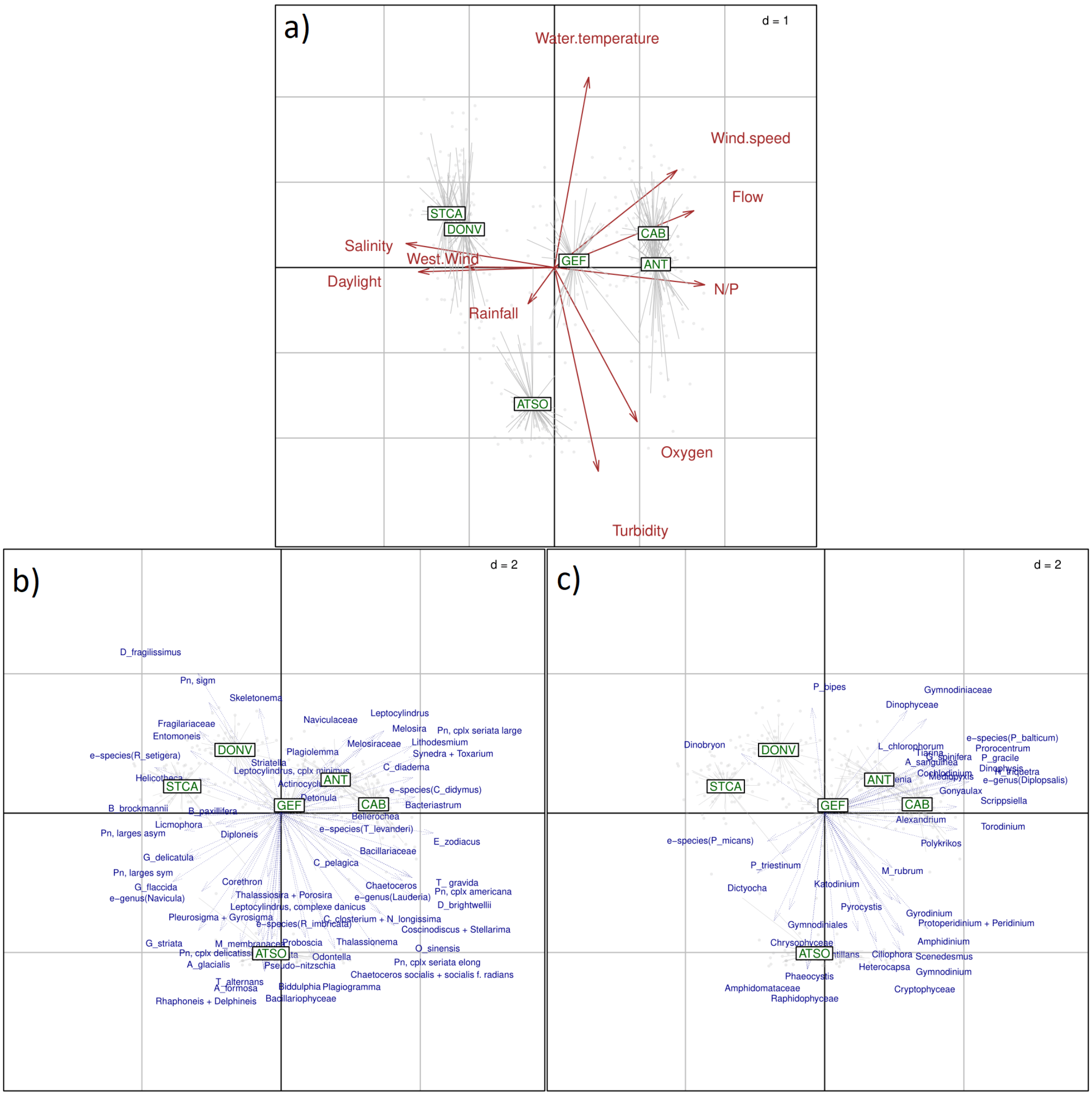


FIGURE 3.5 – 'Intrastructure' of the Costatis representing the community structure for each site superimposed with environment parameters (a) and phytoplankton taxa ; diatoms (b) or other classes (c). Axis 1 and 2 represent respectively 63% and 29% of the variance, RV = 0.809 (correlation between the two k-tables). The grey points and lines represent the variability for each station, the 'd' mention at the upper right is the axes gradation. The detailed nomenclature for the taxa is in the supplementary data.

(1) ANT and CAB, both affected by high value of N/P ratios, river flows and wind speed (with East-North-East wind direction). (2) ATSO that is greatly influenced

by oxygen, low temperatures and turbidity. (3) DONV and STCA are mainly under the influence of oceanic waters and weather changes (daylight durations). (4) GEF is not driven by of any abiotic parameter more than another but displays a pattern closer to ANT and CAB.

On the other hand, looking at the species influences on the community structure, the four communities listed above are still distinct. At first look, the affinity of some species for certain area is noticeable. Thus, many diatoms are driven by ATSO's conditions, and most dinoflagellates by primarily ANT's and CAB's conditions and secondarily ATSO's.

Concerning the species distribution within these contrasted areas, there are a large diversity of taxa at the ANT and CAB stations, with *H. triquetra*, *O. sinensis*, *Prorocentrum* spp., *Lithodesmium* spp., *Leptocylindrus* spp. and some HABs forming species as *Pseudo-nitzschia* spp. complex seriata (large), *Dinophysis* spp., *L. chlorophorum.* ATSO presents higher affinities with many diatoms and lesser other classes ; *Rhaphoneis* spp., *Delphineis* spp., *T. alternans*, *Biddulphia* spp., *A. glacialis*, *Plagiogramma* spp., it is an area highly affected by *Phaeocystis* spp. blooms and some *Pseudo-nitzschia spp.* complex seriata (elongated). The taxa influencing communities at DONV and STCA are not numerous and nearly exclusively diatoms, *D. fragilissimus* and *R. setigera* are the main ones.

3.5 Discussion

The overall analysis indicates an overall stability of the communities for the time-period of 2008–2019. Nevertheless, historical analysis of environmental parameters highlight consequent variations between years for the temperature (increase) and nutrients (higher N/P ratio), with a notable shift in 2013. Local variations also occur at each station, due to the different environmental influences from their respective geographical areas. However, spatial clusters are noticeable within the selected contrasted estuarine systems depending on local drivers.

3.5.1 Temporal variability over a decade of monitoring

The question of phytoplankton community's stability over time in an unsteady environment is complicated due to seasonal patterns and cycling behaviour, especially in coastal environments being interfaces between tides and fresh water inputs. The similarity analysis applied to all samples, while taking into consideration their different sampling intervals, shows only a slight downward trend. Teubner et al. (2003) found comparable similarity values (average of 35%) between pair of months' samples in stable ecosystem such as alpine lakes, using species biovolumes. Moreover, a temporal study on a Hydroelectric Reservoir in Brazil has shown a decrease from 40% to 25% similarities between samples having 0 and 4 years apart, respectively (Schneck et al., 2011). Within the western Channel in the 70s, Maddock et al. (1981) could not find any trends in their 11 years-long study period, even though inter-annual fluctuations were noticeable. The present study shows Eastern-Channel coastal communities are displaying between 35% and 45% mean similarity from 2008 to 2019. Even with a year-by-year difference, the highest decrease in similarity goes from 40% to 30% between samples set 10 years apart. This suggests a decadal stability on the overall marine phytoplankton community over the studied period in the Eastern-Channel (Fig. 3.3). This also indicates limitations for community variations and highlights the fact that there are no substantial restructurings of the entire community over the studied period. Be that as it may, environmental variables along the western Channel have shown a sudden increase in water temperature and N/P ratio by the year 2013 (Fig. 3.2). Despite having a decade of stability, there is a clear sinusoidal pattern with a 20% amplitude between highest and lowest similarities (Fig. 3.3). This reflects a major 12 months similarity cycle that was also found by Winder & Cloern (2010) in 48% of 125 studied time series. However, only the communities within the Bay of Seine (namely ANT, CAB and GEF) show the most variations and decrease of similarities. The associated stations are under the influence of the main river that is the Seine. Moreover, even if GEF is further away and protected from the west winds in the Bay of Veys, models also indicate a westward water circulation from Seine water input that affects its water (Cugier & Le Hir, 2002).

Besides the overall stability over the decadal period, seasonal trajectories further highlight variabilities within phytoplankton assemblage's changes over time (Fig. 3.4). Autumn and winter seasons indicate, for all sites, a temporal shift in the trajectories around the years 2013–2014 (Table S5). The environment anomalies analysis indicates a corresponding change in abiotic parameters during autumn of 2013 ; sudden drops of N/P ratio and oxygen value that were higher than usual during spring and summer 2013, higher rainfalls from autumn 2013 to summer 2014, stronger flows and water temperature values and mainly ; a strong west wind influence. These parameters changes are the consequence of positive North Atlantic Oscillation (NAO+) occurrences which also caused a very high mortality rate within Oyster farms in 2014 (Thomas et al., 2018). During spring and summer, another shift in the community composition is apparent around 2015 on the second axis of the CTA. No changes within the environmental parameters could be linked to this change. In their article covering 20 years of data for 12 sampling sites from the Bay of Somme, up to the border with Belgium, Hernandez-Farinas et al. (2013) could define 2 distinct periods (1992–2001 and 2002–2007) with different community structures respectively separated by 9 and 5 years. Therefore, a community change around 2015 is not out of the ordinary but is discrete and mostly involves the blooming seasons (spring and summer) when species diversity is higher. Nonetheless, plankton shifts or changes in patterns should not be taken as a global change in forcing parameters ; they could be due to a multitude of internal dynamics, like grazing and filtration by upper levels, as it was not taken into consideration during the analysis (Mazzocchi et al., 2012).

All sites' communities display a very strong seasonal pattern common to plankton communities (Fig. 3.4). Such stability and resilience among plankton communities was noticed in Italy through similar analysis applied to copepods assemblages over a two decades time period (Mazzocchi et al., 2012). In their study, the constant presence of abundant species and clear seasonal succession enabled this constancy. The zoo- and phytoplankton compartments are strongly linked to one another, which makes seasonal patterns very similar and successive (Greve et al., 2004; Wiltshire et al., 2015). The phytoplankton community structure observed is likewise marked by species encountered in high numbers on an annual scale, like *Chaetoceros* spp. and *Paralia sulcata*, and by the clear seasonal succession between species

(Table S4). Amongst these species, *Skeletonema* spp., *Pseudo-nitzschia* spp., *Dactiliosolen fragilissimus*, *Leptocylindrus* spp., *Asterionellopsis glacialis*, *Phaeocytis* spp. and *Lepidodinium chlorophorum* present clear seasonal affinities, mainly for spring and summer. These blooming species were found to respond to temperature gradients in other studies (Carstensen et al., 2015). Summer is the most diverse season in terms of number of species observed per sample and bloom occurrences (Cloern & Jassby, 2008; Wiltshire et al., 2008). This season is however structured by the same specific blooming species that highly dominate successively the water composition. They show a fast response when seasonal changes occur in their local environment. This specific structuration, through the dominance of a handful of species, answers why phytoplankton is mostly site specific due to local bloom drivers and species. The low variations run over by few species' dominance also explains why the community's composition is stable from one year to another during this season specifically, in spite of the high species' diversity recorded.

3.5.2 Phytoplankton community responses to different estuarine pressures

Even though the micro-phytoplankton communities at the scale of this epicontinental sea are globally stable over time, they are affected by estuarine conditions, an effect from local environmental parameters on phytoplankton is expected. Beside the influence of the estuaries' size, this study pointed out four communities distinguished by their responses to the environment. The first is deeply impacted or dependant on river inputs and local winds (ANT and CAB). The second is challenged by water turbidity and high dissolved oxygen concentrations (ATSO). The third is mostly affected by oceanic and weather-like influences such as daily light duration and salinity (STCA and DONV). Finally, this study shows a fourth intermediate community structuration around a shellfish farming area (GEF).

The communities of the Seine estuary (ANT and CAB) display overlapping trajectories for each of the four seasons (Fig. 3.4) which can be explained by common environmental pressures due to the coastal drift of the Seine River (Brylinski et al., 1991). The ANT station most likely catches this Northward current of the Seine, while a wind change disturbance (East wind) seems to affect local phytoplankton communities' structure for both stations (Fig. 3.5). Besides their proximity, higher inter-annual variabilities within phytoplankton species assemblage were observed at the mouth of the Seine (ANT and CAB) compared to the northern station (ATSO).

For every season, at the Somme river mouth, ATSO clearly indicates a different phytoplankton community in both trajectory patterns and compositions (Fig. 3.4). This site is located 120 km North of ANT and is also partly affected by the Seine's coastal drift (Brylinski et al., 1996). Looking at the CTA scores, the phytoplankton's response tends to be closer to the ones of the Seine estuary (ANT and CAB) (Figs. 3.4 and 3.5). A first observation indicates that these communities are both under a largely estuarine influence (nutrient ratios, dissolved oxygen) and less under local weather dynamics (Morelle et al., 2018). However, ATSO is closer to the North Sea's influence. It is also known for having large and frequent *Phaeocystis* spp. blooms in spring and summer (Brunet et al., 1996; Dauvin et al., 2008; Lamy et al., 2006) (Table S4, this species is mainly recorded at this station). In that sense, beside the affinity to rivers-related parameters observed at the Seine and Somme stations (ANT, CAB and ATSO), the COSTATIS displays a different pattern between both estuarine systems (Fig. 3.5). The Seine basin and Somme basin are very different. The catchment basin is also ten times wider and the population density (200 inhab/km^2) is the double, mainly concentrated downstream, for the Seine basin compared to the Somme's (Thieu et al., 2009). In their complete comparison study, Thieu et al. (2009) highlight a higher N/P ratio due to lower phosphate in the Somme's estuary, along with higher dissolved oxygen and turbidity values, leading to low chl-*a* content. Moreover, the highly turbid water and high oxygenation of the Somme estuary suggest a well-mixed water column as well which is coherent with the species' life form observed at ATSO. Diatoms with benthic affinities such as the epipelic *Pleurosigma* spp., *Gyrosigma* spp., *Nitzschia longissima*, the set of genus around *Navicula* spp., and the tychoplanktonic *Rhaphoneis* spp., *Delphineis* spp., and *Cylindrotheca closterium* are observed on this site (Fig. 3.5) (Hernández Fariñas et al., 2017).

Considered as more marine influenced, the communities situated west of the

Cotentin peninsula (DONV and STCA) are characterised by a lower diversity but a stable similarity over the studied period. The communities are grouped together in the co-inertia analysis, when taking into consideration their composition and affinities to environmental parameters (Fig. 3.5). They are dependant of local, short-termed variations (rainfalls, daily light availability). Studies indicate that short-term events can mainly affect phytoplankton's structure, as observed in the Bedford Basin in Nova Scotia with the passage of storms and during up-welling periods (Côté & Platt, 1983). Nevertheless, it is unlikely that these punctual events are responsible of significant long-term changes in community composition (Gohin et al., 2015; Henson et al., 2018), but it does explain the resiliency and why there is a decadal stability in this area (Fig. 3.3). The main difference between these two areas is the length of the seasonal trajectories, with the most notable difference for the autumnal and winter periods. This is due to the fact that one of the sites (STCA) is protected from the influence of the major west winds by its closeness to the western coast, unlike the other.

Lastly, the Bay of Veys is a very active shellfish farming area (GEF) (Costil et al., 2005; Timsit et al., 2004). It is a sheltered area from the winds, characterised by a high inter-annual variability and an unstable community composition compared to the stations mentioned above, and displays the smallest sinusoidal amplitude (Fig. 3.3). As previous studies have shown, filter feeders have a "top down" and "bottom-up" influence on primary producers (less chl-a), through grazing and biodeposition (ammonium), they induce changes in turbidity and nutrient ratios and mitigate specific blooms (Gallardi, 2014; Grant & Pastres, 2019; Cugier et al., 2010). For the Bay of Veys, similar conclusions were drawn from models on bivalves and phytoplankton interactions (Grangeré et al., 2010). To conclude, being an intermediate point, the chosen abiotic variables are not the ones structuring the phytoplankton community in the Bay of Veys (Fig. 3.5). However, this study does not include indicators from the shellfish farms, their impact on the local community is thus only an hypothesis.

3.6 Conclusion

This study has highlighted an overall 12 years stability within the microphytoplankton communities thriving in epicontinental Sea (Bay of Seine, Bay of Somme and Northern Brittany). In accordance with Cloern & Jassby (2010) hypothesis, with the slight environmental and community changes in 2013 and with a higher inter-annual variability for a shellfish farming area, our results show that seasonal patterns of community changes were linked to environmental cycling and year-to-year variability was a slow process to be correlated with anthropic or climate shift. Moreover, being in a macro and mega tidal environment, seasonal patterns within each sites are both strong and regular.

As shown through this study, no long-term changes were evident despite environmental variations. Taking a closer look at the functional groups within the phytoplankton could highlight some community variation, as suggested by Zingone et al. (2010). Moreover, a comparative analysis with English estuarine systems along the Channel could give a more detailed and complete mapping of the English Channel's influence on phytoplankton communities (Iriarte & Purdie, 2004; Pirani et al., 2016).

4

Phytoplankton functional diversity and temporal stability within coastal systems

Angéline Lefran, Tania Hernández Fariñas, Pascal Claquin

Ce chapitre s'oriente sur la diversité fonctionnelle de la communauté phytoplanctonique. Après avoir observé que la communauté phytoplanctonique était relativement stable à l'échelle d'une décennie, nous avons mis en avant une diversité spatiale et saisonnière. C'est pourquoi, ce chapitre s'attarde sur ce qui est au coeur de la relation organisme-environnement ; la diversité fonctionnelle. Nous reprenons donc les premiers résultats en intégrant cette fois-ci un tableau décrivant 87 taxons microphytoplanctoniques sur 10 traits morphologiques, physiologiques et comportementaux.

Ce chapitre à été soumis au journal Limnology and Oceanography (janvier 2022), il est actuellement en review.

4.1 Abstract

Phytoplankton communities are of main interest in coastal areas, as upper levels rely on both its resilience and variability for survival. Trait-based approach could enable to understand the effects of major environmental variations or climate change and the potential consequences for trophic chains regardless of phylogenetic relationship. This study begins with observations of chlorophyll-a depletion in coastal areas since 2008, especially within estuarine systems along the Eastern Channel. We have been able to access phytoplankton functional ecology through morphological, physiological and behavioural traits. Numerous phytoplankton taxa identified by local monitoring networks were described for 10 chosen functional traits based on literature. Application of Multiple Correspondence Analysis along with hierarchical classifications led to the creation of 15 functional groups. Results indicate that small, round and colonial diatoms dominate the community, followed by elongated diatoms. Through functional groups, spatial preferences were highlighted ; estuarine systems rather inhabit medium, round, solitary cells rather than large cells with resistance abilities (resting stage, high Surface/Volume ratio), also marine systems have a higher functional diversity. Temporally, possibly due to change in nutrients ratio, trends shift around 2008 with a depletion of traits characteristic to small, mixotrophic and heterotrophic taxa as opposed by medium to large diatoms that increased in autumn and winter.

4.2 Introduction

In coastal ecosystems, environmental changes are frequently affecting local organisms. In order to better apprehend these changes and their effects, it is important to study the stability of its primary trophic level (Lindegren et al., 2016). Indeed, phytoplankton depends on various environmental parameters, and therefore is the reflection of water's variability at a physical, chemical and biological levels. It is clear today that ocean waters are affected by global change through increasing temperature, stratification, changes in currents or nutrients upwelling, heat waves and recurrent storms (Frölicher et al., 2018;

Hallegraeff, 2010). Effects on phytoplankton are already described in various studies ; from changes in community structure and phenology and its impacts on the upper trophic levels (e.g. : “match-mismatches”) to the increase in frequency and intensity of Harmful Algal Blooms (HABs) (Hallegraeff, 2010; Winder & Sommer, 2012; Asch et al., 2019). Since the 70s in the North Sea area have shown that diatoms’ and dinoflagellates’ seasonal assemblages have been homogenised and spring blooms tend to start earlier now compared to 2000’s (Nohe et al., 2020). However, it is still hard to predict how it will reorganise following future environmental changes.

Trait-based approaches are becoming increasingly used to explain environmental changes through community functioning, regardless of the phylogeny. Initially, functional groups are sets of species sharing similar modalities on several traits and consequently are expected to have similar effects on the ecosystem functioning (Tilman, 2001). Different functional approaches have been explored regarding phytoplankton communities. Reynolds (1984) have been publishing different studies on functional grouping of freshwater phytoplankton since the 80s. He argued that species assemblages according to their responses to environmental variability coincide with cell’s morphology and also depend on cell’s resistance, adaptation and behaviour. His work led to the creation of the Reynolds Functional Groups (RFG) reference for freshwater phytoplankton diversity (Kruk et al., 2021). In parallel, Margalef (1978) had conceived a model in which marine phytoplankton is structured by nutrient concentrations and turbulence. The ‘Margalef Mandala’ model, in which r-strategists (diatoms in mixed and rich waters) are followed by K-strategists (dinoflagellates within oligotrophic and stratified water), is still frequently referred to in functional studies (Glibert, 2016; Wentzky et al., 2020). Indeed, trait-based approaches on phytoplankton are increasingly used, especially in freshwater studies, and an entire series of traits exists (morphological characteristics, physiological rates, behaviours). When grouping taxa upon functional criteria, Litchman & Klausmeier (2008) advice to take into consideration traits answering to the reproduction, resources acquisition and predator avoidance functions (see Figure 1 in Litchman & Klausmeier (2008)). Thus, cell size correspond to the most important trait as most cell functions rely on it ; nutrient uptakes, grazing, sinking rates and light acquisition for instance

(Litchman et al., 2010; Salmaso et al., 2015; Bretherton et al., 2020). Additionally, and depending on the problematic of the study area, other traits are commonly used such as shape, phenology and toxicity potential (David et al., 2012), trophic regime (Cloern & Dufford, 2005), resources utilisation and tolerance curves (Litchman et al., 2012).

Such approaches hold the potential to detect and explain past and future environmental changes and is already often used while studying the two main classes of phytoplankton, diatoms and dinoflagellates (Tomas, 1997). Both classes have very different modalities on numerous traits (like shape and trophic behaviour) and have separate relationships with environment. Diatoms prefer nutrients and temperature inputs in mixed waters, whereas dinoflagellates are found preferably in calm and stratified waters (Stanca et al., 2013; Stanca & Parsons, 2017). Since 2006, results from the Plankton Recorder Survey time series in the East Atlantic and North Sea indicated a decrease in dinoflagellates taxa and an increase of diatoms (Hinder et al., 2012) which would suggest that their ecological niches have been affected by changes. Looking deeper in traits variability, studies have also shown an increase of diatoms' and dinoflagellates' biovolumes between 1970 and 2000 (Nohe et al., 2020). However, over the last decade, studies seem to indicate that phytoplankton communities might shift toward smaller cells to fit in a more stratified environment (Finkel et al., 2010). Even though, larger cells could still benefit from a higher flexibility facing climate change's scenario of warmer temperature and higher pCO_2 concentrations (Van de Waal & Litchman, 2020). Additionally, other studies suggest that mixotrophy should be a trait to consider in global change models due to its role on biochemical functions at the ecosystem's scale (Ward & Follows, 2016; Stoecker et al., 2017).

Among European coastal microphytoplankton, hundreds of taxa undergo seasonal cycling, with lower abundance and diversity during winter while a handful of species are triggered to form blooms in spring as light intensity increases (Nohe et al., 2020; Napoléon et al., 2014). During the past decade, studies have shown that despite seasonality and environmental dependency, phytoplankton communities have known a low temporal deviation in their taxonomic assemblage (Lefran et al., 2021; Caracciolo et al., 2021a). However, the french coastlines have known a global decrease of chlorophyll-a (chl-a; proxy of phytoplankton biomass), especially in the French-English Channel mixed waters (Gohin et al., 2019). Such changes in primary producers' biomass raise the question of reorganisation within phytoplankton at a species level. This paper aims at understanding the functional changes within contrasted coastal systems that occurred around this period, and at describing the functional diversity behind phytoplankton's assemblages. The process started with the construction of a trait database covering the description of nearly a hundred taxa from literature investigations. As it has been stated by Roselli et al. (2017), we will test the null hypothesis 'everything is everywhere, all the time' for the Channel area. Along the French coast, coastal systems present different affinities with river flow and tidal range which affect the various phytoplankton assemblage both at spatial and temporal scales (Dauvin, 2012; Gohin et al., 2019; Liénart et al., 2017; Lefran et al., 2021). Therefore, the same systems are expected to present differences in term of functional groups. Each groups' dynamic may enable a better understanding of the major changes observed since the 90s, notably the chlorophyll-a decrease measured a decade ago.

4.3 Material & Methods

4.3.1 Study area

The study area is located on the Northern coast of France and is composed of six stations at different coastal systems (Figure 5.1). Those systems are contrasted both in term of phytoplankton community composition and environmental parameters and four categories among them have already been distinguished and described in literature (Lefran et al., 2021). They are composed of six sampling stations. ATSO is at a dynamic area, driven by colder temperatures and higher amount of dissolved oxygen. ANT and CAB are highly estuarine being under the direct influence of the Seine river flow (average of 315 $m^3.s^{-1}$. GEF is an intermediate point, protected from western winds and under the influence of bivalves farming sites. STCA and DONV are in wider bays, under a dominant marine influence in a megatidal environment. The terms "Dynamic", "Estuarine", "Intermediate" and "Marine" will be used in the following results to distinguish and compare the systems in accordance with our previous study's results.

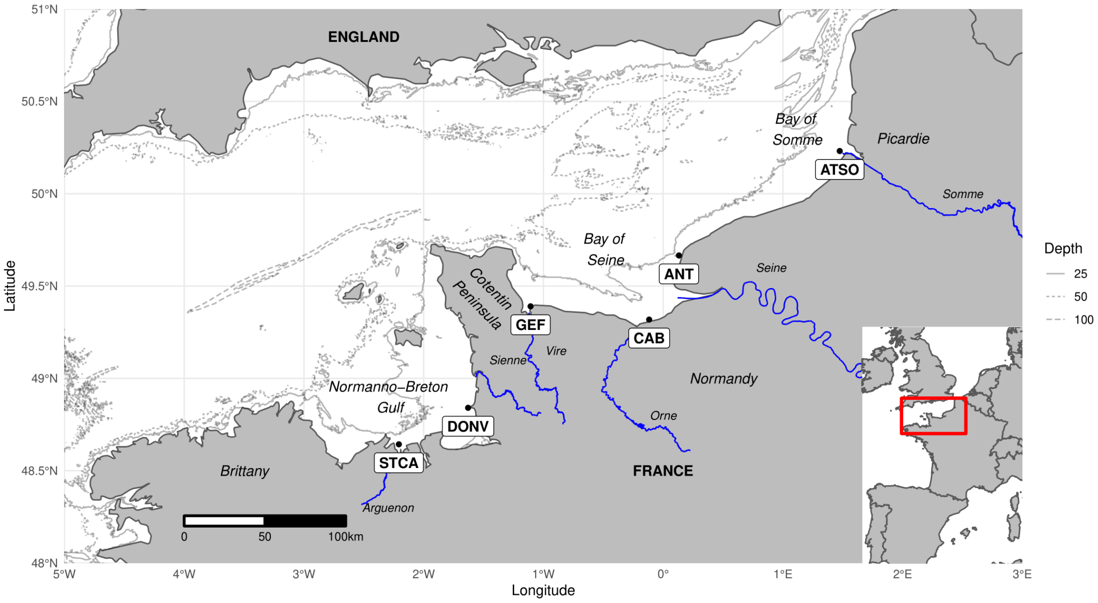


FIGURE 4.1 – English-French Channel and the studied sampling stations (from Lefran et al. (2021)).

4.3.2 Datasets compilations

All data treatments and representations described below were done through the R software (R Core Team, 2018).

Phytoplankton datasets

Over the past two decades, the regional monitoring programs have enabled the acquisition of monthly to bi-monthly records of the abundance of microphytoplanktonic taxa (REPHY – French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters (2019); SRN Regional Observation and Monitoring program for Phytoplankton and Hydrology in the eastern English Channel (2017), and RHLN - Hydrologic Network for the Normandy Littoral). There were different taxonomic levels, we considered 87 taxa to be evaluated through a functional approach.

Functional trait database

The trait database conception starts with the work of Ramond and collaborators (Ramond et al., 2018) who gathered traits information from literature for various marine protists, mostly at a genus level. Most of the modalities regarding the presence of spine, the cover, shape, motility and colonial shape used in this paper result from their work. After filling part of the traits for the taxa present in our studied areas (the taxa above the genus level were not considered for the trait database), additional research were done to complete the missing modalities, add informations at a species level and eventually adapt some other to better suit the study location particularities. Morphological data (size and surface/volume ration calculation) also results from Nordic Microalgae (`http://www.nordicmicroalgae.org`). The objectives during the creation of this dataset were to have the most representative traits and limit the number of correlated traits. As highlighted by Weithoff & Beisner (2019), the choice of traits had to reflect both bottom-up and top-down related functions, by covering morphological, behavioural and physiological aspects. However, due to the lack of information on physiological parameters (e.g. Nitrogen, Phosphate and Silicate uptakes parameters and light acclimation) for such a number of taxa, some of these processes related to nutrient acquisition are being considered through morphological traits (Finkel et al., 2010). All details can be found in the species-trait dataset (Lefran et al 2021b, *in press*) ; and a summary of the 10 chosen traits and their modalities is presented in Table 5.2

4.3.3 Numerical analyses

Functional groups construction

While doing test and trials for the traits' selection and grouping, the first observation was the natural division into two groups of our taxa list, between the silicates (mostly diatoms) and the non-silicates. This is why we applied the same method on both table separately. The method consists of a Multiple Correspondence Analysis (MCA) followed by a Hierarchical Classification on Principal Components (HCPC) on the species-trait dataset (packages FactomineR ; (Lê et al., 2008; Kassambara & Mundt, 2017)). The first creates a n-dimensions representation of the trait's mo-

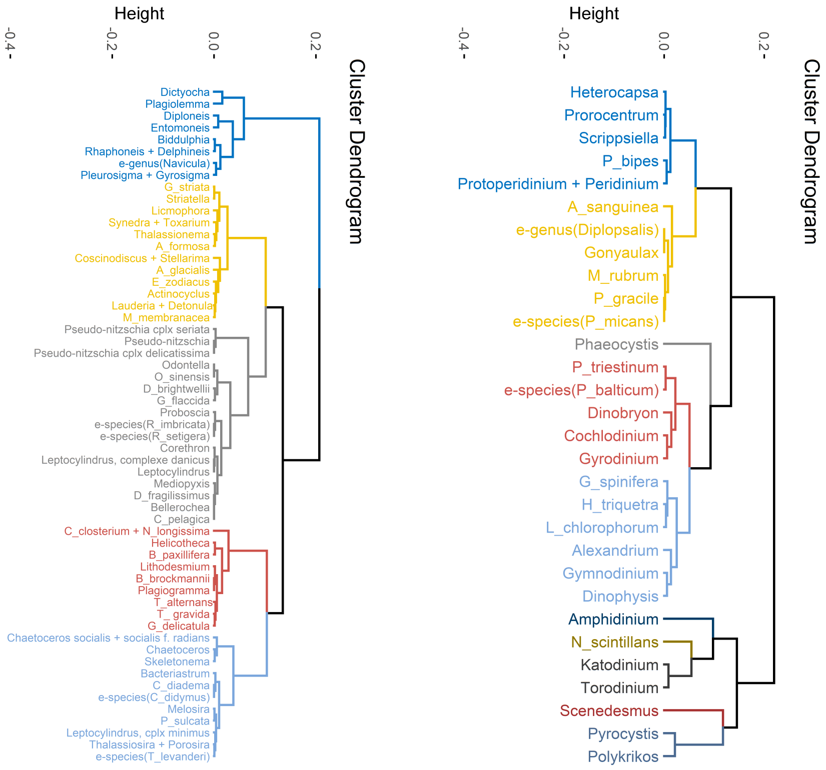
Table 4.1 – Functional traits used and their modalities (* : trait used to divide the taxa into two tables to be analysed separately).

Traits	**Modalities**	**Trait Type**	**Ecological Function**
Size max (µm)	0-25 / 25-50 / 50-100 / 100-200 / 200-500 / 500-1500	Morphological	Resource acquisition Predation avoidance Sinking speed
Surface / Volume ratio	0-1 / 1-10 / 10-30 / 30-60	Morphological	Nutrient uptake
Spines or setae	Spines / Setae / None	Morphological	Predation avoidance
Shape	Round / Elongated	Morphological	Resource acquisition Predation avoidance
Motility	Floater / Gliding / Swimmer	Behavioural	Water column movement Light acquisition
Colonial shape	Curved / Straight / None	Behavioural	Sinking facilitation Predation avoidance
Trophic diet	Autotrophic / Heterotrophic / Mixotrophic	Behavioural	Nutrient limitation avoidance
Habitat preference	Planktonic / Epiphytic / Benthic / Tychoplanktonic	Behavioural	Light affinities Filtering pressure
Resting Stage	1 (yes) / 0 (no)	Physiological	Fitness
Substance producer	Toxic / Harmful / No	Physiological	Predator avoidance Biotic interaction
*Cover**	*Silicated / Naked / Organic*	Physiological	Nutrient facilitation, class division

dalities according to their affinities to one another and then disposes the species at the centroid position of all its modalities. The second uses the coordinates of the species' locations in the n-dimensions and build a hierarchical clustering tree highlighting the most pertinent groups. The dimensions representing at least 5% of the variance explained were kept for the distances estimation for the tree construction (Figure 4.2). This approach enabled the creation of 15 groups (5 within silicates, 6 within non-silicates, 4 mono-specifics) (Table 4.2).

Numerical analysis

A Generalized Procrustes Analysis (GPA) is used to compare a number of matrices all containing functional group representation over time for the common period 2008-2019 (Dijksterhuis & Gower, 1991; Gower, 1975; Legendre & Legendre, 2012). Similarly to the associated Greek mythology (Procrustes was compelling travellers to share his bed and wanted them to fit perfectly ; cutting limbs or stretching them), the analysis is composed of an algorithm that minimizes the sum of squared distances between points in a joint ordination



(a) (b)

FIGURE 4.2 – Clustered dendrograms based on the trait database (Table 5.2) for 87 taxa for silicates (a) and non-silicates (b). Colors separate phytoplankton functional groups.

TABLE 4.2 – The functional groups obtained and their indicative species.

Functional Group (FG)	**Indicative taxa**
S1 : Small, round, chain forming, with resting stage	*T. levanderi, Chaetoceros, Bacteriastrum*
NS1 : Phaeocystis, forming curved colonies	*Phaeocystis*
S2 : Elongated, Xlarge and chain forming, with low S/Vratio	*Mediopyxis, Bellerochea, D. fragilissimus, C. pelagica*
S4 : Tychoplanktonic, medium sized, chain forming	*Odontella, O. sinensis, G. flaccida*
S3 : Large, diverse colonial aspects, low S/V ratio	*E. zodiacus, A.formosa, M. membranacea*
NS3 : Mixotrophic, large, round, single, swimming	*P. gracile, P. micans, M. rubrum*
S5 : Benthic and mobile, medium sized, single cells	*Navicula, Raphoneis + Delphineis, Pleurosigma + Girosigma*
NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	*Heterocapsa, P. bipes, Scripsiella*
NS2 : Mixotrophic, medium, round, swimming and toxic	*L. chlorophorum, H. triquetera, Dinophysis, Alexandrium*
NS4 : Small, high S/V ratio, swimming, mix or autotrophic	*Cochlodinium, P ; triestinum, Gyrodinium*
NS8 : Heterotrophic, elongated, with high S/V ratio	*Katodinium, Torodinium*
NS10 : Large, elongated, with resting stage	*Polykrikos, Pyrocystis*
NS9 : Scenedesmus, chain forming with spines	*Scenedesmus*
NS6 : Amphidinium, small, heterotrophic and tychoplanktonic	*Amphidinium*
NS7 : N. scintillans, XXL-size, round and heterotrophic	*N. scintillans*

(Legendre & Legendre, 2012). The purpose of this analysis is to compare the spatial relationship between the studied stations based on their functional group composition and to compare the results with previous ones obtained by taxonomic and environmental affinities (Lefran et al., 2021).

Following Gohin et al. (2019)'s statement of chl-a depletion, our monitoring data enabled to illustrated this depletion for the studied stations. To assess the effects of the chlorophyll-a depletion on phytoplankton community reorganisation, we targeted two periods before and after 2008 which corresponds to the year after which a general and substantial drop in chl-a occurs (according to a cumulative sum approach). However, due to a wide study area that covers different laboratories, the sampling periods before 2008 are different from a station to another. Data before 2008 at ANT, CAB and GEF and DONV correspond to the period 2003-2007, for ATSO it goes back to 1992 to 2007 and for STCA it covers 1990-2003.

First, for the common period of 2008-2019, Spearman's correlation was used to detect monotonic trends in the traits themselves. The correlations on the traits' modalities (through the study of the taxa's abundance that bear them) versus time was done on a matrix built thanks to the 'FD' package (Laliberté et al., 2014). It enables a description of the traits variability shown through a compilation of the significant correlations for each modalities per system, apart from the Marine system that shows no significant changes during this period.

The functional distribution of the phytoplankton community is then described by the display of the relative proportion of the abundance of each functional group per system and per season from the records of the period of 2008-2019. Finally, Spearman's correlations enables to assess the difference in trends between the functional groups dynamic through time for the periods before and after 2008 for each system and each season. A specific graphical representation gathers and highlight the significant changes that occurred over this period.

4.4 Results

4.4.1 Spatial distinction within the Eastern Channel

The Generalized Procrustes Analysis enables a system distinction based on the functional groups structuration at each station. Without environmental information taken into consideration within this analysis, we can distinguish three systems (Figure 4.3). GEF is close to STCA and DONV on both axis in the category defined as "Marine" systems. ANT and CAB's coordinates are closer to one another, as both estuarine systems under the Seine's influence. And ATSO is separated from the other stations.

4.4.2 Overview of the main change in community traits

The first important observation concerns the traits modalities. The classification of the trait's influence on the functional groups' temporal evolution is given through the study of each modalities' variation (Table 4.3 4.4). All of the traits have modalities that are significantly evolving over the period 2008-2019. The intermediate system (GEF station) is the one displaying major changes whereas

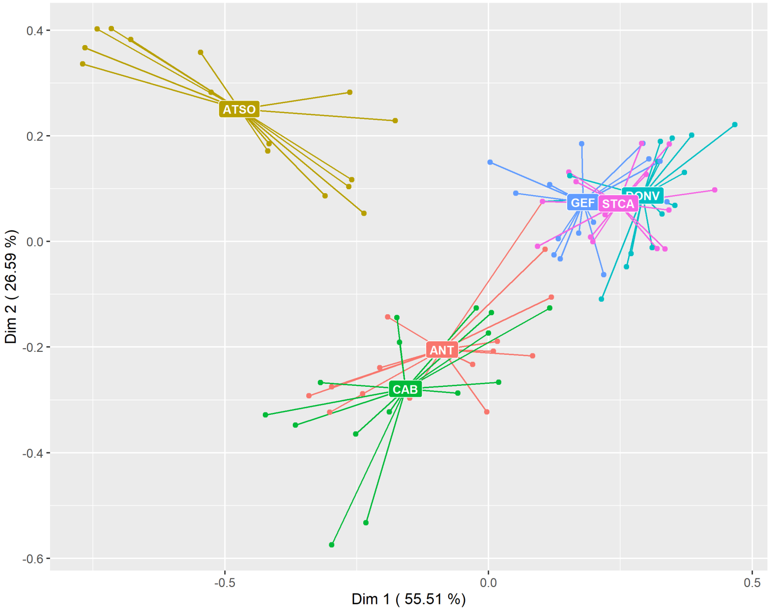


FIGURE 4.3 – Generalized Procrustes Analysis displaying the six stations' relationship on two axis in an ordination plot. Their closeness relates of their proximity in composition considering the period 2008-2019. Each dot per station corresponds to a functional group's position.

the marine system does not display any significant trend. 32 over 37 modalities display significant changes within one or two systems.

In terms of colonies, chain-forming taxa are increasingly found in estuarine systems but are decreasing in the intermediate in favour of single cells or curved colonies. Silicates and floaters are increasingly found in estuarine systems while calcareous taxa are growing in the intermediate system. Taxa with benthic affinities are also favouring the intermediate systems compared to planktonic ones. Elongated long cells and toxin producers are more found in the intermediate system, round cells are however decreasing. In addition, species without resting stages are increasingly found in this latter system whereas, species with the ability to form resting stage are decreasing. In the estuarine systems only, there is a reduction of mixotrophic taxa but an increase of autotrophic ones.

Table 4.3 – Significant results for Spearman correlations applied for each modalities against time from 2008 to 2019. Note : * : p-value < 0.05 and ** : p-value < 0.01. No significant trends are found for the Marine system which is thus not represented.

Trait	**Dynamic**	**Estuarine**	**Intermediate**
	Positive correlations :		
Colony		Straight *	None **
Cover	Siliceous *	Siliceous *	Calcareous **
Habitat preference			Benthic **
			Epiphytic*
			Tychoplanktonic**
Motility	Floater *	Floater *	Gliding *
Resting Stage			No **
S.V ratio		1-10**	10-30**
Shape			Elongated **
Spine or Setae			No *
Substance producer			Toxic **
Size max (µm)		0-25*	100-200**
			200-500**
			25-50**
Trophic regime		Autotrophic*	
	Negative correlations :		
Motility	Swimmer*	Swimmer **	
Colony			Straight **
Cover	Naked *		
	Organic*		
Resting Stage			Yes **
S/V ratio		0-1*	
Shape			Round **
Spine or Setae			Setae *
Size max (µm)	500-1500	50-100*	0-25*
Trophic Regime			Planktonic**

4.4.3 Context of chlorophyll-*a* depletion

The reality of the chlorophyll-*a* depletion is shown through the display of the total annual chl-*a* encountered at each system (addition of monthly values) in Figure 4.4. It shows from the period 2000 to 2019 a global decrease in chl-*a* concentration, and a common acceleration from 2008 for most systems. The 'Estuarine' and 'Dynamic' systems are indeed the most affected. However, while the Estuarine system's decrease is steady in time until 2019, both 'Dynamic' and 'Intermediate' systems are seeing their chlorophyll-*a* concentrations increase since 2013.

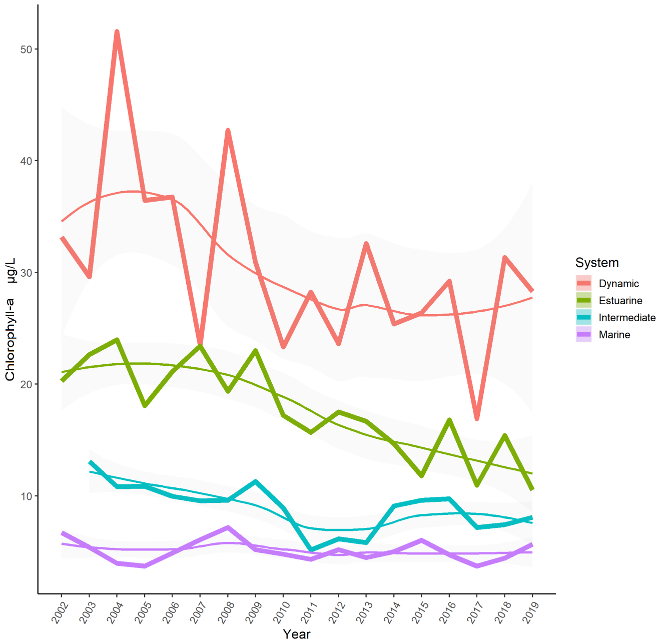


FIGURE 4.4 – Chlorophyll-*a* depletion observed from annual primary production per system's type between 2000 and 2019.

4.4.4 Global density distribution

The relative proportion of each functional group indicates that the community is indeed dominated in abundance by few groups (Table 4.4). S1 (Small, round, chain forming, with resting stage) is specifically dominant and widespread in space and time followed by S2 (Elongated, large and chain forming, with low S/V ratio). The monospecific group NS1 (Phaeocystis, forming curved colonies) displays also high proportions ; however, it is specific to the dynamic system and to the spring season. Most of the dominant groups (S1 and S2) are major during summer and autumn, two (NS1 and S4) thrive in spring preferably, and the less dominant groups (mainly dinoflagellates in NS8, NS10, NS9, NS6 and NS7) in abundance are more specific to the autumn and winter periods.

All the groups are recorded at each studied location, however, spatial differences and affinities dissociated them. The large, diverse colonial aspects, low S/V ratio (group S3) are less found in estuarine system by opposition with the mixotrophic, round, single, swimming cells (NS3 & NS2). The intermediate and marine systems both display the highest proportion of various groups with low S/V ratio ; planktonic, elongated chains (S2), tychoplanktonic, medium-size (S4) and of the least abundant groups like the moving, benthic solitary cells (S5) and also the mixotrophic and heterotrophic, swimming group (NS5) for the marine system.

4.4.5 Temporal stability

Spearman's correlation enabled a comparison between trends for each functional group (Figure 4.5). The first observation concerns the functional groups in the estuarine systems that are the most stable throughout the periods (green point located in the centre of the graph).

However, changes in trends (Spearman's correlations) are observed in certain functional groups (FG) before *versus* after 2008. Most points are located on the right side of the graph which means that all these FG were increasing in abundance before 2008. Mostly within non-silicate groups like NS2 (Mixotrophic, medium, round, swimming and toxic), NS3 (Mix/heterotrophic round, swimming, low S/V ratio, with resting stage), NS5 (Mix/heterotrophic round, swimming, low S/V ratio, with resting stage), Amphidinium and Scenedesmus (NS6 & NS9), the FG shifted from an increasing trend to a decreasing trend between 2008. For the silicates, S5 (Benthic and mobile, medium sized, single cells), S4 (Tychoplanktonic, medium size, chain forming) and S3 (Large, diverse colonial aspects, low S/V ratio), their trends before 2008 are first negatives in most systems but specifically for the 'Dynamic' system and on winter and spring, indicating a decrease in the abundance of the concerned taxa. After 2008, trends

TABLE 4.4 – General abundance repartition for each functional groups per system and season. All column's sum is equal to 100%. In grey, the conditions in which the functional groups' presence is above the average (Total).

Functional Group (FG)	Total (%)	Dynamic	Estuarine	Inter-	Marine	Spring	Summer	Autumn	Winter
S1 : Small, round, chain forming, with resting stage	35.43	12.32	74.25	43.58	32.44	10.55	62.03	55.74	64.33
NS1 : Phaeocystis, forming curved colonies	40.17	69.33	2.92	13.27	12.05	73.51	4.22	0.7	19.04
S2 : Elongated, Xlarge and chain forming, with low S/Vratio	11.32	7.78	10.41	25.58	27.36	7.38	16.25	19.94	3.94
S4 : Tychoplanktonic, medium sized, chain forming	4.57	2.37	3.41	8.74	19.85	4.85	3.94	6.21	4.4
S3 : Large, diverse colonial aspects, low S/V ratio	5.67	6.74	3.67	7.27	5.22	2.92	9.07	8.86	4.31
NS3 : Mixotrophic, large, round, single, swimming	0.87	0.22	2.21	0.24	0.44	0.07	1.92	1.4	0.41
S5 : Benthic and mobile, medium sized, single cells	0.53	0.69	0.22	0.4	0.8	0.25	0.39	2.66	1.82
NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	0.49	0.17	1.09	0.24	0.51	0.1	0.73	2.33	0.41
NS2 : Mixotrophic, medium, round, swimming and toxic	0.52	0.17	1.18	0.24	0.43	0.22	0.84	0.96	0.53
NS4 : Small, high S/V ratio, swimming, mix or autotrophic	0.28	0.12	0.51	0.2	0.46	0.08	0.48	0.58	0.34
NS8 : Heterotrophic, elongated, with high S/V ratio	0.06	0.04	0.06	0.08	0.14	0.02	0.06	0.22	0.14
NS10 : Large, elongated, with resting stage	0.03	0.02	0.04	0.06	0.13	0.01	0.03	0.15	0.14
NS9 : Scenedesmus, chain forming with spines	0.03	0.03	0.02	0.04	0.07	0.02	0.02	0.11	0.08
NS6 : Amphidinium, small, heterotrophic and tychoplanktonic	0.02	0.01	0.02	0.03	0.06	0.01	0.02	0.07	0.07
NS7 : N. scintillans, XXL-size, round and heterotrophic	0.01	0.01	0.01	0.03	0.06	0.01	0.01	0.06	0.06

for the taxa within S4 and S3 but also NS10 (Large, elongated, with resting stage) are positives, specifically in the 'Intermediate' system, which indicate an increase of their abundance.

In term of spatial observations, significant changes are pointed out in the 'Dynamic' system which first underwent a decrease of medium size diatoms (S3) and an increase in swimming dinoflagellates predators (NS5, NS6, NS8 and NS9) before 2008. Since 2008, this system shows a reversed tendency with

FIGURE 4.5 – Graphical comparison of spearman correlations' changes around 2008. The trends followed by FGs are highlighted in orange. FG per system consider all seasons, and the functional groups per season consider all systems all together. Only FGs with one or two significant trends have their name indicated (S : group of silicate organisms, NS : group of non-silicate organisms).

the decrease of taxa within NS5, NS6. The 'Estuarine' systems are affected by a strong decrease of NS4 and NS7 since 2008. Only the 'Intermediate' and 'Marine' systems are having an increase of large mixotrophic dinoflagellates (NS3).

After studying the spatial difference, the temporal differences indicate that the dominant silicates S1 (Small, round, chain forming, with resting stage) and S2 (Elongated, Xlarge and chain forming, with low S/Vratio) were increasing before 2008, mainly during spring and summer. After 2008 however, only S2 in summer continues its positive trend while the rest stabilises. The amount of significant correlations show an increasing trend among the functional groups from spring to autumn before 2008 (72% of the FG have a positive index) while an overall stability is mostly observed after or even decreases (41% FG still display positive correlations).

Concerning the changes in abundances observed through spatial distinction, similar tendencies can be found through seasonal approach. First, the most stricking observation is the amount of significant increase among the functional groups throughout the seasons before 2008 while an overall stability is mostly observed after. From this temporal perspective, all station considered, we can notice the changes in the most representative functional group, S1 which correspond to the small colonial diatoms, that used to be thriving in Spring, Summer and Winter but is now significantly decreasing in autumn and winter.

More precisely, for the silicates' decrease seen before 2008, it concerned mainly spring and winter (S3, S4 and S5) while the increasing trends noticed are recorded in summer and autumn for most non silicate groups. Winter is thus hosting larger species with low S/V ratio (S3) since 2008 (compared to before). Silicates in S5 (benthic and mobile, medium sized, single cells) are showing significant negative trends in winter and spring before 2008 but the indexes are displaying stability after this date. Additionally, since 2008, elongated chains (S2) are more found in summer. Concerning non-silicates, the increasing trends were recorded for Amphidinium (NS6) and Scenedesmus (NS9) but shifted toward a negative trend in winter after 2008.

4.5 Discussion

Increasingly used in freshwater but also in marine phytoplankton since Reynolds (1984) and Margalef (1978), the trait-based approach is an alternative method for understanding community changes regardless of phylogenetic relationships. It leads to the description of these organisms in terms of function, which could be considered as an intermediate step, more precise than a chl-a proxy, for studies on upper levels and at an ecosystem scale. Moreover, ecosystem modelling could beneficiate from such an approach (Dutkiewicz et al., 2020; Zwart et al., 2015). Additionally, various datasets coming from a wide range of monitoring networks could be compiled according to the functional traits shared between taxa (e.g. the Plankton Lifeform Extraction Tool of Ostle et al. (2021)).

4.5.1 A trait-based approach that highlights spatial differences

Trait-based analysis aims at grouping species according to their common traits and that are expected to share similar effects from environment (Tilman, 2001). As primary producers, the specificity of phytoplankton's compartment resides in its reliability upon environmental variables such as nutrient, light and temperature, which drives numerous species' seasonal successions (Carstensen et al., 2015; Rhee, 1982; Spatharis et al., 2007). As Salmaso et al. (2015) explained, the choice of traits and methods is key, the misuse of this method could have consequence on the comprehension of the ecological processes. In our approach,the traits were selected to answer all the main abilities that characterise phytoplankton considering their resources needs and pressures avoidance but eliminating the redundant traits following suggestions from other studies (Litchman et al., 2010; Litchman & Klausmeier, 2008). Looking deeper within the traits combination enables to answer the problematic of changes within microphytoplankton's assemblage and their meaning in a context of global change rather than only exploring the dominant classes (Widdicombe et al., 2010). A classification only build from morphological traits was not considered as this study focuses on different stations situated on a specific coastline along the French-Channel area and did not cover a wide enough range of environmental condition to do a morpho-functional comparison (Roselli et al., 2017). The resulting functional groups from this approach have the specificity to be made from numeric clusterisations which permit an optimised grouping method considering the amount of taxa covered. They were in agreement with the groups described in a study from the South of France which made its groups using traits characteristics to preys for oysters feeders ; notably using taxa's abilities to form colonies, their shape, the size, spines presence and toxicity (David et al., 2012).

Looking at the functional groups' distribution in our study, there is a pattern that dissociates the stations from one another based on the functional groups variability. The General Procrustes Analysis separates the stations into three main systems (called 'Dynamics', 'Estuarine' and 'Marine') corresponding to the ones highlighted in our previous study that was based on taxonomical entities, regardless environmental influences (Lefran et al., 2021). However, the COSTATIS ordination in the previous paper highlighted a separate site (GEF), which is located in the Bay of Veys and was called ‘Intermediate’ system, its isolation was due to its lack of affinities with the chosen environmental variables while here the analysis only focus on the functional groups. This indicates that through a ‘compressed’ approach that is the trait-based approach, it is possible to discriminate spatial communities as well as through taxonomical diversity, which confirm the interest of this approach to characterise ecosystem trajectories (Graco-Roza et al., 2021).

Even though *Phaeocystis*’ abundance during spring blooms can highly influence community composition, especially in the dynamic system (Bonato et al., 2015; Karasiewicz et al., 2018), our study pointed out that microphytoplankton in the French-English Channel is largely dominated by organisms that are small, round, with resting stage, Chaetoceros-like (S1) regardless of the location or the season. Such characteristics key traits as they favour nutrient uptake, metabolic rate, light absorption, growth rates, trophic interactions with filter feeders and grazers and sinking process (Barton et al., 2013b; David et al., 2012; Finkel et al., 2010). In their review exploring the spatial distribution of phytoplankton traits, Barton et al. (2013b) also highlighted the general dominance of small cells compared to larger ones.

The functional grouping that was made in this paper bases its analysis on a fixed database build for the complete description of 87 taxa on 10 traits covering morphological, physiological and behavioural functions. It is an approach on microphytoplankton functional diversity, and it cannot answer the problematic of trait’s changes within a given taxonomic entity. Indeed, approaches on intra-specific trait variability could lead to a better understanding of acclimation through cell volume or growth rates changes in response to temperature or stoichiometry for example (Hofmann et al., 2019) but are often estimated through cultures experiments. Other traits can be of interest to answer fitness problematics, such as N2-fixation (Barton et al., 2013b), growth rates (Edwards et al., 2013), fatty acid composition (Cañavate et al., 2019), carbon allocation (Wagner et al., 2016) or other smaller phytoplankton classes through pigment, molecular or cytometry approaches for i.e.

cryptophytes, cyanobacteria, pico and nanophytoplankton proportion (Paerl et al., 2003). However, our study does not consider any intra-cellular rates as traits due to their high variability and the complexity to be obtained for a large dataset that describe 87 taxa.

4.5.2 A changing community

The changes in chlorophyll-a has been observed along the french Atlantic coast (Gohin et al., 2019) but also predicted at a global scale over a century (Hofmann et al., 2011). Our data confirm that the chl-a depletion was affecting systems with high river influence. Such changes were induced by the drop of phosphorus content within river flow all across Western-Europe (Romero et al., 2013). Microphytoplankton contribute grandly to chl-a concentrations on shelf areas (Lamont et al., 2019), therefore this work also aimed at describing a potential community restructuration around this biomass depletion.

Over the period 2008-2019, our results from trait's modalities indeed show an increase of larger species with length over 100 µm in the Bay of Veys while smaller cells are decreasing. This could be the cause of various effects but we know that the Bay of Veys is under 'top-down' pressure from filters in shellfish farms (Costil et al., 2005; Ubertini et al., 2012). Such pressure from benthic filter has already been proven to affect chlorophyll-a at a local scale (Cugier et al., 2010). However, the increase in the tychoplanktonic group (S4) is interesting as they could be targets for filter feeders in this area. Nevertheless, since 2008, abnormal mortalities in oysters due to a new type of herpes virus (OsHV-1) are investigated all over France, this could have reduced the 'top-down' biomass control (Segarra et al., 2010; EFSA Panel on Animal Health and Welfare (AHAW), 2015). This area is also under higher toxic risk, mainly from *Pseudo-nitzschia* spp. blooms (Klein et al., 2010).

Around 2008 there are changes within the functional groups ; in estuarine systems, we specifically observe a decrease of dinoflagellates with mixotrophic and heterotrophic regime (NS5) and of *Scenedesmus* in spring and autumn, and also of *Phaeocystis*. In the dynamic systems, mixotrophic taxa (NS2 &

NS5) are also affected by a decrease since 2008, as opposed with silicates within S3 (large cells with spines). Only the marine and intermediate systems, less concerned by the chl-a depletion, beneficiates of increases from medium to large diatoms with low S/V ratio in autumn and winter periods. In the Channel area, community changes thus seem driven by river inputs as explained by Cloern (2001). Nevertheless, our opposite results are not surprising and follow a tendency at a larger scale, observed also through the Plankton Recorder Survey time series for the Northeast Atlantic and North Sea (Hinder et al., 2012). While small cells dominate microphytoplankton community, there is a change in trends that used to be grandly increasing before 2008 and one can wonder if this also affects the pico- and nano-phytoplankton which would contribute and partly explain the biomass depletion. In a context of global change, various theories exist on the future impacts on phytoplankton. Finkel et al. (2010) explored the effect of increase CO_2 through the review of literature and suggested two hypotheses ; on one hand larger cells are more likely to take advantage of this increase, on the other hand picophytoplankton (smaller cells) are enhanced following increases of ocean stratification.

It is interesting to notice the decrease of mixotrophic dinoflagellates in the estuarine and dynamic systems. It could have been expected to see more of this regime considering the increasing irradiance and temperature in the area (Figure 2 in Lefran et al. (2021)) which are known to trigger stratification and enhance their abundance (Stoecker et al., 2017). However, those parameters may not be the drivers in our case. Indeed, Hinder et al. (2012) explained the decrease in dinoflagellates in the North East Atlantic by an increase in wind and associated turbulence, which causes the water to homogenize. Also, there could be a link between the global decrease in chl-a and the prey availability for mixotrophs and heterotrophs. Indeed, there is a decrease within the smaller round cells (S1), mostly in autumn and winter, which may affect mixotrophs. Mixotrophy is an essential trait enabling carbon accumulation without nutrients limitations which can be transferred in the upper levels (Ward & Follows, 2016). Changes of functional diversity of the first trophic level as pointed out in this work may affect the ecosystem function in term of carbon flux and food web structures (Edwards et al., 2013; Chakraborty et al., 2020; Litchman et al., 2007).

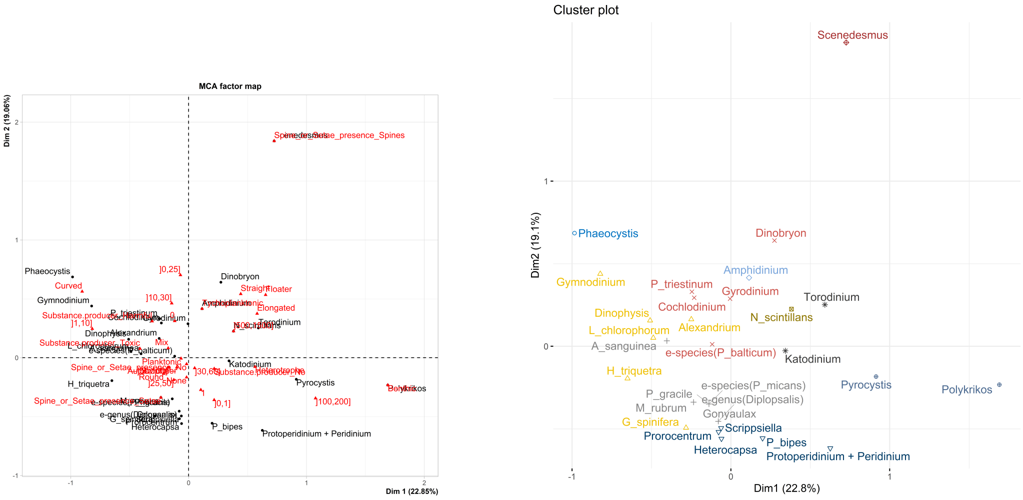
Following the various scenarios of changes at a global scale suggested by Henson et al. (2021), temperate systems are likely to lose diatoms and mixotrophic dinoflagellates types, in favour of diazotrophic taxa. Nitrogen being not a limiting factor in the studied area as in many temperate coastal ecosystems, diazotrophic taxa are not expected to find a niche but other cyanobacteria or small phytoplankton groups can be favoured. Phytoplankton having a very flexible, diverse and adaptative compartment with a resilient cycling, it cannot be enough to study a couple of decades to predict nor conclude from local trends, but effort for considering smaller phytoplankton groups beside microphytoplankton has to be done by monitoring network for phytoplankton. We believe that the functional groups created in this work is an efficient step when considering primary producers, more precise than the chl-a proxy, to explain recruitment, mortalities, trophic transfer at upper levels or any coastal ecosystemic model development.

4.6 Conclusion

This study is the first step toward a functional approach on the primary producers in temperate coastal ecosystems. It describes the phytoplankton diversity and changes in the light of morphological, physiological and behavioural characteristics, and in a context of changes in biomass around 2008. If most groups are represented within the several systems, they are not equally distributed, each functional groups have spatial and seasonal preferences. Regarding the chl-a depletion observed around the year 2008, our results highlighted a depletion in functional groups mostly of small to medium organisms that could explain lower biomass, especially if this effects also affected the smaller division of pico and nano-phytoplankton. There are also a depletion seen in certain smaller dinoflagellates with mixotrophic or heterotrophic regime and high S/V ratio for systems under high river inflow but an increase in benthic or tychoplanktonic organisms in surface waters. No major depletion is seen in parallel in the marine or intermediate (farming) areas, the latter being the most subject to community variability.

Trait-based approaches are in-between cell and environment, which confers to this study a specificity regarding the variability of community behind environmental changes. Considering the proximity of this approach with environmental parameters, a next step could be to explore the relationship between functional groups and ecological niches in order to better understand this link and eventually predict the effects of future environmental changes onto the primary producers in coastal areas.

4.7 Supplementary material



(a) (b)

FIGURE 4.6 – Graphical representations of the methodological steps to the trees construction and the functional groups creation. (a) MCA displaying modalities and the taxa. (b) The taxa and the clusters build from their coordinates.

5

Does sharing functional similarities lead to similar ecological niches in coastal phytoplankton ?

Angéline Lefran, Stéphane Karasiewicz, Tania Hernández Fariñas, Pascal Claquin

Ce chapitre reprend les groupements fonctionnels dits "théoriques" du chapitre précédent et s'interroge sur la possibilité de groupements écologiques plus réalistes, notamment avec la prise en compte des interactions espèces-environnement. En effet, si le premier chapitre a permis de mettre en lumière une communauté phytoplanctonique structurellement stable durant la dernière décennie, il a aussi montré une nette différenciation spatiale en lien avec l'environnement et son interaction avec la communauté de ces producteurs primaires. Face aux enjeux des changements globaux, il est important de pouvoir prédire les réponses du compartiment primaire, notamment en terme de déplacement de niche écologique. Pour ce faire, associer à la fois le concept de niche et celui des traits fonctionnel devrait apporter une meilleure compréhension des mécanismes de réponse du phytoplancton.

5.1 Abstract

On one hand, ecological niche concept is becoming increasingly used in various fields of ecological research to apprehend species-environment relationships. Indeed, understanding the environmental conditions in which a species can grow and reproduce with effectiveness is essential for predicting its invasive or harmful potentials, but also to protect endangered organisms from it, as they are already under major environmental or anthropogenic pressures. However, estimating phytoplankton's ecological niches relies on biotic and abiotic drivers that are not always accessible through field monitoring. On the other hand, functional approach gathers essential information on community structure and its capacity to answer to ecological needs such as nutrient and light uptakes, predation avoidance or buoyancy for better position in the water column. Such characteristics maximise fitness and adaptation to environmental conditions. In many studies using trait-based approaches, it has been hypothesised that organisms sharing similar traits would have similar ecological responses ; that is to say share environmental preferences. This study aims at answering this question for a community composed of nearly a hundred taxa, in the English-French Channel area. Phytoplankton characteristics are compared through both functional characteristics, issued from literature, and real ecological position within an environmental space. In our results, clustering methods are able to create groups either having most traits in common or displaying similar affinities along environmental gradients. Despite high variability, well established for this compartment, comparison between clusters indicates that organisms sharing traits also tend to share similar environmental space. It is even more true for diatoms, compared to dinoflagellates.

5.2 Introduction

Phytoplankton is well-known for its diversity and density in the world's marine and fresh waters. With sufficient nutrient supply, global ecosystem models indicate that diversity is directly linked with enhanced primary production (Vallina et al., 2014). There are numerous scales for diversity as organisms can be described on morphological levels, but also on behaviour, physiology and metabolic processes. All these characteristics are part of the functional approach, which aims at assembling phytoplankton taxa according to their similarities over certain functional traits. The resulting groups are then used to explore spatial or temporal dynamics, and to study their relationship with one another and with environmental gradients (Litchman et al., 2007; Roselli et al., 2017). Specifically, trait-based approaches are becoming a new window toward the comprehension of communities' reorganisation under climate change (Litchman & Klausmeier, 2008).

In such context, ecological niche approaches would enable the understanding of community composition facing environmental drivers. Hutchinson (1957)'s famous concept defines a *fundamental* niche as the theoretical n-dimension hypervolume, for n-ecological factors relative to a species, in which every point corresponds to "a state of the environment which would permit the species to exist indefinitely". *In situ*, scientists explore the *realised* niche, which represents the species' distribution in an environment where interactions between organisms and between parameters affect survival. Phytoplankton's structure highly relies on temperature, nutrient inputs, hydrodynamic events, grazing pressure and the interactive effects of these parameters (Anderson et al., 2022). This is the reason for species succession following seasonal changes.

Niches approaches have lead to enhanced comprehension of species dynamics and distribution spatially and temporally. Reynolds distinguishes three strategies among phytoplankton which would display three distinct niches, it is the C-S-R model (C-colonist, S-nutrient stress tolerant and R-ruderal) (Smayda & Reynolds, 2001; Reynolds, 2006). Colonists are small, fast growing, and typical of coastal areas, not limited by either nutrient nor light. Organisms described as tolerant to nutrient depletion were found to have niches displaying lower nutrients limits but higher irradiance conditions compared to light stress tolerant taxa (Brun et al., 2015). Ruderals are light stress tolerant, displaying peculiar morphological adaptation to maximise resource uptake. Exploring hundreds of taxa from the Continuous Plankton Recorder, Irwin et al. (2012) and Caracciolo et al. (2021a) noticed that salinity, mixed layer depth, irradiance and temperature were the most important predictors by opposition to macronutrients in the North Atlantic. Hence, phytoplankton structure depends on various environmental parameters and their functional differences could lead to divergence within their responses to environmental changes and *vice versa.*

Studying functional phytoplankton groups is an active area of research that tends to indicate a better comprehension of community composition along with environmental change and could be a better predictor of ecosystem functioning (Abonyi et al., 2018; Wentzky et al., 2020). There are multiple ways to define functional groups depending on the studies' problematic. They can be made by gathering organisms having common traits through ordination and clustering (Benedetti et al., 2016; Mammola & Cardoso, 2020), by identifying morpho-functional groups (Allende et al., 2019) or survival strategies (Smayda & Reynolds, 2001), by grouping individuals according specific prey-predator interaction (David et al., 2012), or through a combination of these processes (Alves-de Souza et al., 2008). Nevertheless, in order to study the most of phytoplankton community and due to the amount of data needed to get the community's diversity, the approach itself relies on literature resources from all over the world (Edwards et al., 2016; Ramond et al., 2018; Laplace-Treyture et al., 2021). However, ecological niche approaches applied to a frequently monitored phytoplankton community can access the local species-environment relationship (Karasiewicz et al., 2018). Therefore, combining both local distribution and traits could reveal mechanisms behind community structure.

In this study, the complexity of functional trait analysis at a community's scale is challenged by the ecological relevance of the functional groups obtained. Based on the hypothesis that taxa sharing a functional group also respond to similar environmental conditions, this paper aims at comparing inter-taxa functional affinities with *in situ* similarities when facing environmental pressures. Indeed, on one hand, we used the functional groups built from the French's coastal micro-phytoplankton composition in the Channel (Chapitre, 4, *in review*) and extracted clusters of taxa sharing similar traits. On the other hand, the information on the same micro-phytoplankton taxa for the past decade is used to obtain each taxa's distribution along environmental variables for a parallel data clustering process based on similar ecological affinities.

5.3 Material & Methods

5.3.1 Study area

This study covers French coastal ecosystem along the Channel area. Thanks to a unique configuration of this epicontinental sea, systems present contrasted phytoplankton communities and environmental influences (Delavenne et al., 2013; Lefran et al., 2021). The southern stations STCA and DONV are characterized by marine influences such as high tidal range, and lower river inputs, therefore more saline waters. The Bay of Seine stations are divided between an intermediate system located at a thriving but vulnerable shellfish farming area in the Bay of Veys (GEF) and stations close to the Seine river flows with therefore estuarine influences (ANT and CAB). At the northern Bay of Somme, ATSO is a station with dynamic waters (Figure 5.1).

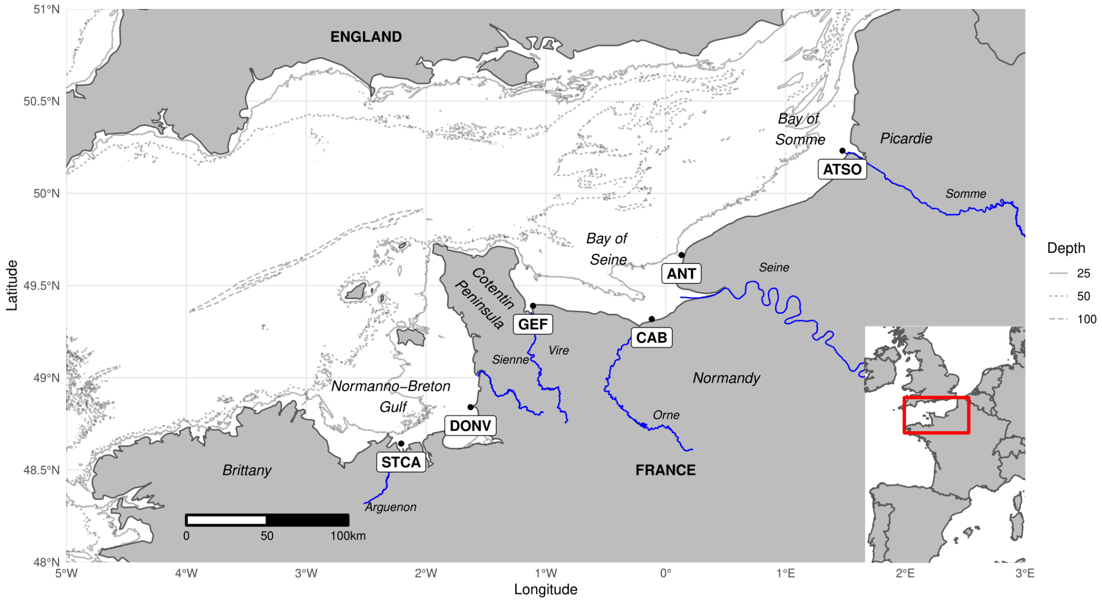


Figure 5.1 – Study area, from Lefran et al. (2021)

5.3.2 Data composition

This works relies on the datasets made available by the local and national monitoring networks (SRN Regional Observation and Monitoring program for Phytoplankton and Hydrology in the eastern English Channel (2017); REPHY – French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters (2019) and RHLN - Hydrologic Network for the Normandy Littoral). Up to bi-monthly records of 87 micro-phytoplankton taxa are available for all six stations for the period from 2008 to 2019. In addition, environmental variables are also available through MétéoFrance and the Hydrologic bank (details in Table 5.1).

Table 5.1 – Summary of the abiotic variables (with their unit) used for the numerical analyses and their measuring or calculation methods.

Parameter	Method		
Temperature (°C)	*In situ* temperature sensor		
Salinity (PSU)	*In situ* conductivity sensor		
Dissolved oxygen ($mg.L^{-1}$)	*In situ* oxygen sensor		
Turbidity (FNU)	Optical turbidimeter		
N/P ratio	Spectrophotometry flows for the ammonium, nitrate, nitrite and phosphate nutrient $N/P = ([NH_4^+] + [NO_3^-] + [NO_2^-])/[H_3PO_4]$		
Rainfall (mm)	Amount of rainfall gathered between 06H00 UTC Day D and 06H00 UTC Day D+1 (1 mm = 1 $L.m^{-2}$)		
Wind Speed (m.s^{-1})	Average of the maximum speeds recorded over 10 min		
Wind direction (% of a West wind)	Similarity of the wind direction (realWD) with a West wind (270°). $NewWD = abs(100 - abs(realWD - 270)/180 * 100)$		
Daylight duration (min)	Duration of light (intensity over 120 W m^{-2}, enough to create distinct shades) over a period of 24h (from 00H00 UTC)		
Inflow ($m^3.s^{-1}$)	River	Average	Basin
	Seine (at Paris, Austerlitz)	315	78650km^2
	Somme (at Bray sur Somme)	8.5	6650km^2
	Vire (at Malloué)	7	1969km^2
	Sienne (at St Cécile)	2	794km^2
	Arguenon (at Jugon Les Lacs)	0.8	534km^2

Prior to the direct comparative study of functional and ecological clusters, an ordination for a multi-tables representation of the dataset introduces its composition and the relationship between the variables. The RLQ analysis (Chessel et al., 2004; Dray et al., 2007) enables to visualise in a couple of dimension the relationship linking phytoplankton composition at the samplings stations (L), with the local environmental variables (R) and the trait's modalities of each phytoplankton taxa (Q) (Figure 5.4). The taxa are selected from an annual average for analysis requirement.

5.3.3 Comparing functional and ecological approach through OMI analysis

In a previous study (Chapitre 4), a complete database was built to describe 87 phytoplankton taxa on 10 traits covering morphological, physiological and behavioural aspects of each one (Table 5.2). Silicates and non-silicates organisms, due to their initial numerous functional and ecological dissimilarities, were given separately the same analytical treatment and will still be analysed separately in the following ecological clustering.

TABLE 5.2 – Functional traits used and their modalities (* : trait used to divide the taxa into two tables to be analysed separately).

Traits	**Modalities**	**Trait Type**	**Functional Interest**
Size max (µm)	0-25 / 25-50 / 50-100 / 100-200 / 200-500 / 500-1500	Morphological	Ressource acquisition Predation avoidance Sinking speed
Surface / Volume ratio	0-1 / 1-10 / 10-30 / 30-60	Morphological	Nutrient uptake
Spines or setae ?	Spines / Setae / None	Morphological	Predation avoidance
Shape	Round / Elongated	Morphological	Ressource acquisition Predation avoidance
Motility	Floater / Gliding / Swimmer	Behavioural	Water column movement Light acquisition
Colonial shape	Curved / Straight / None	Behavioural	Sinking facilitation Predation avoidance
Trophic diet	Autotrophic / Heterotrophic / Mixotrophic	Behavioural	Nutrient limitation avoidance
Habitat preference	Planktonic / Epiphytic / Benthic / Tychoplanktonic	Behavioural	Light affinities Filtering pressure
Resting Stage	1 (yes) / 0 (no)	Physiological	Fitness
Substance producer	Toxic / Harmful / No	Physiological	Predator avoidance Biotic interaction
*Cover**	*Silicated / Naked / Organic*	Physiological	Nutrient facilitation, class division

This database enabled to access a functional clusterisation of these taxa following the number of traits they have in common. A combination of a Multiple Correspondence Analysis (MCA) and Hierarchical Clustering on Principal Components (HCPC) were applied directly on the species-traits database (packages

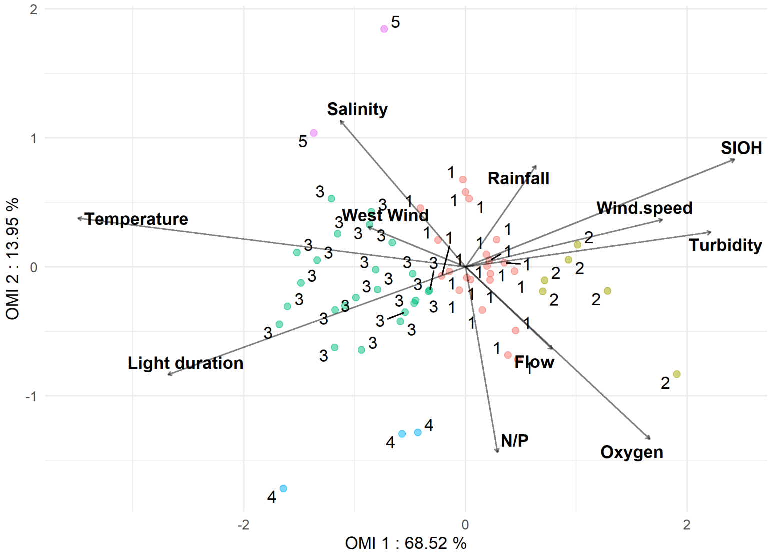
FactomineR ; Lê et al. (2008); Kassambara & Mundt (2017)). It led to the distinction of 15 functional groups ; 5 within silicate organisms, 6 within non-silicate, and 4 mono-specific organisms (Table 5.3).

Table 5.3 – The functional groups obtained and their indicative taxa. The order is given according the group's place in proportion within the studied phytoplankton community (Chapitre 4).

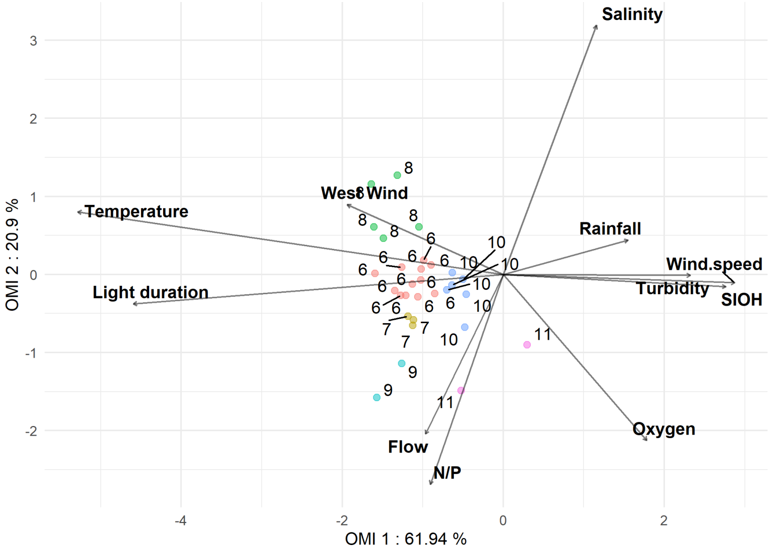
Functional Group (FG)	**Indicative taxa**
S1 : Round with setae and resting stage, small and colonial	*Chaetoceros, Skeletonema, Bacteriastrum*
NS1 : Phaeocystis, forming curved colonies	*Phaeocystis*
S3 : Planktonic, elongated, long chain, with low S/V	*Bellerochea, C. pelagica, D. fragilissimus, Pseudo-nitzschia*
S5 : Tychoplanktonic, medium sized with low S/V	*Lithodesmium, Plagiogramma, B. brockmannii, Thalassiosira*
S6 : Medium, colonial, low S/V	*A.formosa, M. membranacea, E. zodiacus*
S2 : XXL-size, with resting stage and low S/V	*R. imbricate, R. setigera, Proboscia*
NS3 : Mixotrophic, swimming with high S/V	*P. gracile, P. micans, Dinophysis*
NS2 : M-size, round, organic and swimming	*Heterocapsa, Prorocentrum*
S4 : XL-size, with spines and low S/V	*Odontella, O. sinensis, G. flaccida*
S7 : Moving, benthic, single cell	*Navicula, Diploneis, Entomoneis*
NS4 : Mix/heterotrophic , swimming with high S/V	*Katodinium, Tiarina, Torodinium, Gyrodinium*
NS7 : Scenedesmus, chain forming with spines	*Scenedesmus*
NS6 : Polykrikos, chain forming benthic, heterotrophic	*Polykrikos*
NS5 : N. scintillans, XXL-size, round and heterotrophic	*N. scintillans*

In this study, a similar approach was applied ; using an ordination method then a clustering to separate the taxa into relevant groups. However, in this case, phytoplankton is not considered as organisms through their fixed life-history traits but through their relationship with environmental variables. Therefore, a Principal Component Analysis (PCA) was performed on environmental variables then ecological niches gave the relationship between taxa and environment through the Outlying Mean Index (OMI), which compares species' habitat condition to a mean within a sampling area (Dolédec et al., 2000) (Figure 5.2). The further the species is from the mean habitat (average environmental condition, ordination's center), the more the species needs specific conditions to have an optimal development.

The clustering using Ward's criteria enabled to build a hierarchic tree (or dendrogram) based on the proximity between taxa on the niche ordination. The optimal number of clusters was estimated using the package NbClust (Charrad et al., 2014). For a first comparison we re-attributed the indicative taxa in Table



(a) Silicates (diatoms)



(b) Non silicates (mainly dinoflagellates)

Figure 5.2 – Details of the taxa's clustering into ecological groups depending of their relationship with environmental variables along OMI analysis, for both analysis of silicate (a) and non silicate (b) phytoplankton cells.

5.3 to their respective ecological group (Table 5.4).

From the two clustering results, built over the same taxa but through two

Table 5.4 – The ecological groups obtained from niche ordination and the corresponding indicative species obtained from the functional clustering. The group number indicate the location on the OMI space (Figure 5.2).

Ecological Group	N°OMI	Indicative taxa from the functional groups
Diatoms ; In dynamic, turbid, colder waters, affected by eastern winds	2	*T. levanderi, Plagiogramma, B. brockmanii, A.formosa*
Diatoms ; In warm waters with long light exposure, less relations with flows or nutrients	3	*Bacteriastrum, D. fragilissimus, C. pelagica, Lithodesmium, E. zodiacus, M. membranacea, Pleurosigma + Gyrosigma*
Diatoms ; Need long light exposure, with high N/P ratio	4	*Mediopyxis*
Diatoms ; Generalist, appreciate water runoffs	1	*Chaetoceros, Bellerochea, Navicula, Raphoneis + Delphineis*
Diatoms ; With marine affinities, high salinities and low N/P ratio	5	*(Entomoneis, Proboscia)*
Dino ; Appears during west winds in stratified waters	8	*P. micans, L. chlorophorum*
Dino ; Need light and freshwater inputs, and N/P ratio	7	*Alexandrium*
Dino ; Present with fresh water inputs, dissolved oxygen and high N/P ratio	11	*H. triquetra, Scenedesmus*
Dino ; Present with high flows and high N/P ratio	9	*Pyrocystis*
Dino ; Generalist, in-between conditions	10	*Phaeocystis, Scripsiella, Gyrodinium, Torodinium*
Dino ; Under temperature and daylight duration influence	6	*P. gracile, M. rubrum, Heterocapsa, P. bipes Dinophysis, Cochlodinium, Katodinium, Polykrikos, Amphidinium, N. scintillans*

different approaches, a comparison is made to estimate the similarities between taxa's relationships (using the package dendextend, Galili (2015)). First, the trees are untangled to find the best alignment between the taxa and their relationships. From this, a value of entanglement (from the package dendextend) can be estimated, from 0 (aligned) to 1 (entangled). This index can estimate the comparison quality considering the quantity of taxa and the approaches that have led naturally to low correlations between dendrograms' matrices (a visual summary of each steps is given Figure 5.3). The final output is given by a table summarising the relationship between phytoplankton considered through functional clustering and the ecological groups obtained through phytoplankton-environment interaction.

5.4 Results

5.4.1 Traits and environment, spatial preference

The RLQ analysis highlights in a couple of dimensions the relationship between samplings stations, environmental variables and a functional description of phytoplankton taxa (Figure 5.4). More than 90% of the variance is explained with this ordination.

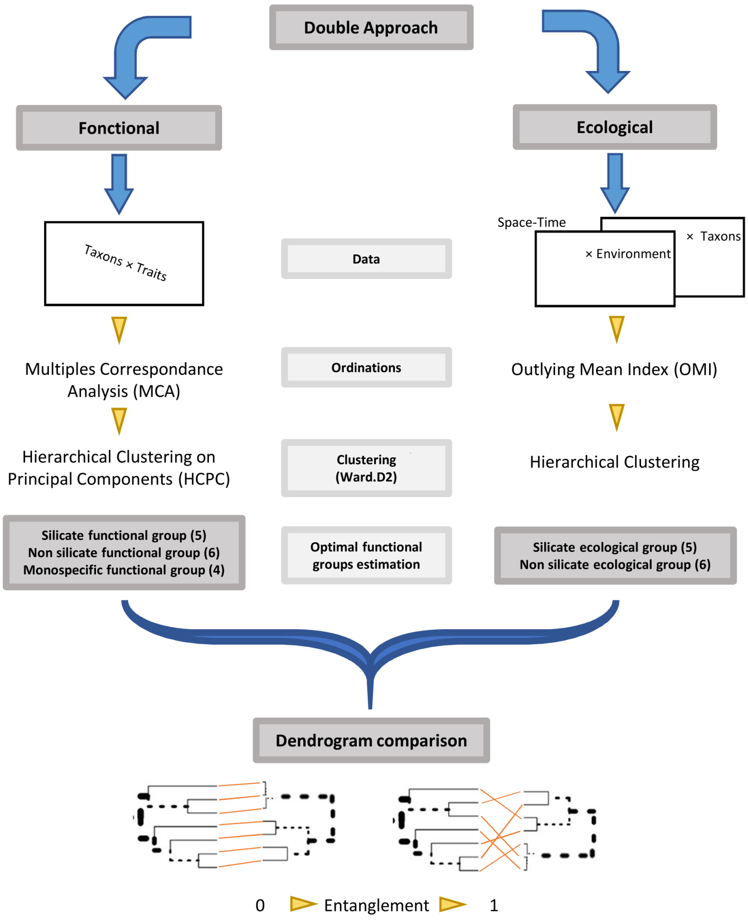


FIGURE 5.3 – Schematic step-by-step representation of the approach.

The Channel's french coast is clearly characterised spatially by different systems. The dynamic system displaying affinities with western wind, turbidity and oxygen and daylight duration (clear weather), is distinguished by large cells (above 200µm), forming curved colonies and/or possessing spines. The marine system has higher salinity influences, longer light exposure duration and, with lesser importance, rainfalls that affect community composition. It displays fewer characteristics within cells traits, elongated and gliding cells mainly, also tychoplanktonic and benthic organisms can be found in this system even if they have more proximity with the intermediate system. The latter is under the main influence of rainfall, temperature and wind speed and as its nomination says, between marine and estuarine systems. Additionally, this system hosts preferably smaller cells (below

50µm) but with higher Surface/Volume ratio (from 30 to 60) which is related with wind speed. Finally, the estuarine system displays the characteristics of the Seine river inputs but is also under wind speed influence. Many cell's traits, competitive ones, preferably occur in this system : toxic and harmful algae, mixotrophic regimes are along the N/P ratio parameter, and cells are also described as round, swimming and with higher S/V ratio.

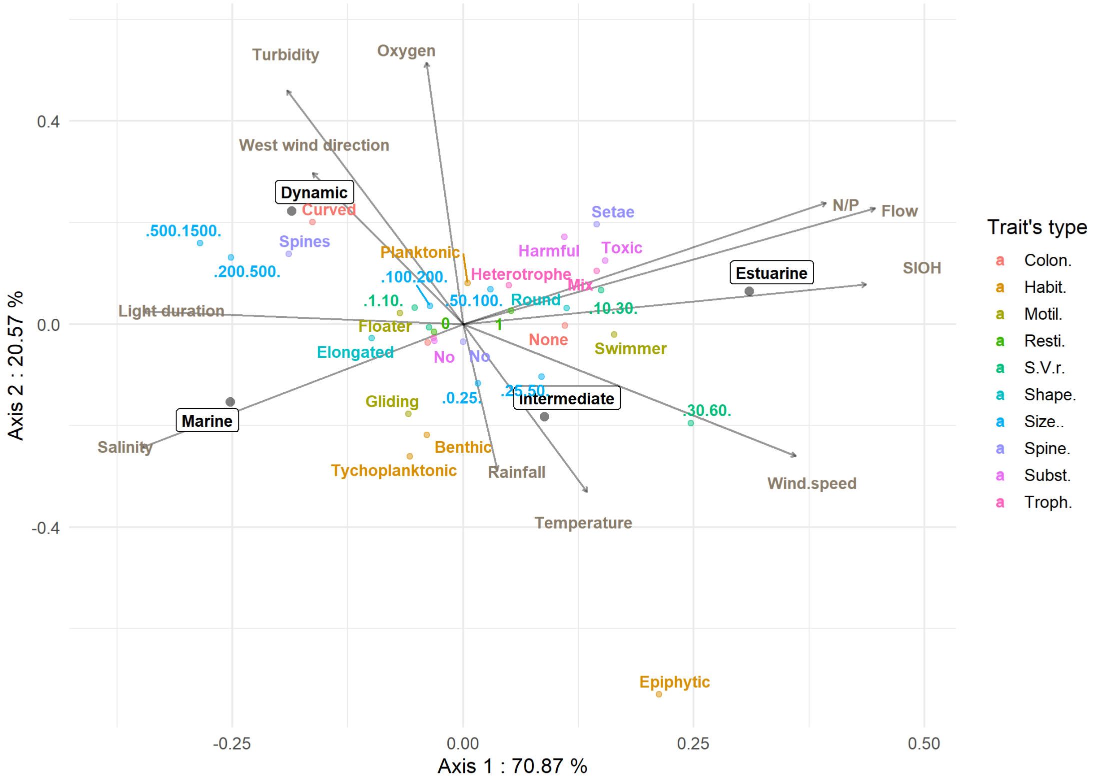


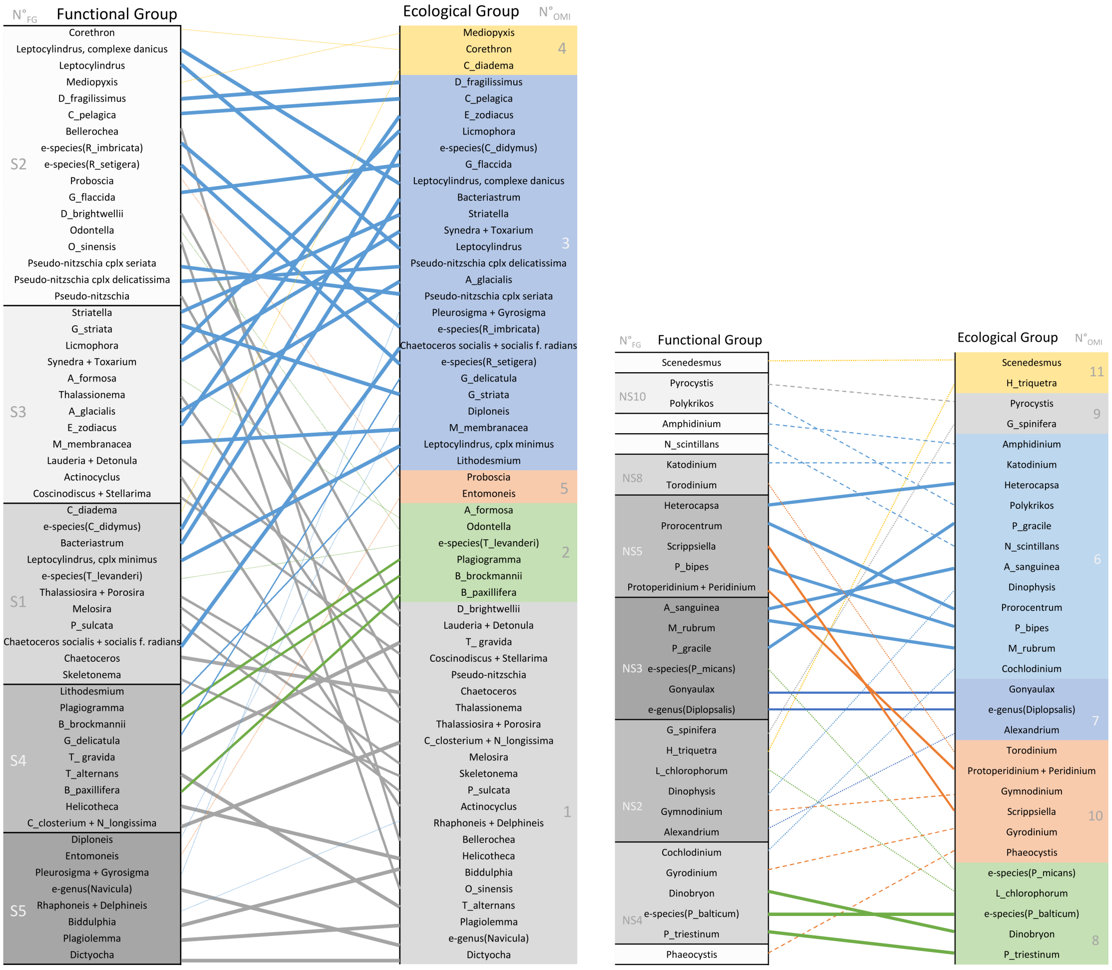
FIGURE 5.4 – Graphical representation of the relationship between traits' modalities (colouring differentiates 10 types, respectively ; colonies, habitat preference, motility, resting stage, S/V ratio, shape, size, Spine or setae presence, substance producer, trophic diet), environment variables and the 4 sampling areas. It results from a RLQ analysis.

5.4.2 Comparing functional and ecological clusters

To achieve a global representation of the dendrograms similarities and differences, the trees are displayed aside one another and taxa's positions are joined. Even considering the basic complexity of functional and ecological diversity within phytoplankton compartment, both silicate and non silicate organisms (diatoms and dinoflagellates mainly), display an entanglement below 30% between functional and ecological organisation of the same taxonomic entities. Therefore, while the dendrograms comparison seems quite unorganised at first, it does show that taxa that are close to one another on the functional clustering tree are found also close on the ecological clustering tree (highlighted by links' coloration and thickness in Figure 5.5).

Considering that the level of entanglement does not take into account directly the groups but rather the overall hierarchic distribution of each taxa, and due to the numerous taxa taken into consideration for this approach, a summary of this comparison is directly given in Table 5.5. The first observation is that functional groups amongst diatoms are more likely to be found in the same ecological environment than dinoflagellates (in average 50% of the taxa in each silicated FG are in the same EG). Indeed, in each S_n functional group, at least 40% of the taxa are found in the same ecological group. However, as dinoflagellates are located along similar parameters on the OMI analysis ; daylight and temperature influence, taxa's differentiation relies on the relationship with fresh water, nutrients variables and salinity (Figure 5.2).

Specifically, taxa in S1 (small, round, chain forming, with resting stage diatoms) are distributed within two major environments ; globally generalists (without specific environmental needs), 36% are also displayed in area under high temperature and light exposure. Within large diatoms groups (S2 and S3), 50% taxa favour environment with higher temperature and light exposure, a fourth to a third of them are generalists. Tychoplanktonic and benthic organisms (found in S4 and S5) are amongst generalists (tolerant) organisms, a third of tychoplanktonic taxa are preferably found in dynamic and turbid waters. Taxa within NS2 (mixotrophic, medium, round, swimming and toxic) are spread within different environmental



(a) Silicates (diatoms) ; entanglement rate = 0.288

(b) Non silicates (mainly dinoflagellates) ; entanglement rate = 0.227

Figure 5.5 – Ordered dendrograms comparison between functional groups (FG, left dendrograms) and ecological groups (EG, right dendrograms). Coloring differentiates the groups, links are colored according to their respective ecological groups. Trait's thickness is dependant on the proportion of taxa in FG sharing the same EG. Numbering correspond to those found in Table 5.3 & 5.4

.

conditions. However, NS3 (mixotrophic, large) and NS4 (small, autotrophic and with high S/V ratio) seem to be more competitive ; they are distributed according to temperature, and daylight duration values but under reduced wind speed, low silicate and not turbid conditions. NS4 specifically displays high affinities with western winds and stratified waters.

5.5 Discussion

Trait-based approach often results in giving insights on growth and survival strategies in dynamic environment. Classifications into functional groups enable to access to phytoplankton's roles within a compartment and at the ecosystem level while reducing the complexity of taxonomic diversity. Various grouping approaches emerged ; they can be based on the number of traits species share (ordination), or made directly from morphological characteristics (morpho-functional groups) ; or from a selection of specific characteristics to answer ecological needs (e.g. shellfish predation selectivity) (Smayda & Reynolds, 2001; Alves-de Souza et al., 2008; Allende et al., 2019; Mammola & Cardoso, 2020). However, choosing traits and clusterisation methods is still subject to debate and no standard approach to functional traits exist, nor is there an approach that give weight to a specific trait compared to another in an ecological context (e.g. colonies > growth rates regarding predation avoidance), and this needs to be further improved (Petchey & Gaston, 2006). Moreover, as Loewen et al. (2021) noticed, the underlying assumption that organisms sharing similar traits also share similar ecological niches is rarely brought to light. The present study benefits of both functional information and environmental preferences over the last decade for 87 identical micro-phytoplankton taxa, in order to confront both approaches and answer this implicit hypothesis on the eastern Channel area.

5.5.1 Spatial trait distribution

Spatially, the eastern Channel has been described in previous study as divided into four systems characteristic of both environmental specificity and phytoplankton structure (Lefran et al., 2021). As highlighted by Loewen et al. (2021), trait-environment relationships within functional approaches are often implicit. In their approach within lakes phytoplankton communities, they indicated the importance of the understanding trait's relationship along environmental gradient to better predict anthropogenic and climate change effects on ecosystem functioning.

The RLQ approach confirms the presence of this spatial diversity and integrates phytoplankton trait affinities along environmental gradients. More specifically, the dynamic system is known for frequent *Phaeocystis* spp. blooms which explain the high affinity of this system with taxa possessing curved colonies, typical of *Phaeocystis* spp. (Lamy et al., 2006). Turbidity and high dissolved oxygen concentrations, characteristic of this area, are often the results of high turbulence, and indeed favours organisms with high sinking rates and density such as large cells, cells displaying ornaments (spines) or forming colonies, in agreement with results found in Fraisse et al. (2015). In a previous approach, taxa with benthic affinities were closely related with position in this dynamic system due to its turbulence (Lefran et al., 2021). However, in this case they are better correlated with the intermediate system, which could be the result of the temporal resolution considered. Using annual average may smooth the seasonal community composition and its distribution which may results in some divergences within spatial distribution, both results are still relevant considering each system.

The intermediate area is located in the Bay of Veys, between marine and estuarine influence, in a macrotidal environment which is stratified by salinity (Bazin et al., 2014). Small cells (below 50µm) can be favoured within such environment due to higher Surface/Volume ratio and therefore faster nutrient uptake rates (Friebele et al., 1978). This location also displays influence of wind speed and rainfalls, therefore physical disturbance that are also affecting the marine area, which can lead to resuspension of small benthic and tychopelagic species in surface water (Alpine & Cloern, 1992). Indeed, abundances of *Navicula, Fragilaria* and *Actinoptychus senarus* were monitored during a local survey on primary production in autumn and winter 2002-2003 (Jouenne et al., 2007).

Finally, the estuarine system is under the influence of the large Seine river plume. Compared to other systems, its characteristics of elevated nutrient inputs are pulling the traits of harmful and toxic algae. Historically, the Seine estuary is indeed regularly impacted by *Pseudo-nitzschia* spp. and *Dinophysis* spp. blooms (Belin & Soudant, 2018). Thus, it is not surprising to find this affinity knowing the effects of eutrophication on Harmful Algal Blooms (HABs) in marine and freshwater environment (Heisler et al., 2008). Large estuarine systems like the Seine (catchment basin of nearly 80 000 km^2, including the city of Paris) are most likely to be under substantial effects of wastewater discharge, agriculture and other anthropogenic impacts that lead to greater nitrogen and phophaste inputs overriding natural processes (Moss et al., 2013), even though management measures started to improve water quality over the past few years (Garnier et al., 2019). To conclude with estuary-traits relationship, the presence of setae, characteristic of *Chaetoceros* sp. that is a dominant genus in most, if not all, estuarine waters, is found in higher abundance at proximity of river's flow influence to gain maximum nutrient input (María Trigueros & Orive, 2001; Muylaert et al., 2009; Tas & Hernández-Becerril, 2017). Phytoplankton biomass is globally higher near river inputs which also attract predators, thus the presence of setae as a defense mechanism may protect the cell or even epiphytic organism within the setae in system under high risk of predation (Gómez, 2007).

5.5.2 Functional group and ecological relevance

First of all, many functional-niche approaches base their study on functional traits rather than functional groups, certainly because of the trade-off that has to be made while clustering taxa according to the traits they share (among dozen chosen traits). Indeed, physiological traits such as light utilisation, growth rate, nutrient acquisition and utilisation are preferred to predict phytoplankton response to environmental changes (Litchman et al., 2007; Litchman & Klausmeier, 2008; Edwards et al., 2013). Additionally, temperature related traits also differentiate species as many physiological processes rely on this parameter (photosynthesis, respiration, growth rate, resource acquisition to motility) but associated temperature maxima varies from a species to another due to high cell plasticity (Litchman & Klausmeier, 2008). Temperature holds the potential to trigger blooms and species' seasonal successions, it is highlighted as a major driver. However, its co-occurring environmental influence from wind, flow or even tide can structure furthermore phytoplankton in coastal areas. In our approach, functional groups are made according to trade-offs on many taxa's similarities in traits characteristics. Indeed, we highlighted that certain species can be found in similar ecological groups, but not in the same functional group. While, functional groups have fixed delimitation between taxonomic entities, facts are that two taxa may be close in the hierarchical tree, and could be found in similar environment, without necessarily being in the same functional group.

Phytoplankton is well known for its diversity, abundance and plasticity in marine waters. Despite the odds due to traits' choices and clusterisation approaches to assemble functional groups, this study shows that hierarchical trees built from literature knowledge on functional traits are less than 30% entangled when compared with hierarchical trees made of the same taxa's ecological distribution through an OMI analysis. Indeed, it is found for all diatoms' functional groups and for 3 pluri-taxonomical groups amongst dinoflagellates that nearly half of the taxa shared common *in situ* environmental preferences, that is to say ecological niches. Such comparison have been carried out on a hundred copepods in the Mediterranean Sea (Benedetti et al., 2018). The 7 functional groups were placed in niche space along environmental variables including sea temperature, salinity, mixed layer depth (MLD), radiation and chlorophyll-*a*. While some functional groups shared similar niches, they displayed a gradual distribution along temperature and MLD characteristics indicating that they also differ in environmental preference. In their approach Brun et al. (2015), could associate realized niche to plankton functional types (PFTs, species sharing similar role and biogeochemical functions) and to Reynolds C-S-R classification (namely separating colonists, nutrient stress tolerants and ruderals taxa). Nevertheless, the authors also note uncertainties due to the limited choice of environmental variables and considering the broad range of the different niches and their natural overlaps for a compartment like phytoplankton.

Secondly, this study is showing that functional groups, composed of various taxa sharing similar modalities on dozen of traits types also are more likely to be found sharing similar niches. Such observations could raise the question of competition among those taxa, as it could be argued that sharing similar niches would lead to inter-specific competition for scarce resources and lead to competitive exclusion (Hardin, 1960). It has been investigated in upper trophic levels, for example flatfish species share specific morpho-functional traits, thus their diets rely exclusively on the same benthic fauna for which they can compete (Piet et al., 1998; Rault et al., 2017). Coexistence among phytoplankton species within unstable environments, known to be regularly under nutrient stress, was the initial issue raised by Hutchinson (1961) in the paradox of plankton. Nevertheless, our observations are not surprising for a compartment with a rapid turnover that relies exclusively on surrounding conditions for growth and survival. Some findings argue that inner processes such as allelopathy facilitate diversity within phytoplankton (Roy & Chattopadhyay, 2007; Felpeto et al., 2018), which in turn enhance primary production (Vallina et al., 2014).

To conclude this approach, we note that this study highlights overlapping niches between organisms sharing similar functional characteristics. While this choice is initially based on the functional groups classification established in a previous study, it was justified regarding the very different role they have in an ecosystems which is illustrated within seasonal successions (diatoms are blooming during the spring season, dinoflagellates' blooms follow in the summer). By showing closeness between taxa displaying literature-base functional similarities and *in situ* distribution along environmental variable, this paper also validates the relevance of the clusterisation approach that builds the functional groups, specially regarding diatoms. However, diatoms are more ubiquitous organisms compared to dinoflagellate that favors warmer temperature, stratification and therefore thrives during certain months. Our study period may have been too wide to better differentiate dinoflagellates' niches, or also key environmental variable may be missing (preys abundance). It also still lacks of cells' plasticity consideration, it is poorly and indirectly included within its niche as the organism can change its buoyancy or nutrient and light acquisitions through various processes to better apprehend its environment resources (Groß et al., 2021; Sauterey & Ward, 2022). Functional-niche concepts could both beneficiate of traits' range of variations to assess the limits to cells' plasticity, and thus limits in niche deviation facing environmental changes (Litchman et al., 2012). Additionally, this study is based on the bottom up effects supposed to enhance primary production but does not include top down effects (predation) on trait selection in coastal waters because of the lack of information on zooplankton pressure within the chosen studied stations. We would suggest that a better monitoring of zooplankton grazers within ecosystems along with phytoplankton monitoring will enhance the comprehension of how biotic and abiotic environment can lead or not to better fitness among phytoplankton taxa. It is a compartment often forgotten between primary production and upper consumers of commercial interest, even though their presence is deeply related with cell's morphological selection during predation.

5.6 Conclusion

While functional traits are at the interface between cell functioning and environment, literature-based datasets are often fixed temporally and also spatially. Therefore, the related approaches poorly take into account the effective environmental influence on local communities. Moreover, functional approach is widely used and still better developed for freshwater ecosystems, specially following the work of Reynolds (Reynolds, 1984; Reynolds et al., 2002). As Loewen et al. (2021) and Kruk & Segura (2012) noticed in aquatic ecosystems, taxa within the same functional groups are not always linked to a specific ecological niche. Nevertheless, our results indicate that species sharing functional similarities, which by the way imply that they are not functionally identical only that they are the most similar within a diverse community, are also favouring similar environmental condition to grow, specifically diatoms. Dinoflagellates are more competitive organisms in coastal ecosystem, triggered by environmental conditions such as temperature and light duration, but also resistant to nutrient stress. While specific to eastern Channel micro-phytoplankton community over the last decade and specific for its choice of traits and clustering methods, this study is finally giving insights on the long known and implicit hypothesis that functional and ecological similarities within primary producers are deeply related.

Table 5.5 – Table indicating the distribution of each functional groups taxa within the ecological group/niche. The percentage value correspond to the proportion of taxa in functional groups that are found in the same ecological group.

Functional group	(%)	Ecological group/niche
S1 : Small, round, chain forming, with resting stage	45.45	Generalist, appreciate water runoffs
	36.36	In warm waters with long daylight exposure, less relations with flows or nutrients
	9.09	In dynamic, turbid, colder waters, affected by eastern winds
	9.09	Need long light exposure, with high N/P ratio
S2 : Elongated, Xlarge and chain forming, with low S/V ratio	52.94	In warm waters with long light exposure, less relations with flows or nutrients
	23.53	Generalist, appreciate water runoffs
	11.76	Need long light exposure, with high N/P ratio
	5.88	In dynamic, turbid, colder waters, affected by eastern winds
	5.88	With marine affinities, high salinity and low N/P ratio
S3 : Large, diverse colonial aspects, low S/V ratio	58.33	In warm waters with long light exposure, less relations with flows or nutrients
	33.33	Generalist, appreciate water runoffs
	8.33	In dynamic, turbid, colder waters, affected by eastern winds
S4 : Tychoplanktonic, medium sized, chain forming	44.44	Generalist, appreciate water runoffs
	33.33	In dynamic, turbid, colder waters, affected by eastern winds
	22.22	In warm waters with long light exposure, less relations with flows or nutrients
S5 : Benthic and mobile, medium sized, single cells	62.5	Generalist, appreciate water runoffs
	25	In warm waters with long light exposure, less relations with flows or nutrients
	12.5	With marine affinities, high salinity and low N/P ratio
NS1 : Phaeocystis, forming curved colonies	100	Generalist, in-between conditions
NS2 : Mixotrophic, medium, round, swimming and toxic	16.67	Appears during west winds in stratified waters
	16.67	Need light and freshwater inputs, and high N/P ratio
	16.67	Present with fresh water inputs, dissolved oxygen and high N/P ratio
	16.67	Present with high flows and high N/P ratio
	16.67	Generalist, in-between conditions
	16.67	Under temperature and daylight duration influence
NS3 : Mixotrophic, large, round, single, swimming	50	Under temperature and daylight duration influence
	33.33	Need light and freshwater inputs, and high N/P ratio
	16.67	Appears during west winds in stratified waters
NS4 : Small, high S/V ratio, swimming, mix or autotrophic	60	Appears during west winds in stratified waters
	20	Generalist, in-between conditions
	20	Under temperature and daylight duration influence
NS6 : Amphidinium, small, heterotrophic and tychoplanktonic	100	Under temperature and daylight duration influence
NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	60	Under temperature and daylight duration influence
	40	Generalist, in-between conditions
NS7 : N. scintillans, XXL-size, round and heterotrophic	100	Under temperature and daylight duration influence
NS8 : Heterotrophic, elongated, with high S/V ratio	50	Generalist, in-between conditions
	50	Under temperature and daylight duration influence
NS9 : Scenedesmus, chain forming with spines	100	Present with fresh water inputs, dissolved oxygen and high N/P ratio
NS10 : Large, elongated, with resting stage	50	Present with high flows and high N/P ratio
	50	Under temperature and daylight duration influence

6

Monitoring the variations of annual phytoplankton's lipids and chlorophyll-a content per confocal microscopy

Angéline Lefran, Nicolas Elie, Léon Serre-Fredj, Tania Hernández Fariñas, Pascal Claquin

Ce chapitre présente un aspect expérimental original, mené de septembre 2020 à août 2021, pour l'étude de la variabilité de deux traits physiologiques ; les teneurs en lipides et en chlorophylle-a. Le chapitre 2 de ce travail a mis en avant une base de traits figés qui, au regard du nombre de traits et de taxons, ne peut être qu'issue de la littérature. Construire une telle base pour l'ensemble de la communauté microphytoplanctonique littorale aux échelles régionales ou nationales n'est pas encore envisageable. Pour autant, le chapitre 3 montre que les traits, de part la répartition des espèces qui les possèdent, sont sensibles à certaines conditions environnementales. Le microphytoplancton ayant une période de *turn-over* extrêmement rapide, notamment en période printanière et estivale, l'approche décrite dans ce chapitre met en lumière la variabilité annuelle de composants intracellulaires d'intérêts.

6.1 Abstract

Trait-based approaches hold the potential to describe and access mechanisms behind community structure. More and more studies investigate this field of research to better understand climate change's effect on biodiversity. As the first link of most marine trophic networks, phytoplankton's responses to environmental changes are key to the comprehension of ecosystem's dynamic. However, it is no secret that phytoplankton also holds important range of variability at numerous scales ; from inter-annual to daily range. Morpho-functional traits are key as they enable to estimate intra-cellular physiological rates (e.g. growth, nutrient and light uptakes). However, phytoplankton cells have high plasticity in response to surrounding environmental conditions. This plasticity is acknowledged but poorly investigated *in situ*. In our study, two major components of the cell ; chlorophyll-*a* (photosynthesis efficiency) and lipids (energy storage) contents are estimated through confocal microscopy and 3D imaging reconstruction. Monthly samples coming from three contrasted stations of the northern French coast are investigated to better understand the seasonality of intracellular chlorophyll-*a* and lipids contents. Results showed that chlorophyll-*a* content, while variable, displayed no clear seasonality (in average it represented 25% of cells biovolume). Spatially, its content was higher in cells coming from area under high turbidity, in response to limited light (photo-acclimation process). However, lipids content displayed seasonality at all spatial points, with higher content in winter and early spring (around 25% of cells biovolume) and lower content in summer (5%). Reasons behind such variability is not clear, rapid cell's division during this time of the year is an hypothesis, but more studies are needed to understand these results.

6.2 Introduction

Phytoplankton is a compartment extremely diverse in size, shape, behaviour and content. With community composition, using the functional diversity is essential to understand an organism's relationship with environmental parameters. Specifically, morphological traits are key and largely influence growth and fitness of a cell. That is to say for instance that shape affects nutrient and light acquisition, predation and sinking rates. It was studied that round cells are found to have more surface in contact with environment (higher surface/volume ratio) and thus are better suited for nutrient acquisition while elongated cells are more efficient toward light acquisition (Friebele et al., 1978; Stanca et al., 2013). These functional characteristics are already known and found through the seasonal cycling of primary producers, triggered by environmental changes in coastal ecosystems. On the eastern Atlantic, after a cold winter and the increase of water discharge, diatoms' blooms occur in spring, followed by dinoflagellates' in summer when nutrients availability become scarce, and sometimes another diatoms' proliferation occurs in early autumn (Napoléon et al., 2014; Carstensen et al., 2015).

Chlorophyll-*a* (chl-*a*) is the main pigment within phytoplankton cells. Productivity and biomass are estimated as a function of chl-*a* concentration (Behrenfeld & Falkowski, 1997). The chl-*a* content per cell is known to be highly variable, depending on the cell's phylogeny (Álvarez et al., 2017) but also on the light condition (Legendre et al., 1985; Stæhr et al., 2004) and nutrient availability (Riemann et al., 1989). Such plasticity following environmental parameters is part of the photosynthesis optimisation process. Lipids represent a part of the cells' energy storage and are also susceptible to variations depending mainly on phylogeny, but also on environmental conditions (nutrients, light duration and salinity correlations were found for certain classes in freshwater phytoplankton) (Galloway & Winder, 2015; West et al., 2015; White et al., 2015). Fatty acids are the most abundant lipidic component within marine plankton and are essential to the cell's functioning, division and growth (White et al., 2015). They can be impacted by nitrogen in the different life stages through an increase of tryacyglycerols for example, a major lipid component, especially in aged cells (Fidalgo et al., 1998). Fatty acids can be used as marker to study phytoplankton diversity as seen with the use of pigments (Dijkman & Kromkamp, 2006). The "quality" of a resource for a given consumer is partly attributed to its content of essential nutrients (additionally to edibility and toxicity) (Galloway & Winder, 2015). Certain upper levels consumers even select the cells according to the amount of energy it contains (Cotonnec et al., 2001). Moreover, zooplankton growth rate has been correlated with highly unsaturated fatty acids content in their diet (Brett

& Müller-Navarra, 1997). It is essential to understand the variability of such components as upper levels rely on them, especially as they depend on environmental conditions (Hellessey et al., 2020). In a period of climate change issues, ocean acidification (pCO_2 increase), by reducing resource's quality at the cellular level, could affect zooplankton's fitness through a decrease in egg production and hatching success, as it has been demonstrated with copepods (Meyers et al., 2019).

Traits-based approaches have the potential to elucidate processes at the base of phytoplankton organisation. To better appreciate phytoplankton's responses to environmental changes, both in short and long term, it is often recommended to look at resources utilisation traits or tolerance curves besides morphological characteristics (Litchman et al., 2012; Weithoff & Beisner, 2019). However, such approaches often need the use of cultures, mainly monospecific with few strains, resulting in insights of species's plasticity but difficulties to relate with actual environmental conditions, especially in marine environment. To study marine functional assemblage it is therefore easier to rely on literature-based traits to form functional groups and study their relationship with environmental changes (Edwards et al., 2016; Ramond et al., 2018; Laplace-Treyture et al., 2021; Kruk et al., 2021).

Functional traits approaches to cell's plasticity and its drivers (phylogeny or environmental) are rare due to the complexity of data acquisition. Nevertheless, this work aims at understanding the plasticity of marine phytoplankton cells' physiology based on local monitoring of seawater samples. The chosen study area covers various sites that have been described as contrasted in term of environment but also in term of phytoplankton community structure (Lefran et al., 2021). Moreover, a monthly water sampling covers continuously all seasons and their particular environmental conditions. The estimation of both chlorophyll-a and lipid monthly content per cell was done on an annual basis using confocal microscopy. This method is poorly used in phytoplankton ecology due to the time consuming image acquisition, but few studies beneficiate from this method for biovolume estimation (Roselli et al., 2015; Mcnair et al., 2021). Considering the actual knowledge of phytoplankton's seasonality in temperate waters, chlorophyll-a is expected to vary in response to light conditions. It is also expected that spring and summer conditions, favourable for rapid cell division and blooms, may not permit lipid accumulation within cells, by opposition to winter that enables slow growth and therefore probably higher cellular content.

6.3 Material & Methods

During a year, from September 2020 to August 2021, samples were taken every month on three coastal sites along the French coast of the Channel (Fig 6.1). They are considered contrasted in term of phytoplankton community following previous work on the area that describe, Cabourg (CAB) as a estuarine system, Donville (DON) as a marine system, and Géfosse (GEF) as an in-between system with a higher biotic pressure coming from filters feeders (Lefran et al., 2021). Due to sampling protocols hazards, an additional sampling was done on Cabourg in November 2020, another sample was missing on Donville in February 2021

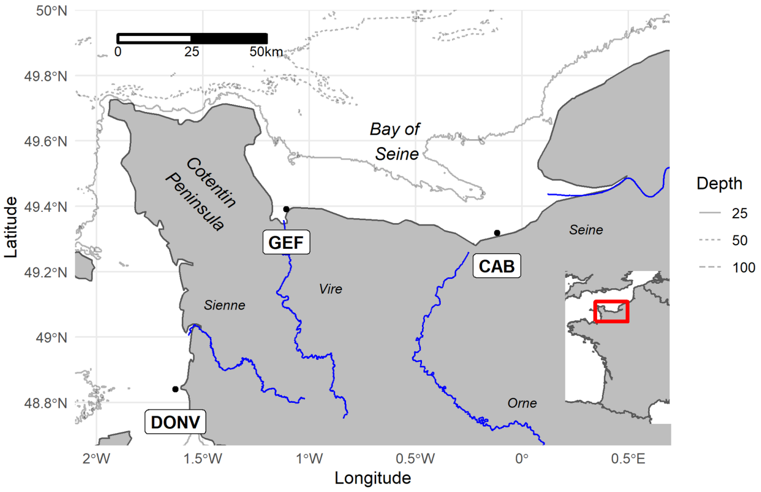
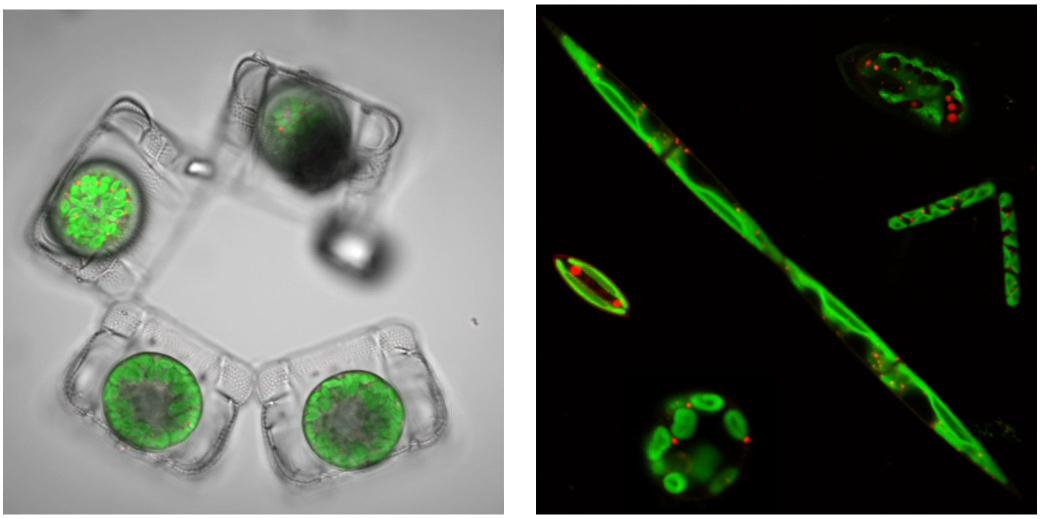


FIGURE 6.1 – Study area displaying the three stations covered by the experiment.

Water sampling followed the REPHY and RHLN standardised protocols (Neaud-Masson, 2016), in order to access environmental biotic and abiotic information surrounding confocal microscopy observations. To observe both the chloroplasts and lipids fluorescence, our samples needed to be alive. Therefore they were taken for analysis in the few hours following the sampling. A volume of approximately 800 ml of water sample was filtered using a 10 µm filter to concentrate the cells amounts. Few drops were placed in 5 ml in cell culture dish (35/10 mm, Greiner Bio-One GmBh, Frickenhausen, Germany), a drop of Nile Red (1 g.ml^{-1}, pounder diluted with DMSO-dimethylsulfoxyde) was added and spread around the sample. The Nile Red is a solution which can enter the cells and stain the lipids compounds to give them a fluorescence response (Greenspan & Fowler, 1985). A cover glass was positioned above the sample and the extra liquid was removed so that the cells could not be under any kind of flow movement during the analysis. Only few minutes are necessary for the staining.

Our next approach is based on the use of confocal laser scanning microscopy (FV1000, Olympus, Rungis, France) which enables to access biovolume and fluorescence at different wavelength (Govender et al., 2012; Roselli et al., 2015). We used λ = 633 nm and λ = 488 nm to observe the chlorophyll-a and lipids fluorescence respectively in addition a third channel of transmitted light from 488 nm LASER for a bright-field observation. The cell culture dish is observed under a ×60 objective. In order to avoid inter-operators effects, only one was assigned to gather all the observations. Transects were realized starting at the top-right corner of the cell culture dish. The observations paused each time a live cell was fit for acquisition, maximizing the diversity of observations. At each targeted cell, the fluorescence saturation level was adjusted for both wavelengths. Then, the upper and lower limits of the cells were roughly selected manually thanks to the chlorophyll-a fluorescence channel. The software was then able to scan layers of 0.56 μm (estimated upstream as an optimal value considering the time of acquisition and the cell size) between the given limits. The output is a compilation of n-scanned layers for the three channels (white light, λ = 633 nm and λ = 488 nm) (Fig 6.2). The method is very time consuming. Up to a dozen scans per sample could be done, depending on the time and location of the sampling, and also the number of samples to analyse in a row.

Through ImageJ (Rasband, 2018), a first script was used to redraw the upper and lower limits of the cells as the initial acquisitions were mostly taken with caution not to cut the cells which resulted in too many layers. The second script enabled to access the bright-field images, draw the cells limits on the main layers



(a) (b)

Figure 6.2 – Examples of outputs of the confocal microscopy acquisition ; a) the 3 channels overlap on *Trigonium alternans*, b) the channels displaying lipids (red) and chlorophyll-*a* (green) for *Pseudo-nitzschia* spp (center), *Prorocentrum micans*, *Thalassionema* sp., a cell of Naviculaceae family and a centric diatom (from top to bottom). For higher image clarity, proportions in the latter are not accurate.

and extrapolate to reconstruct the whole cell's shape. Afterwards, the script calculated the volume of the cell, the volume highlighted by chlorophyll-*a*'s fluorescence of and by lipids' fluorescence (Bolte & Cordelières, 2006). Those values were then converted into chlorophyll-*a* content and lipids content per cell's biovolume (ratio of fluorescence's volume over total biovolume).

Part of our samples were used to add photobiological parameters through variable fluorimetry method. A lab-STAF (Chelsea Technologies, UK) was used to estimate the phytoplankton community productivity as described by Boatman et al. (2019) using a fluorescence light curve (FLC). The method and calculation details are available in Oxborough et al. (2012) and Boatman et al. (2019). As a summary, we considered the following elements ; the maximum quantum efficiency of the photosystem II (F_v/F_m) which allows to assess the physiological state of the phytoplankton community, was calculated as (Genty et al., 1989) :

$$\frac{F_v}{F_m} = \frac{(F_m - F_0)}{F_m}$$

with F_0 ; minimum fluorescence and F_m ; maximum fluorescence in the dark.

The FLCs allowed to determined the maximal photosynthetic production, JVPII_{max} (expressed in µmole-.m^{-3}.s^{-1}), using the absorption algorithm of Oxborough et al. (2012). The electron transport rate, ETR$_{IImax}$ (expressed mmol e-. mgChla^{-1}.h^{-1}), which corresponds to the maximal photosynthetic productivity (production per Chl-a unit), was calculated as followed :

$$ETR_{IImax} = \frac{JVP_{IImax}}{[Chl - a]}$$

In addition, two photosynthetic parameters were estimated using FLCs, α (Photosynthetic efficiency) the initial slope of the FLCs and Ek (light saturation coefficient) with corresponds to the ratio between ETR$_{IImax}$ and α.

Also, flow cytometry analysis using a CytoSense (Cytobuoy, The Netherlands) were performed to discriminate groups of phytoplankton using cell size and fluorescence, notably concentrations of pico- and nano-phytoplankton (converted to cells.L^{-1}) as described in Serre-Fredj et al. (2021).

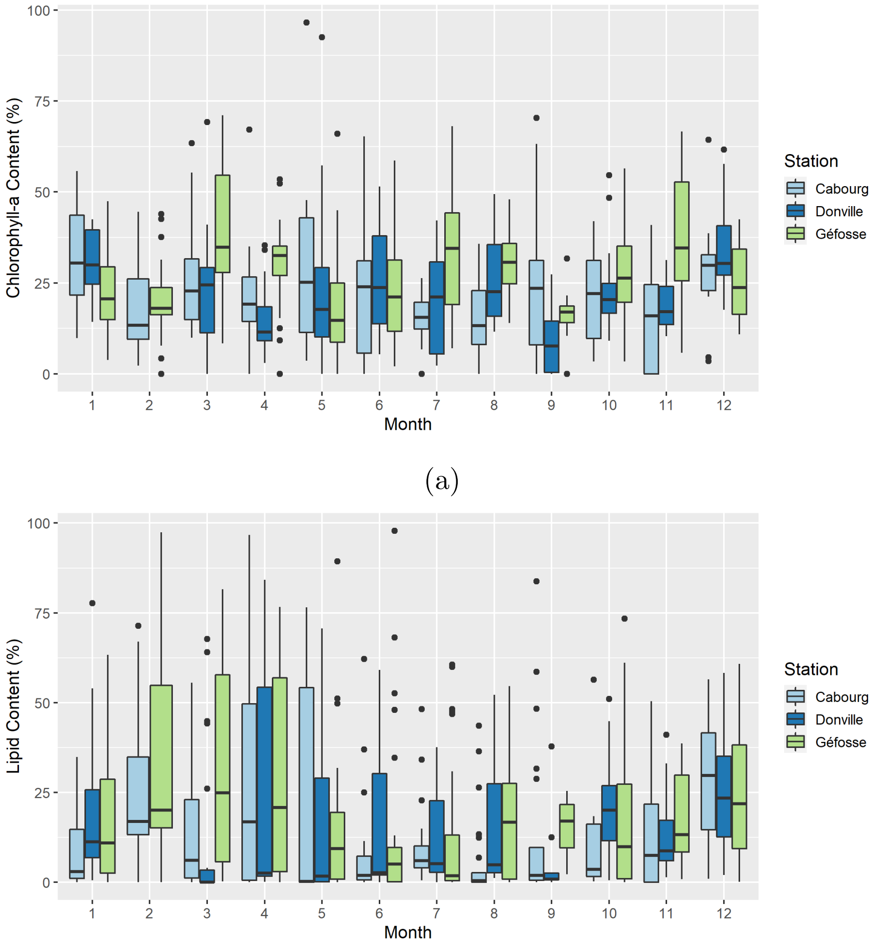
In term of data analysis, correlations between cells' content and environmental parameters were built from monthly values. For each water samples, the aim was to obtain as much information on the abiotic conditions surrounding the sample as possible. The most common parameters, such as nutrients, temperature, salinity, turbidity and dissolved oxygen were measured or calculated (details in Table 6.1). Information on cell efficiency regarding the photosynthesis process (described above) were also taken into consideration. Each pair of complete variable were compared and a correlation value is establish following either Spearman or Pearson's index (depending on normality). A coloured matrix is used to better highlight the meaningful values.

Table 6.1 – Environmental parameters considered and their methods of acquisition

Parameter	Method		
Temperature (°C)	*In situ* temperature sensor		
Salinity (PSU)	*In situ* conductivity sensor		
Dissolved oxygen ($mg.L^{-1}$)	*In situ* oxygen sensor		
Turbidity (FNU)	Optical turbidimeter		
Pheophytin & Chl-*a* (µmol.L^{-1})	Flow spectrophotometry (Aminot & Kérouel, 2004)		
N/P ratio	Flow spectrophotometry for the ammonium, nitrate, nitrite and phosphate nutrient (Aminot & Kérouel, 2004) : $N/P = ([NH_4^+] + [NO_3^-] + [NO_2^-])/[H_3PO_4]$		
Rainfall (mm)	Amount of rainfall gathered between 06H00 UTC Day D and 06H00 UTC Day D+1 (1 mm = 1 $L.m^{-2}$)		
Wind Speed (m.s^{-1})	Average of the maximum speeds recorded over 10 min		
Wind direction (% of a West wind)	Similarity of the wind direction (realWD) with a West wind (270°). $NewWD = abs(100 - abs(realWD - 270)/180 * 100)$		
Daylight duration (min)	Duration of light (intensity over 120 W m^{-2}, enough to create distinct shades) over a period of 24h (from 00H00 UTC)		
Inflow ($m^3.s^{-1}$)	River	Average	Catchment Basin
	Seine (at Paris, Austerlitz)	315	78650km^2
	Vire (at Malloué)	7	1969km^2
	Sienne (at St Cécile)	2	794km^2

6.4 Results

Our monthly results tend to indicate that the chlorophyll-*a* content is unstable from a month to another with content representing 8 to 38% of the total cell biovolume. Spatially, Géfosse showed the highest values except during the winter period (Fig 6.3a). Concerning lipids content, the values were between 5 to 35% of the total biovolume, there were a progressive decline from April to August then a progressive increase until December. Both Cabourg and Géfosse displayed lower content in January, but higher value in February and April (Fig 6.3b). Looking at the significant relationships ($p < 0.05$, details in supplementary data 1), Cabourg samples possessed lower chlorophyll-*a* content in summer compared to spring and winter ; Donville's samples values in Winter were greater than those found in all other seasons but it's the opposite for Géfosse for which winter chorophyll-*a* contents were the lowest. For lipids content, Cabourg displayed significant higher values in winter compared to summer and autumn ; Donville displayed the lowest values in spring and highest in winter compared to the other seasons ; and Géfosse's lipids content in summer were the lowest compared to all other seasons.



(a)

(b)

FIGURE 6.3 – Monthly average distribution of (a) chlorophyll-*a* and (b) lipids content (% per cell biovolume) for the three coastal stations for the period between September 2020 to August 2021.

To pin point the origin of the lipids content depletion over the summer months, a subset of the previous figure displayed the lipids content for the most frequent taxa. It shows high temporal variability and follows the general tendency observed on the average monthly lipid content, especially regarding *Skeletonema* spp. and *Paralia sulcata* (Fig 6.4).

The seasonal display per station indicated few significant differences (Fig 6.5).

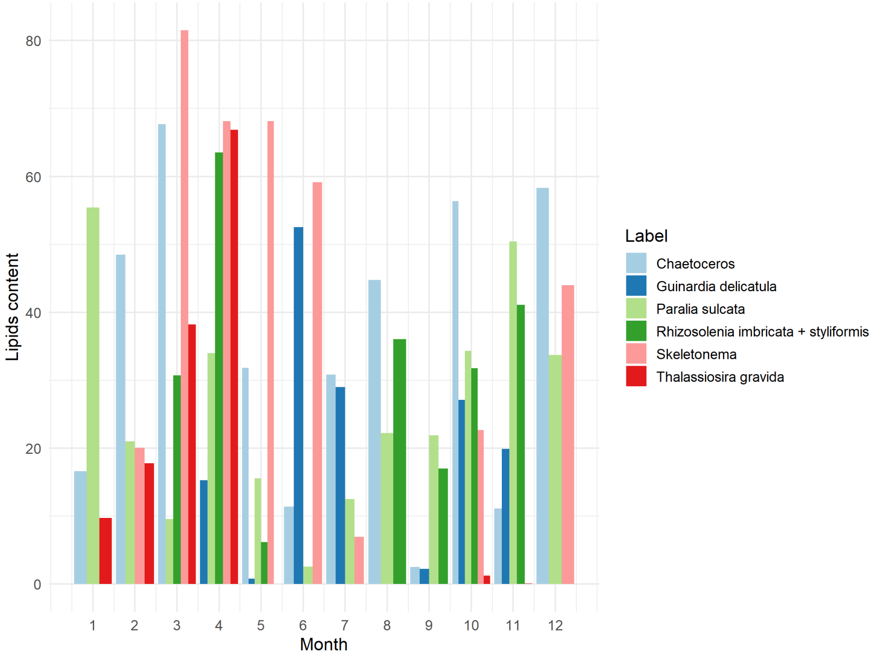


FIGURE 6.4 – Illustration of the average lipids content (% per cell's biovolume) on the most frequent taxa observed over the study period.

Regarding chlorophyll-a content per cell, the major spatial difference appeared in summer with Cabourg having lower content than Géfosse. Moreover, while those stations were displaying similar content per cell in winter, Donville possessed the highest chlorophyll-a content during this season. The content's range was wider for cells gathered in winter and spring. Spatially, fewer differences appeared regarding lipids content, notably Géfosse cells' content in spring was higher than the other stations'.

The previous observations highlight seasonal contrast between chl-a and lipid content (Fig 6.6). Therefore, looking at correlations with environmental variables highlights affinities between variables co-occuring at the same time. All stations considered, lipids contents per cells were negatively correlated with temperature, pheophytin and *in-situ* chl-a and positively correlated with the chlorophyll-a content, PO_4^{3-} and turbidity. The chlorophyll-a content displayed lower absolute correlation values but the latter indicated negative correlation with temperature and also weak positive correlations with turbidity, PO_4^{3-}, $Si(OH)_4$ and $NO_2^- + NO_3^-$. Most specifically, few spatial variations exist, Donville displayed mostly po-

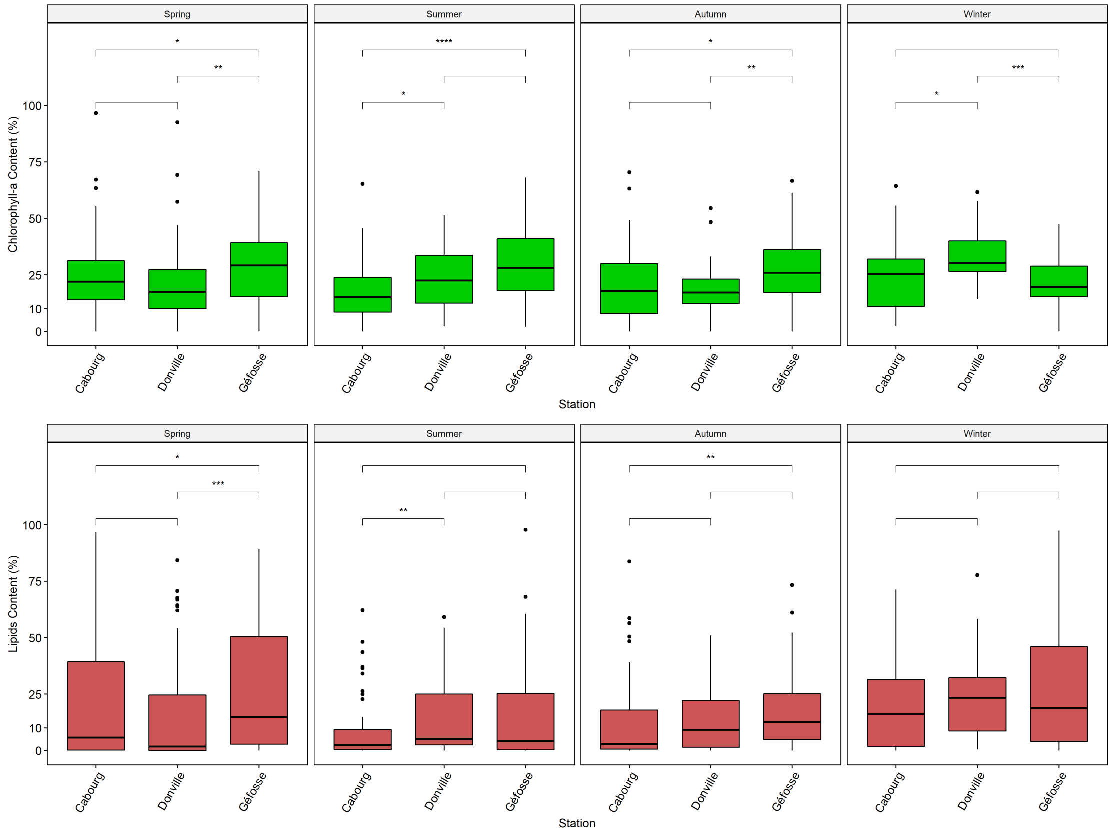


FIGURE 6.5 – Seasonal boxplots comparing station's content (% of cell's biovolume) in chlorophyll-*a* (green) and lipids (red). The stars indicate the level of significance given after a Wilcoxon test (significance symbols : "****", "***", "**", "*" are respectively associated with the p-value = 0, 0.0001, 0.001, 0.01, 0.05).

sitives correlations for both chlorophyll-*a* and lipidic contents with environmental parameters (flow, salinity). In Donville and Géfosse, lipids contents were positively correlated with nutrients concentrations. Lipids content in Géfosse was negatively correlated with pico-phytoplankton and rainfall.

6.5 Discussion

Environmental changes are affecting the oceans and specially coastal areas through multiples processes from eutrophication to global change (Halpern et al., 2008). In temperate systems, seasonality is a strong component of phytoplankton cycling and results from environmental drivers (Beliaeff et al., 2001; Hernandez-

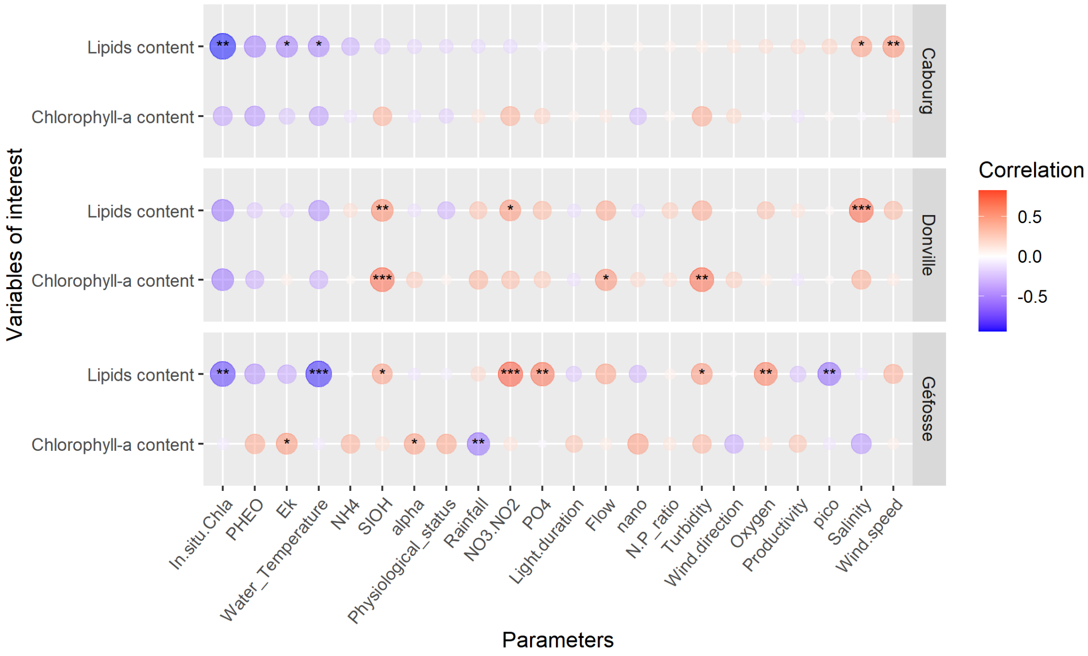


FIGURE 6.6 – Environmental correlations between biotic and abiotic variables. The size of the dots depend on the correlation's value, the colours indicate positive (red) or negative (blue) relationship. The parameters are ordered according to their correlations value with lipids content in Cabourg. Significant values are indicated as ; * : p-value < 0.1, ** : p-value < 0.05 or *** : p-value < 0.01

Farinas et al., 2013). But at the scale of cellular variability, daily changes play a significant role in intra-cellular mechanisms. It is suggested in Becker et al. (2018) that phytoplankton (specially haptophytes and dinoflagellates) could contain up to 40% more calories at sunset compare to sunrise. Chlorophyll-*a* is a major pigment signature of chloroplasts, which are distributed in various number, shape and size among phytoplankton taxa (Larkum & Vesk, 2003). It has many facets of use on which is based primary production and is widely known to be a proxy of phytoplankton biomass (Huot et al., 2007). In this study, through confocal microscopy, we have been able to access both chlorophyll-*a* and lipid contents with a cell by cell multi-specific analysis during an annual survey. While most physiological approaches are the result of laboratory cultures in different conditions of one or two abiotic variable at a time, to our knowledge, this approach from *in-situ* continuous marine water samples is one of a kind.

6.5.1 Exploring cell's physiology and plasticity

In trait-based approaches, the morphological traits, specially size, are essential characteristics on which depend many physiological processes such as nutrient uptake or growth rate, and also influence grazing and sinking rates (Litchman et al., 2010; Salmaso et al., 2015; Bretherton et al., 2020). Cells' fitness relies on their ability to catch and make use of light through photosynthesis (Berges & Falkowski, 1998; Key et al., 2010) and using it with environmental nutrients to produce energy and maximise their development (Jónasdóttir, 2019). It then defines the cells' "quality" and richness as preys on which whole trophic chains depend on (Cotonnec et al., 2001; Galloway & Winder, 2015). However, estimating the inner cells' physiological processes is complex and relies mostly on cultures to apprehend cellular plasticity. On a community level, from field sampling, our results indicate that the average annual lipids content corresponded 17% of cell's biovolume (up to 25% in winter and spring, and down to 5% in summer). Chlorophyll-*a* content covered an average 25% of cell's biovolume throughout the study period.

Confocal microscopy is an optical imaging approach using lasers as excitation light to trigger fluorescence of certain components of interest within targeted cells (Nwaneshiudu et al., 2012). It is widely used in medicine, notably in cancer research (Dubois et al., 2020), but has also been used for immunofluorescence in marine organisms such as oysters (Maillard et al., 2021) or through bacteria-phytoplankton interactions (Cheng et al., 2021). Confocal analysis along with 3D reconstruction imaging enables to access information on cellular biovolume, size and shape. This is central considering the proximity between phytoplankton organisms and their immediate surrounding environment. Usually, biovolume is estimated through models estimations, not from field samples (Roselli et al., 2013, 2015). A more recent study used confocal microscopy to highlights the effects of micro- and nano- plastic on phytoplankton cells, and noticed that plastic aggregating around large cells impacted their overall density (Dedman et al., 2022). This is therefore an approach, whilst not recent, that holds the potential of revealing inner processes of marine phytoplankton organisms that scientists long for.

In our experience, this approach is of high quality, both confocal images and fluorescence were satisfying in order to access chl-a and lipids content from 3D cell reconstructions. It enables high contrast acquisitions, and 3D biovolume reconstruction thanks to images analysis. Unfortunately, not being able to fix the cells' content to access a higher amount of information (as chl-a's wide range of fluorescence overlapped the lipids' at cell's death) lead to a very narrow time interval to perform the acquisitions after the sampling. Regarding our main targeted compound, the lipids, few studies opted for fluorescence approaches ; it has been done mainly on cultures, for example *Heterosigma akashiwo* (Sengupta et al., 2021) and *Thalassiosira weissflogii* (Chansawang et al., 2016). Most approaches rather use high performance liquid chromatography (HPLC) mass spectrometry (MS) on cultures experiments (Becker et al., 2018) or on communities with seawater samples (Falk-Petersen et al., 1998; White et al., 2015) but not at individual cell level.

6.5.2 Exploring environmental drivers of intracellular plasticity

A consequent spatial variability has been highlighted, mostly regarding chlorophyll-a content, between the three coastal stations of either marine, estuarine or intermediate (but with shellfish farms) influence.

The station Géfosse, has the highest chl-a cellular content in each seasons except for winter compared to the other stations. Chl-a is the only one displaying positive correlation with the two indicators of the production *versus* irradiance curve (E_k and α), which could be evidence that phytoplankton organisms in this area are more efficient at light acquisition (Bouman et al., 2018). This data can be explain by photoacclimation processes (Dubinsky & Stambler, 2009). Géfosse shows high turbitidy level in comparison with other sites. Light penetration being limited, phytoplankton required higher chl-a concentration to better harvest light flux and maintain their growth. In parallel, cells also display higher content in lipid, which, in addition with the previous statement, would indicates that, at

Géfosse, the microphytoplankton compartment is richer and with higher fitness, benefiting predators. This would be in agreement with Winder et al. (2017), who argued that salinity is an important factor conditioning the quality of phytoplankton cells (that is to say its long-chain essential fatty acids (LCEFA) content, major component of lipids). They found that intermediate to higher salinity regions inhabit phytoplankton with higher LCEFA content compared to areas with too much salinity (offshore oligotrophic areas) or not enough. Such results, if confirmed on longer survey, would beneficiate (and explain) the shellfish productivity in the Bay of Veys, already known to be an important host for oysters farms (Timsit et al., 2004; Costil et al., 2005).

The most anthropised and estuarine station, Cabourg, displays the opposite results ; it gathers the lowest chl-*a* contents, except in spring and mostly in summer compared to the other two areas. Chl-*a* content displays a low but still negative correlation with cellular physiological status and Ek (from the PE curve) which would indicate lower fitness and ability to use the light received. Turbidity in this area is indeed lower than the one found at Géfosse. Moreover, the lipid contents are also lower in phytoplankton cells this region, especially in summer and autumn. Additionally, the correlations show negative relationships between lipid content and water temperature and chl-*a*, two indicators of summer conditions in the Seine estuary. Such observations raise the question of river inflow influence on phytoplankton cells' status. Indeed, phytoplankton lipid contents are correlated with higher level of salinity in this area. The Seine pollutants (Gardes et al., 2020) could also be causing lower fitness ; trace metals, even though essential to phytoplankton growth, lead to a decrease in intra-cellular lipid content in diatoms when too concentrated (Anantharaj et al., 2011).

The most marine station shows intermediate values in both lipid and chl-*a* content compared to the other two areas. It differentiates itself in winter during which phytoplankton cells contain higher chl-*a* and lipids. According to the correlations with the local parameters, the lipid contents are correlated with salinity and silicate and nitrate+nitrite concentrations and the chl-*a* content is correlated with silicate, flow and turbidity. This coastal area is known for its megatidal environment, and well-mixed seawater. The saline correlation with lipid content is in agreement with Winder et al. (2017), as seen with the previous observation at Géfosse. Moreover, like at Géfosse, the relation between lipids and turbidity could be a sign of light limitation which would lead to higher lipid content that increase cell's buoyancy for a better position in the water column. It has been illustrated with *Scenedesmus* sp. that lipids are useful element to help cell buoyancy (Pančić & Kiørboe, 2018). Indeed, the colonial form of *Scenedesmus* sp. is a defensive strategy to avoid predation but it would cause higher sinking rate compare to single cells, driving the colony out of the euphotic zone due to higher cell density. The authors note that lipid contents in colonial cells can be more than twice the amount found in single cell, at an energy cost that is slowing growth rates (Pančić & Kiørboe, 2018).

On a yearly basis, monthly sampling has been successful at showing both temporal and spatial variability of chlorophyll-a and lipid contents within phytoplankton organisms. However, chlorophyll-a content's variability did not display a clear pattern justifying the changes and very few environmental drivers were correlated to these. Turbidity and $\mathrm{Si(OH)_4}$ parameters only seemed to be positively correlated with higher chlorophyll-a content in all stations, but significantly for the marine station Donville. While the link with turbidity is relevant, it would have been expected to have additional seasonal variations, notably following the day length as it has been seen in experimental studies (Blatt et al., 1981; Chansawang et al., 2016). Indeed, in their experiment on *Thalassiosira weissflogii*, Chansawang et al. (2016) observed lower chloroplasts and biovolume in low light condition compared to high light, which could actually be due to how chloroplast are distributed in the cell, either evenly (in low light) or condensed (in high light) (Blatt et al., 1981).

Concerning lipid content, from September 2020 to August 2021, all stations display a cycle with higher values during winter to April and then decreasing values until September. Additionally, in summer, the values are less spread and below 25%. Between spring and summer, phytoplankton blooms occur which means that rapid cell divisions enable to increase cells density in the water (Romero et al., 2013). Reduced lipid content per cell confirm our study hypothesis of lower content during a period of cells' proliferation. This is also in adequacy with the results at a species level, especially *Skeletonema* sp. and *Paralia sulcata* which possess lower intra-cellular lipid content in spring and summer following the overall community trend. However, no literature at our knowledge confirms the variations of inner cells compound during the expansion phase of phytoplankton.

Regarding the possible environmental drivers of such variability, studies indicate that nutrients limitations (nitrate/nitrogen, silicate) tend to enhance total lipid contents in various species (Shifrin & Chisholm, 1981; Madariaga & Joint, 1992; Wainman & Smith, 1997; Schwenk et al., 2013). For example, *Skeletonema* sp. was seen with higher lipid content under nitrogen limitation (Bertozzini et al., 2013). Nutrient limitation can modify the relative proportions of the various inner lipid fractions (neutral lipids, phospholipids, saturated and poly unsaturated fatty acids), decreasing its overall "quality" which could affect zooplankton (Fidalgo et al., 1998; Cotonnec et al., 2001). However, even though a nutrient limitation could explain the sudden rise of lipid content in April when spring blooms of diatoms take advantage of daylight increase, it does not justify the lipid content decrease in summer as this season is more subject to nutrients limitations compared to autumn and winter (Napoléon et al., 2014; Carstensen et al., 2015). Looking at another driver, experimental studies have shown that contents of highly unsaturated fatty acid increase at cold temperature in order to maintain permeability and flexibility of membrane phospholipid layers (Mortensen et al., 1988). This would also explain the higher lipid content per cell during winter.

6.6 Conclusion

Functional traits are key to explain the cell-environment relationship. In a context of environmental change, it is essential to understand the functioning of the primary producers and assure they meet the needs of the consumers. Among physiological traits, lipidic content and chlorophyll-*a* are major elements constitutive of a cell, displaying high plasticity on a seasonal but also daily scale. Both of them enable the phytoplankton cell to grow, reproduce and survive in a highly variable environment that are coastal ecosystems where parameters depend on season, weather and tide. For both components, effects of selected parameters such as light and nutrients has been described as affecting the contents of one or another (Riemann et al., 1989; Stæhr et al., 2004; Galloway & Winder, 2015; White et al., 2015). Most studies explore cellular activity in monospecific environments facing no more than two parameters limitations or enhancement for industrial production purposes, which is not representative of the real cell-environment interaction within marine water, especially in a coastal ecosystems. The confocal approach enables a certain quality and precision to the image but at the cost of a time consuming analysis. This approach beneficiates from wild samples, covering mainly diatoms cells, that still need investigation on a species level to expand our understanding of intra-cellular plasticity. As our three contrasted coastal stations displayed a similar significant pattern of a seasonal lipid content over the studied period, it would be interesting to further investigate zooplankton's predation behaviour and to understand how lower prey quality in spring, through less lipid content, affects the upper levels. Or, if quantity suffice to answer predators' needs.

6.7 Supplementary material

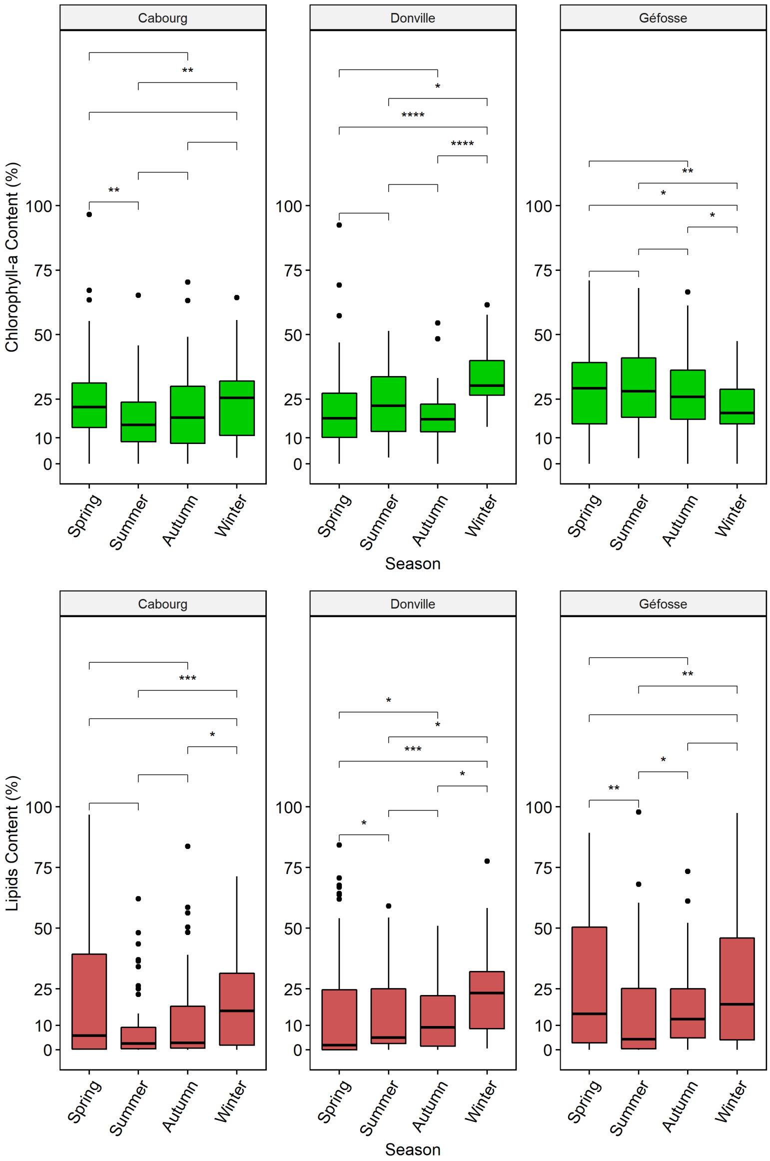


FIGURE 6.7 – Spatial boxplots comparing seasonal content (% of cell's biovolume) in chlorophyll-*a* (green) and lipids (red). The start indicates the level of significance given after a Wilcoxon test (significance symbols : "****", "***", "**", "*" are respectively associated with the p-value = 0, 0.0001, 0.001, 0.01, 0.05).

7

Harmful Algal Blooms : I- Comparative study of *Dinophysis* sp. ecology and environmental drivers along English and French shores

Angéline Lefran, Anouska Panton, Duncan Purdie, Tania Hernández Fariñas

Les deux derniers chapitres s'orientent sur l'écologie et les impacts de blooms algaux toxiques en Manche dans le cadre direct du projet Interreg S3-Eurohab. Ce dernier a pour objectif la détection et prévention des épisodes de contaminations chez les bivalves marins.

Cette première partie explore deux vastes baies, la baie au large de Plymouth (UK) et la baie de Seine (Fr), toutes deux affectées par des blooms récurrents de *Dinophysis* sp., dont la toxine produite peut entraîner des contaminations de type diarrhéique chez l'homme. L'objectif est de comprendre la synergie entre ces baies vis-à-vis des évènements toxiques et le rôle des facteurs environnementaux.

7.1 Abstract

Climate change has been rising many concerns due to its effects on marine ecosystems in terms of temperature increase, stratification, and changes in hydrodynamics but also by enhancing phenomena of extreme events and eutrophication. One of the problematic consequences is the increase of harmful algal blooms (HABs) in coastal ecosystems and their impacts on local fauna and consequently human health. *Dinophysis* sp. is composed of toxin producers (mainly *D. acuta* and *D. acuminata* in Europe) that are causing Diarrhetic Shellfish Poisoning (DSP). Since 2015, DSP outbreaks have been intensifying along the northeast Atlantic, causing closures in farm and fisheries. The S3-EUROHAB project (2018-2022, `https://www.s3eurohab.eu/`) aimed at building a real-time satellite-based portal to follow HABs in the Channel area. However, *Dinophysis* sp. has been difficult to monitor as DSP events occur at low cell density and the genus is mostly found in mixed layer depth, few meters below the surface that is usually sampled by local monitoring networks. It is also a mixotrophic organism, known to predate on a smaller ciliate *Mesodinium rubrum* also hard to detect through satellite. In this context, this study gathers cross-Channel information on *Dinophysis* spp. and potential environmental drivers. It shows that *Dinophysis* spp. is likely to be initiated by warming water coming from the South in the English area as early as May, whereas the Bay of Seine in France is not initiated before June. Among the drivers, there is high spatial variability ; only stratification (mainly at the offshore station L4, UK) and temperature are found commonly correlated with high *Dinophysis* sp. abundance. Futhermore, ecological subniches (WitOMI) between both areas display similar environmental affinities but no overlapping realised niche indicating that environmental conditions are very different and that *Dinophysis* spp. seems to be responding to specific combination of local drivers.

7.2 Introduction

Phytoplankton is an essential link within the marine food chain. However, certain species are known for having dramatic consequences on the local wildlife through toxins productions in quantities that can reach the human consumers

(Fleming et al., 2006). Those Harmful Algal Blooms (HABs) are sudden, rapid and mostly annual events triggered by optimal environmental conditions which have risen a major concern worldwide because of the toxins they produced, among other impacts. Studies tend to indicate that with climate change, notably warmer and more stratified waters among other factors, an increase of intensities and frequencies of HABs events could be expected (Hallegraeff, 2010; Griffith & Gobler, 2020; Gobler, 2020). For instance, in 2011, the US East coast experienced its first major *Dinophysis acuminata* outbreak with toxins amount in blue mussels nearly eight times higher than the sanitary limit (Hattenrath-Lehmann et al., 2013).

Discovered after contamination outbreaks in the mid 70s in Japan, *Dinophysis* spp. are known for affecting bivalves with Diarrhetic Shellfish Poisoning (DSP) even at low cell densities (Reguera et al., 2012). This poisoning is caused by lipophilic toxins ; okadaic acid (OA), its derivates dinophysistoxins (DTXs) and pectenotoxins (PTXs) and are closely monitored in case concentrations exceed the European sanitary limit of 0.16 mg OA eq./kg of dry matter (EFSA, 2009; Reguera et al., 2012). This is the main form of contamination among HABs along the coast of western Europe and United Kingdom considering its widespread and frequency characteristics (Bresnan et al., 2021). Consequences of *Dinophysis* spp. blooms result in shellfish farms and fisheries ground closures with important associated economic impacts. A study in Scotland estimated that for a 1% change (fraction of the OA eq. sanitary limit) above the sanitary threshold, the corresponding shellfish production was reduced by 0.66% (Martino et al., 2020). It is even more concerning considering that the average change in toxin production over the last decade has been reported at 24% above the sanitary limit in this area. Even though there is various species among *Dinophysis* genera, studies described *Dinophysis acuminata* and *Dinophysis acuta* as the main species to be responsible for toxin production over Europe (Salas & Clarke, 2019; Bresnan et al., 2021; Séchet et al., 2021).

Dinophysis sp. is a mixotrophic dinoflagellate, known to combine both photoautotrophic and phagotrophic processes (Riisgaard & Hansen, 2009; Hernández-Urcera et al., 2018). It is a predator of the small ciliate *Mesodinium* *rubrum* as demonstrated in cultures (Park et al., 2006) and through marine observations (Moita et al., 2016) and which itself is a predator of cryptophyte organisms (Park et al., 2006). As these preys are very small and hard to monitor compared to microphytoplankton (Moita et al., 2016), abiotic environmental parameters are usually investigated to elaborate an appropriate ecological realised niche. In the eastern Atlantic, *Dinophysis* spp. blooms appear and intensify when water temperature is rising and leads to stratification in the water column (Peperzak et al., 1996). Besides temperature, transport and most specifically, wind pressure seems to be influencing the blooms (Whyte et al., 2014; Panton & Purdie, 2022).

In the Channel, both the South West coast of England and the Normandy region in France have been under DSP pressure during the summer period, with numerous annual shellfish farms and fisheries spots closures (Belin & Soudant, 2018; Panton & Purdie, 2022). Mussels farming is the second largest aquaculture sector in the United Kingdom (Regan et al., 2021), Normandy is the first and second region for the production of scallops and mussels respectively (CCI Normandie, 2020). Both countries account for more than 90% of scallops catches in Europe (FAO, 2021). In their review on mussel aquaculture situation in Europe, Avdelas et al. (2021) cite HABs as one of the main environmental cause that led to the decline in mussel production for the past two decades. This study aims at understanding *Dinophysis* spp. occurrences through a comparative study of two locations across the Channel, both known to be frequently under HABs pressure, however both facing differently the Channel main stream. Through the investigation of historical events and thanks to local monitoring networks, this approach will highlight the relationship between *Dinophysis* sp. blooms and environmental drivers and compare both niches along key parameters.

7.3 Material & Methods

7.3.1 Cross-Channel study area

The studied stations are located on both side of the Channel (Figure 7.1). At the coastal areas, several events of shellfish farms and fisheries grounds closures have been occurring the past few years, on both French and English side (Belin & Soudant, 2018; Panton & Purdie, 2022). The English coastal stations are St Austell, Fowey and Lantivet, close from one another and close to the Fowey river. L4 is a monitoring station further offshore, south of Plymouth and the Tamar river. The French stations, Antifer and Cabourg, are both located by the coast, on the Seine river plume's path. The stations were chosen in order to maximise similar grounds for comparison purposes, notably ; their open bay configuration, their relative positions from the coast, the quality of the monitoring datasets for both biotic and abiotic variables.

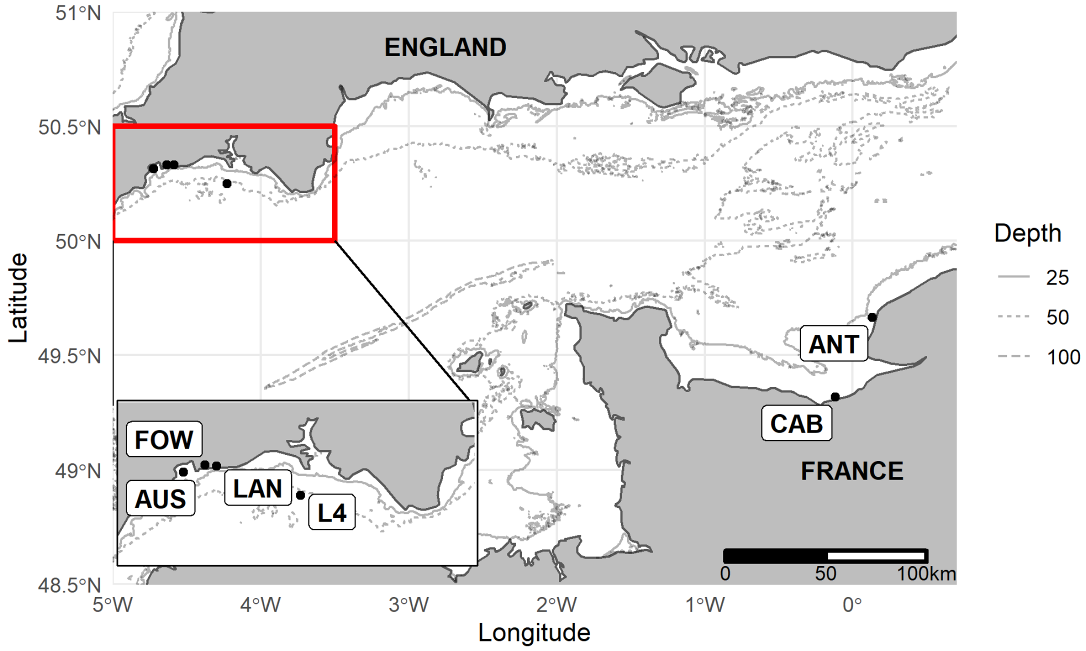


FIGURE 7.1 – Study area displaying the stations of both side of the Channel. Stations acronymes : AUS = St Austell, FOW = Fowey and LAN = Lantivet, ANT = Antifer, CAB = Cabourg. Depth is shown in meters.

7.3.2 Dataset composition

For the three coastal stations south of England, the local Food Standards Agency operated a monthly to weekly (in growing season for primary producers) subsurface (0-1m) sampling for toxin producing species and toxins in bivalves since 2014, with a detection limit of 40 cells.L^{-1} for phytoplankton data. Additional parameters are obtained through a WaveRider buoy (10 meters deep, and approximately 2.75 km offshore) and through meteorological stations inland, located at Looe and Bodmin. The L4 dataset is a long-term weekly time series covering phytoplankton diversity at a depth of 10 m since 1992 with a resolution of 20 cells.L^{-1} (Widdicombe et al., 2010; Widdicombe & Harbour, 2021). Along with the abundance, abiotic parameters are recorded on site (CTD or at a weather station for wind data). The French stations are monitored bi-monthly for microphytoplankton abundance in sub-surface and environmental parameters by the REPHY (REPHY – French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters, 2019), RHLN (Hydrologic Network for the Normandy Littoral). Additional environmental parameters were accessed thanks to weather monitoring stations (Météo France, Hydrological bank and Met Office only archive ; `https://archive.ceda.ac.uk/`). All environmental detail are given in Table 7.1. The Northern Atlantic Oscillation index was extracted from Hurrell (2020). The toxicity levels found in *Mytilus edulis* and *Pecten maximus* since 2010 were extracted from the REPHYTOX network (REPHYTOX – French Monitoring Program For Phycotoxins In Marine Organisms, 2021) for the Bay of Seine area. The toxicity information were consulted from the Cefas annual reports of the years 2014 to 2019 (`https://www.cefas.co.uk/data-and-publications/habs/`).

For all datasets, we considered the overall *Dinophysis* genera and did not find relevant to analyse species-specific patterns as *Dinophysis acuminata* dominates the data on both location, even though *Dinophysis acuta* is also observed in the English waters, but at half *D. acuminata's* numbers.

7.3.3 Data analysis

The various datasets were explored and analysed through the software R (R Core Team, 2021). For the phenology comparison, the direct display of the data on an annual basis was done for the longest time series ; UK offshore station (L4) and the French ones. A straight line shows abundance difference between two successive dates (not exceeding a month) in order to pinpoint the exponential bloom period for each area. Then the three datasets were compared through

Table 7.1 – Summary of the abiotic variables (with their unit) used for the numerical analyses and their measuring or calculation methods.

Parameter	Method		
Temperature (°C)	*In situ* temperature sensor		
Stratification (°C)	Proxy given by difference between surface and bottom temperature		
Light intensity (J.m^{-2})	Light sensor at onshore weather station		
Salinity (PSU)	*In situ* conductivity sensor		
Dissolved oxygen (mg.L^{-1})	*In situ* oxygen sensor		
N/P ratio	Spectrophotometry flows for the ammonium, nitrate, nitrite and phosphate nutrient $N/P = ([NH_4^+] + [NO_3^-] + [NO_2^-])/[H_3PO_4]$		
Rainfall (mm)	Amount of rainfall gathered between 06H00 UTC Day D and 06H00 UTC Day D+1 (1 mm = 1 L.m^{-2})		
Wind/wave Speed (m.s^{-1})	Average of the maximum speed recorded over 10 min		
Wind/wave direction (%)	Similarity of the direction (realWD) with a South West direction (225°). $NewWD = abs(100 - abs(realWD - 225)/180 * 100)$		
Daylight duration (min)	Duration of light (intensity over 120 W m^{-2}, enough to create distinct shades) over a period of 24h (from 00H00 UTC)		
Inflow (m^3.s^{-1})	River	Average	Basin
	Seine (at Paris, Austerlitz)	315	78650km^2
	Tamar (at Gunnislake)	20	1000km^2
	Fowey (at Restormel)	5	170km^2

the years with regard to the maximum DSP contaminations (OA eq.) that were recorded at each closed shellfish areas (*Mytilus edulis* and *Pecten maximus* for the Bay of Seine).

Spearman correlations index (*rho*) were calculated for each environmental parameters with its local *Dinophysis* spp. records. In order to characterise the processes that could explain the high densities of *Dinophysis* spp., and not only its presence, samples with *Dinophysis* spp. presence above detection limit were kept for this analysis. The period was between 2008-2019 for more complete and richer datasets comparison in term of environmental variables access. Mapping correlations through a solar plot representation gives the opportunity to display all parameters and their relative influence on *Dinophysis*'s bloom per area.

Additional information for the most relevant correlations are given through thresholds, that is to say for the main common driver (temperature) and for area-specific parameters (N/P ratio for France, stratification for the UK offshore station, and wind direction for the coastal English station). The graphical representation gives parameter's values above which most (with a 95% confidence) *Dinophysis* spp. records have reached certain concentrations ; from a 100 cells.L^{-1} to 10^4 cells.L^{-1}.

Additionally, co-occurring patterns were investigated between *Dinophysis* spp. and other phytoplankton taxa. For L4 (UK_offshore) and French areas, micro-phytoplankton community diversity is being frequently monitored and was acquired for the period of 2008-2019. The community matrices cover a hundred of taxa at each location. Spearman's correlation was applied to identify the taxa with the most similarities. As a correlation is not always enough to assess a relationship or the similarity between two dynamics, the linear regression index R^2 was also estimated for the most correlated taxa to certify or not the similarities of each pre-selected species with *Dinophysis* spp. in term of occurrences and distribution. A table summarises the main results for both areas.

Finally, this study aims at comparing environmental drivers between cross-Channel stations. Ecological niches using the WitOMI approach (Karasiewicz et al., 2017) were drawn using common and the most complete environmental drivers for both areas (subsets or subniches) for the months between April and November of the period 2008-2019. As explained in their methodological paper, this approach allows to build subniches for a single species (*Dinophysis* spp. in this study) taking into account spatial differences. The potential subniche (SP) for *Dinophysis* spp. is determined for each station and compared to the realized subniche (SN). Theoretically, if a species does not occupy its full environmental niche, it implies the existence of biotic interactions (SB) (Jackson & Overpeck, 2000). The niche position (marginality) is the distance between the average habitat conditions and the average habitat of the subset. The further from average it is, the most atypical is the habitat. The WitOMIG$_K$ (represented by an arrow) represents the habitat used by the species of interest. Using this approach to construct ecological subniches will allow to investigate the spatial differences between both French and English sites as well as how *Dinophysis* spp. interacts with its biotic and abiotic environment.

7.4 Results

7.4.1 Historical *Dinophysis* spp. blooms and impacts

Looking closely to the similarity between English sampling stations (Figure 7.2), *Dinophysis*'s distribution is very similar for the common period of 2014-2020 with high abundances for the years 2014, 2015, 2016 and 2018 and a very low presence in 2017, 2019 and 2020. Looking at England offshore, the 2014 marks also the beginning of a wider range of representation of the genera.
Over the past two decades, *Dinophysis* spp. blooms in France are found to be recurrent and with abundance nearly 10 times higher compared to English stations, with 2005, 2006 and 2018 holding the highest records. However, fewer records were registered for the in-between period of 2009-2012. This inter-annual tendency is not similar to the one observed at the offshore English station. Nevertheless, looking at toxicity records, fewer *Pecten maximus* fisheries spots (colored dots, Figure 7.2) are under DSP sanitary closure in 2013, 2017 and 2019 which also correspond to less *Dinophysis* abundance at the offshore English site. In France, toxins in *Mytilus edulis* have been found to reach 3500 µg OA eq. kg^{-1} in 2014, 2017 and 2018, results in England are similar, with a maximum over 3500 µg OA eq. kg^{-1} reached in 2014, 2015 and 2018.

The annual dispersion of *Dinophysis* spp. is concentrated on a wider time period in England, extended from May to October, whereas the cells can be found between June and November on France's sites (Figure 7.3). There is a month delay between events in England and in France. It is also noticeable on lines of abundances' variations which show that UK stations have been affected by cell's rapid proliferation from mid-June until the end of July is reached, while France's sites has a narrower window of two or three weeks in August. The maximum value reached in the UK was nearly at 10^4 cells.L^{-1} in 2016, it was nearly at 10^6 cells.L^{-1} in 2006 in France.

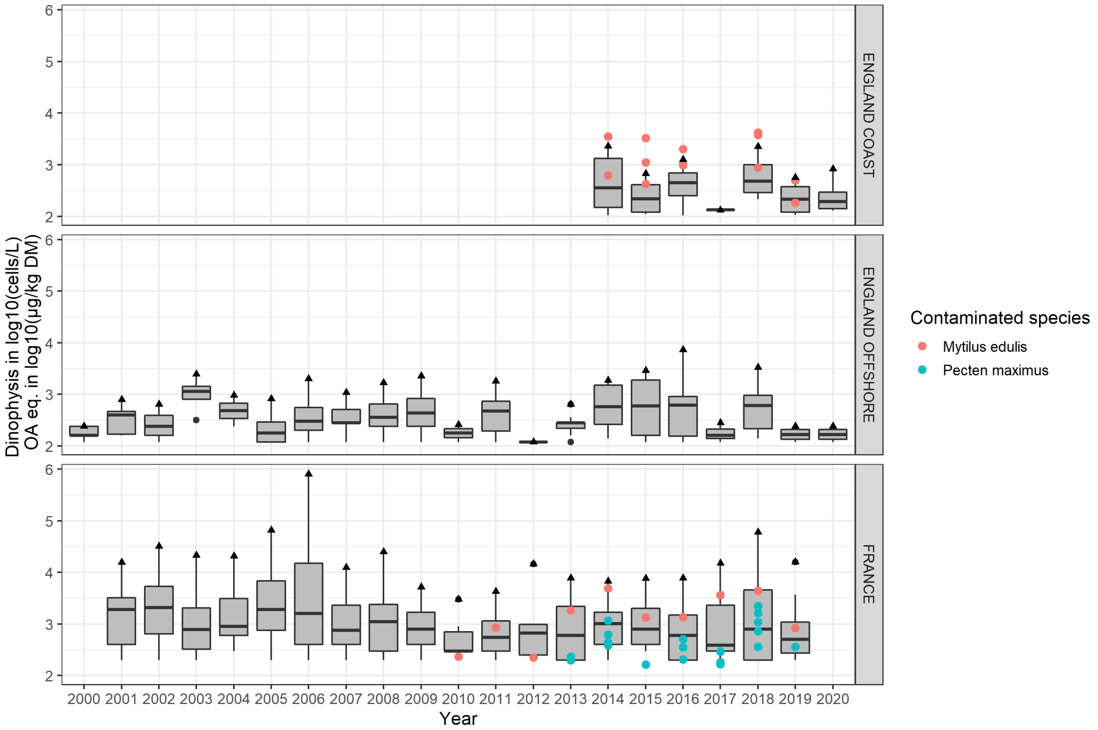
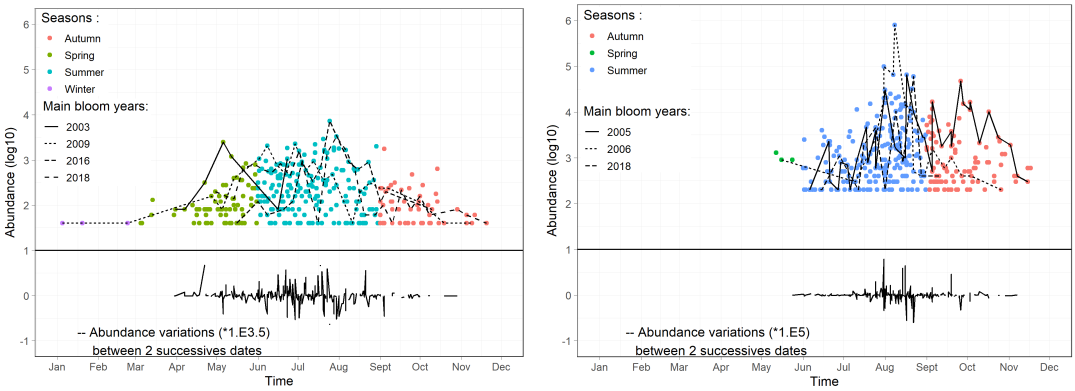


FIGURE 7.2 – Historic of *Dinophysis* spp. densities (> 100 cells.L^{-1}) over the years at locations across the Channel and the maximum toxicity values (> 160 µg OA eq.kg^{-1} in Dry Meat) encountered on two commercial species (*Mytilus edulis* and *Pecten maximus*).

7.4.2 Comparative environmental relationship with *Dinophysis* spp. apparition or bloom

Spearman's *rho* in Figure 7.4 rapidly highlight the most influencing parameters among the various environmental variables for all three areas. Even if correlations values are much lower on the French sites, similarities and differences are found between both side of the Channel. Among the major influencing parameters, temperature is given as the common significant driver for all three areas ($p\text{-value} < 0.05$), but with relatively low correlations of 0.3 (UK) and 0.4 (Fr). The thresholds plots however clearly indicate that *Dinophysis*'s spp. distribution is scaled on temperature values (Figure 7.5) ; with 95% of cells count a thousand cells.L^{-1} being found in water temperature of 15°C in the South West England, and at 17.6°C in France.



(a) UK Offshore

(b) France

FIGURE 7.3 – Historic of *Dinophysis* spp. presence on an annual scale for France and UK offshore stations between 2000 and 2019. Dots on at the bottom of the left graph indicate 2 outliers position (scale at 10^4) following 2016's rapid cells' proliferation in late July.

Daylight duration (indicator of good weather) and temperature play a significant role in water stratification. A *rho* of 0.7 highlights this parameter's importance for the UK offshore area *Dinophysis*'s abundance (Figure 7.4) and 95% of cells counts above a thousand cells.L^{-1} occurred at a stratification of nearly 2°C difference between surface and bottom water (Figure 7.5). Fresh water influence, given by rivers flows, are negatively correlated with high *Dinophysis* counts for all areas, but on French sites, silicates and N/P ratio are positively correlated with cells abundance as much as stratification. Indeed, further looking at thresholds, this variable is correlated with *Dinophysis* spp.'s abundance, 95% of records above a thousand cells.L^{-1} being observed at a N/P ratio of 7.2 which is more than two times lower than the Redfield ratio (16N :1P). Hurell's NAO index is also significantly correlated with *Dinophysis* spp..

For UK coastal areas, water stability is the main variable that can be extrapolated from the negative correlations displayed with weather related parameters such as waves height, period, speed, and also rainfalls. Even though the South-West wind is displayed uncorrelated on the solar plot, the threshold plot for the English coastal areal suggests a positive relationship between wind direction and *Dinophysis* spp. cells counts. This could be due to the amount of records registered during South-West winds but not specifically at high concentrations.

In term of community similarities among micro-phytoplankton taxa, the two dinoflagellate genus *Prorocentrum* and *Scrippsiella* display very similar temporal distribution pattern for both cross Channel areas (Table 7.2).

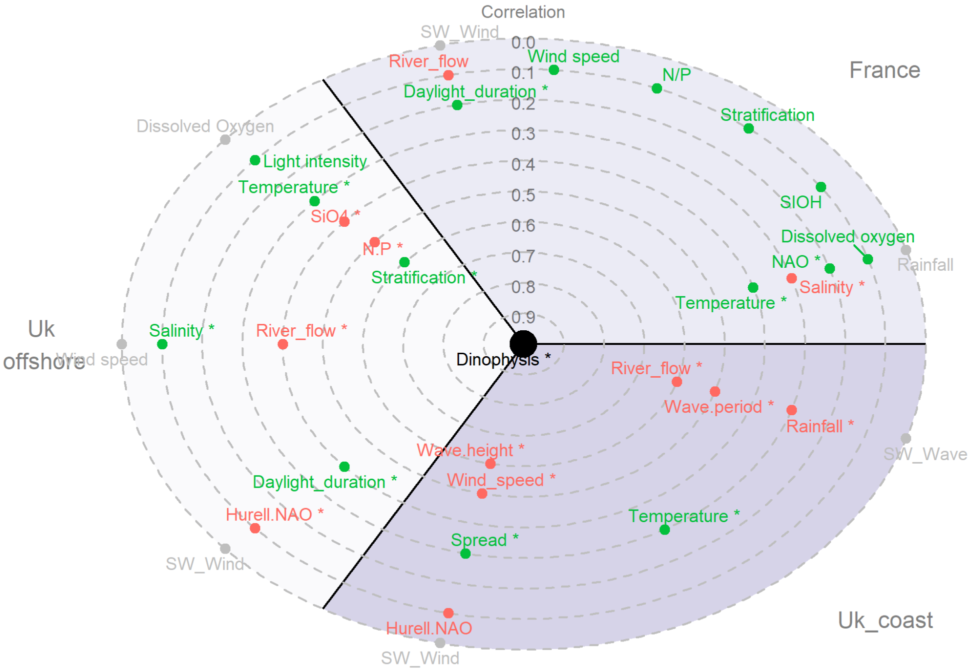


FIGURE 7.4 – Spearman's *rho* between *Dinophysis* spp. and environmental parameters, displayed as a 3 parts solar plot for each location. In green, positive correlation ; in red negative correlation ; * : indicates p-values < 0.05.

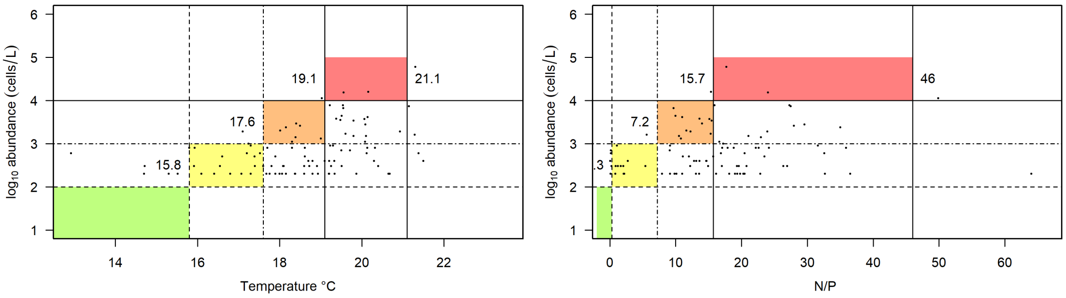
7.4.3 Comparative ecological niches

Looking at the two subsets of *Dinophysis*'s ecological niche, that correspond to the two main monitoring stations in England and France, the environmental space is ordered by three categories of parameters (Figure 7.6). The first is given by water stability through temperature, stratification and daylight influences, then marine influence is highlighted with South-Western wind, dissolved oxygen, salinity and with less importance wind speed, and finally a category of fresh water influence with silicate and N/P ratio. Confirming the previous observation regarding the environmental drivers of *Dinophysis* spp., the English subniche is under stratifi-

Table 7.2 – Spearman's correlations rho and the R^2 indicating the microphytoplankton whose occurences and numbers are related with *Dinophysis*'s over a hundred taxa. Note that e-species gathers species with similar morphological characteristics under the most common species appelation.

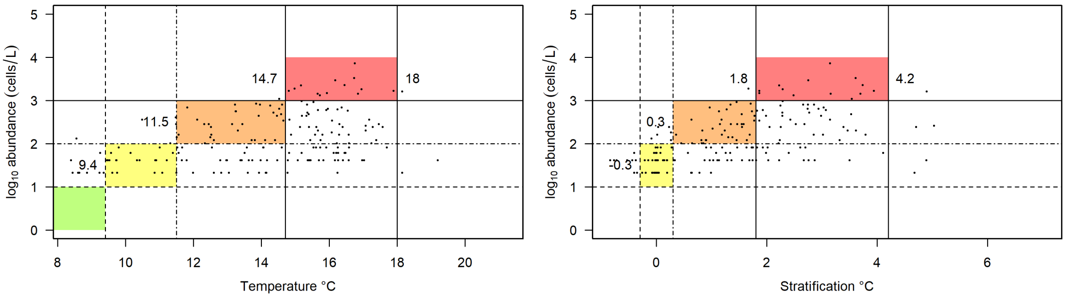
Taxa	Spearman's rho	R^2
France		
Prorocentrum gracile	0.298	0.3
e-species(*Prorocentrum micans*)	0.416	0.236
Protoperidinium + *Peridinium*	0.39	0.148
Scrippsiella	0.345	0.088
UK offshore area		
Gyrodinium spirale	0.34	0.107
Katodinium	0.389	0.136
Tripos lineatus	0.363	0.162
Prorocentrum micans	0.57	0.127
Scripsiella trochoidea	0.523	0.126

cation, temperature, and south-western wind influences while the French subniche are under temperature and fresh water influences. Comparatively, both subniches are isolated and not overlapping on the global environment, however, both *Dinophysis* sub-origins are oriented toward stratification and daylight duration as main drivers. On the English side, most of the local environmental space (K) is used by *Dinophysis* spp.'s realized subniche, while a third of the environmental space is not used by the genera in France. This could be linked to the wider window of appearance in England compared to France. For both areas, only a very small area for biotic interaction within micro-phytoplankton community is displayed. While the years are divided in two periods for the French area with recent years (since 2013) being located on the right part of the subniche, no clear inter-annual pattern is displayed on the English subniche area.



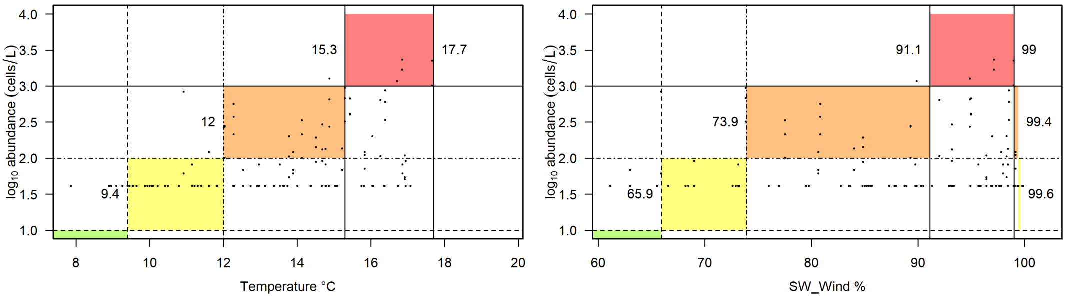
(a) France

(b) France



(c) UK Offshore

(d) UK Offshore



(e) UK coastal

(f) UK coastal

FIGURE 7.5 – Environmental threshold (with 95% confidence) in relation with *Dinophysis* spp. abundance per location. On the left side (a,c,e), the temperature thresholds are highlighted for the three areas. On the right side (b,d,f), various thresholds that highly specific parameters' relationship with species abundance specifically for each area only. Example : 95% of *Dinophysis* records displaying more than a thousand cells.L^{-1} occured at a temperature above 17.6°C.

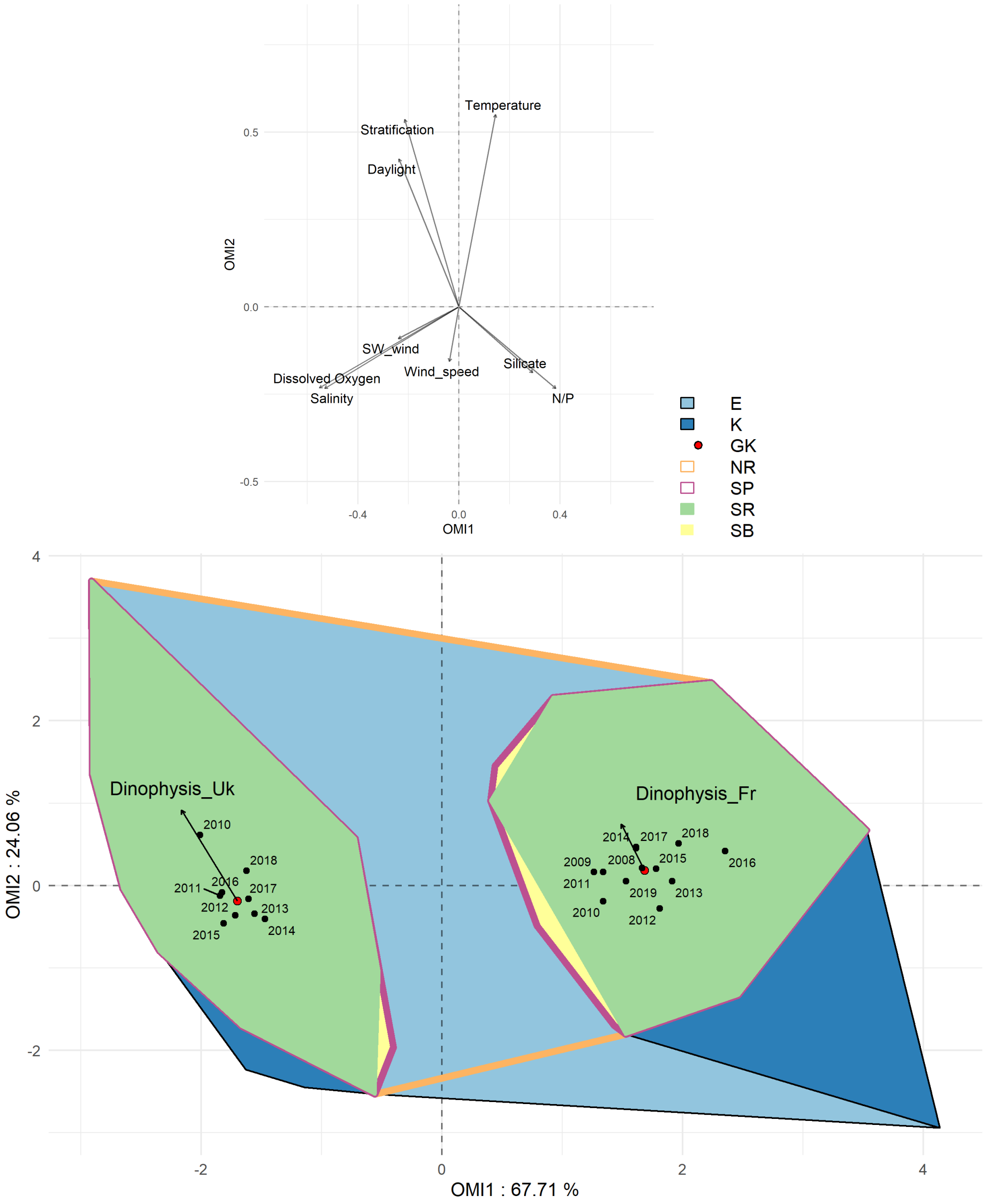


FIGURE 7.6 – Comparison between WitOMI subniches (niche for a selected area within a general environmental space) for both English (L4) and French (ANT and CAB) sites for the months April to November of the period 2008-2019. The years indicate the respective medium position of the corresponding subset area. E : Environment, K : Station subset, GK : Species' marginality within a subset, NR : Realized niche, SP : Potential subniche, SR : Realised subniche, SB : space explained by the influence of biotic interactions. The arrows locate the sub-origin WitOMIGk position for *Dinophysis* spp..

7.5 Discussion

The problematic of HABs raises concern all over the globe because of the risks for human health over the consumption of contaminated shellfish (Kouakou & Poder, 2019; Young et al., 2020) and the economic impact of farm and fisheries closures (Sanseverino et al., 2016; Suddleson & Hoagland, 2021). *Dinophysis* spp. is the cause of numerous DSP contaminations and its toxins are the first cause of closures in Europe (Avdelas et al., 2021). Being a mixotrophic organism, it is predator of smaller phytoplankton cells (such as *Mesodinium rubrum*, Moita et al. (2016)) which are not as well monitored as micro-phytoplankton. Therefore, those prey can not yet be used as indicator in order to predict *Dinophysis* spp. blooms and their intensities. This cross-Channel study on *Dinophysis* spp.'s drivers gives insights on the importance of environmental timing for bloom initiation. Indeed, the studied areas' niches have common affinities with elevated temperatures but also present differences in affinities with water composition and stability for a bloom.

7.5.1 Abiotic drivers of *Dinophysis* sp. bloom

Considering the variables found to be influencing *Dinophysis* spp., temperature was unarguably the most significant driver and could be extended as such at the European scale. In Portugal, *Dinophysis acuminata* events were found to have the same temperature-abundance relationship ; temperature between 13.5°C and 15°C triggering a bloom (from 200 cells.L^{-1}) and between 15.5°C and 17°C for a concentration above a thousand cells.L^{-1} (Moita et al., 2016). However, this specificity is not true worldwide as wider range of temperature were surrounding *Dinophysis* spp.'s blooms in Chilean waters where picnocline arises from saline stratification (Alves-de Souza et al., 2019). Looking at bloom timing, the time lapse of one month between blooms' peaks in England then France is probably related with the early warming of sea water at the South West coast of England prior to the Normandy region in France as shown by satellite data illustrated in Figure 7.7. It may also explain the cells' presence as early as April-May in England.

As listed in the review of Wells et al. (2015), temperature is known to enhance

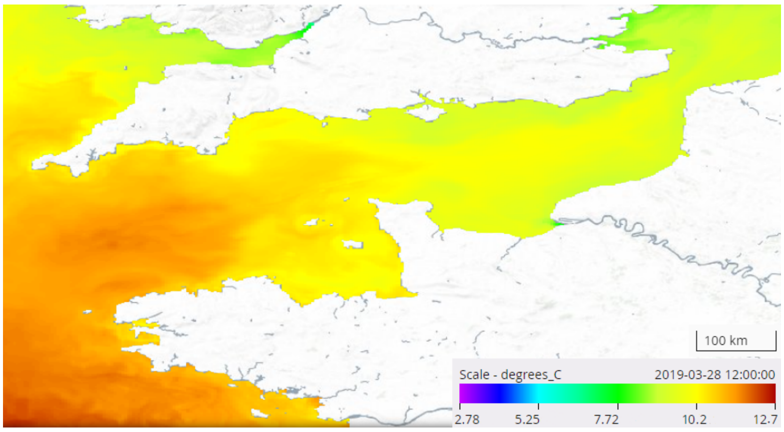


FIGURE 7.7 – Illustration of progressive sea water temperature increase in the western Channel from West to East by the end of March (e.g. of the 28th of March, 2019). Extracted from the satellite-based portal ; `https://www.s3eurohab.eu/portal/`.

many metabolic process such as growth rates, germination, photosynthesis, motility or nutrient uptake. It also leads to stratification when the water column is stable. This parameter is the most correlated with *Dinophysis* spp.'s bloom for the South UK offshore area. Stratification is also known to play a role in dinoflagellates' abundance by improving their mobility and specifically enhancing *Dinophysis* spp. blooms within thin layers, at picnocline depth (Alves-de Souza et al., 2019). The seasonal picnocline on continental shelf is characteristic of chlorophyll-a maxima, which indeed beneficiates from the light above and the nutrient diffusion from below (Raine, 2014). *Dinophysis* spp. was often harder to access through regular monitoring because of its concentrations in thin layers mainly (Park et al., 2006; Raine et al., 2016). Raine (2014)'s review explains also that HABs from this genera were the results of cells transportation toward the coast. This highlights the major hydrodynamic parameter role of wind direction in shaping HABs dynamic and future dispersion. As Panton & Purdie (2022) already described for coastal *Dinophysis* spp. bloom events on the same coastal areas, south-west winds (and wave direction) play a major role in cells transport from offshore area toward the coast. Moreover, following a DSP outbreak in 2013 in Scotland, Whyte et al. (2014) investigated the role of wind direction and found a pattern similar with previous outbreak indicating that a western wind could be the origin of cell transport toward the coast where a periodic upwelling event would give optimal growth conditions. However, none of our correlation highlighted a predominance of wind influence for bloom enhancement, only thresholds could be drawn around *Dinophysis* spp. presence within English coastal waters. This could be due to the southward coast line which catches water currents coming from the south, those same waters warming up in the Channel by the end of March. In France, the south-western wind is the predominant wind direction and was slightly influencing the northern station ANTifer (Soudant et al., 1997), but not enough to clearly be associated with *Dinophysis*'s presence, its major role is directing the Seine's river plume northward (Brylinski et al., 1996). The singular threshold relationship found between N/P ratio and *Dinophysis* spp. records in France is most certainly due to the large influence of the Seine river and its inputs. Mackey et al. (2012) described in Monterey Bay the relatively high alkaline phosphatase activity in dinoflagellates (specifically *Prorocentrum, Dinophysis, Scrippsiella*) which confer them a competitive advantage in case of N increase.

7.5.2 Exploring biotic correlations

While interactions among phytoplankton organisms are still poorly understood, monitoring programs enable the access to hundreds of taxa successively dominating marine waters. However, due to its harder accessibility in regular monitoring, the major prey of *Dinophysis*, *Mesodinium rubrum* could not be explored in this study. Nevertheless, biotic correlations results implied that *Dinophysis* is not the only organism responding to summer environmental condition ; companion dinoflagellates *Prorocentrum gracile* in France, and commonly for both Channel sides *Prorocentrum micans* and *Scrippsiella* were found to have similar and simultaneous intra and inter-annual distribution. The co-occurences of these species do not happen alternatively through the years, the absence of *Dinophysis* is not synonym of increase of these organisms which suggests the absence of competition between them but rather the same needs in environmental conditions. Moreover, the subniche approach in this study does not show any major restriction of the realised subniche of *Dinophysis* spp. due to biotic interactions. Recently, Alves-de Souza et al. (2019) indicated also a common ecological niche shared by *P.*

micans and *D. acuminata* in Chile. Both organisms have functional similarities, *Prorocentrum* is mixotrophic, capable of encystment and certain species have also been identified as DST (Diarrheic Shellfish Toxin) producers (Bravo et al., 2001; Shim et al., 2011). A 48h experiment to examine the vertical distribution of *Dinophysis* spp. at ANT associated the three genus together, *Prorocentrum* sp. and *Scrippsiella* sp. being at the origin of water coloration at the subsurface and influencing *Dinophysis* spp.'s maxima position below this layer (Lassus et al., 1991). Various studies highlight red tides species composition, linking *Dinophysis* spp. and *Scrippsiella* sp. as dominant taxa (Villarino et al., 1995; Yasakova, 2013).

As a final statement, there is no clear evidence that the different sampling strategies (at 10 meters depth or subsurface) impacted the monitoring results. Nevertheless, at L4 (UK offshore area sampled at 10 meters depth), there is a better distinction between years with and without bloom compared to coastal stations. Those years correspond to higher toxin concentrations at the local coastal shellfish farms.

7.6 Conclusion

This study pinpoints the importance of temperature signal for timing *Dinophysis* spp. blooms either directly or through the co-occurences of various community responses to seasonal temperature increase. With stability in the water column, the blooms thrive with stratification and can develop to a thousand cells.L^{-1} and contaminate local organisms. With the upcoming threat of climate change and the various effects on temperature, stratification, irradiance, weather un-stability, it is hard to predict if *Dinophysis* spp. cells will take advantage of those changes, not knowing responses of multiples co-occurring parameters. Recently, a study succeeded to model *Dinophysis* spp.'s past dynamic through the use of multiple complex (not directly measurable) variables such as hydro- and thermo-dynamic parameters, tides, salt fluxes, runoffs and vertical thickness (Boivin-Rioux et al., 2022). The authors, like others before, predict increased frequencies and intensities of *Dinophysis* spp. during the XXIst century (Wells et al., 2015; Boivin-Rioux et al., 2022).

8

Harmful Algal Blooms : II- Effect of the Seine's plume on a *Pseudo-nitzschia* sp. bloom's dispersion

Angéline Lefran, Tania Hernández Fariñas, Pascal Claquin

Enfin, ce dernier chapitre sur l'écologie et les impacts des efflorescences d'algues toxiques reprend les résultats obtenus lors d'une campagne en 2019 en estuaire de Seine. Elle fait suite aux connaissances avancées sur l'effet de l'eutrophisation sur les blooms algaux toxiques du genre *Pseudo-nitzschia* sp. ainsi que la production d'acide domoïque qui peut en résulter, notamment en condition de stress nutritif. Dans ce chapitre, la lumière est faite sur la distribution des cellules de *Pseudo-nitzschia* spp. en embouchure de Seine lors d'un bloom modéré datant du printemps 2019. De nombreuses données abiotiques sont explorées pour chaque prélèvement. Enfin, une analyse des données historiques tente d'expliquer la période 2010-2014 où d'importantes contaminations à l'acide domoïque ont été mesurées dans les coquilles Saint-Jacques de la Baie de Seine.

8.1 Abstract

Consequences of eutrophication, from anoxia to harmful algal blooms (HABs), have forced authorities at different scales to act for water improvements. In Europe, the Atlantic East coasts are under major eutrophication threats due to highly anthropised catchment areas and the release of nutrient from agricultural fields. In Europe and France, reglementations issued in the 1990s and 2000s have indeed led to progressive phosphate reduction but nitrate concentrations remain very high, which cause some changes in nutrient ratio within marine system that phytoplankton assemblage are sensitive to. In 2004, the Bay of Seine registered its first domoic acid (DA) outbreak in the scallops (*Pecten maximus*) due to *Pseudo-nitzschia australis* and *P. multiseries* blooms in spring. Since then, measures of toxicity above sanitary threshold are rare, despite a relatively constant abundance of *Pseudo-nitzschia* sp. in the water over the years. Our approach firstly monitored a *Pseudo-nitzschia* spp.'s bloom distribution at the Seine river plume. Results indicate that the cell density was higher outside the plume's direct influence, in higher salinity. They also highlight two steps of DA release, first dissolved DA was measured at the bloom' expansion phase, then particulate DA was measured, in the same area, at bloom's depletion phase. However, those toxins did not lead to closures of fisheries areas. The second part of this approach aimed at understanding historical data to highlight the circumstances that lead to toxicity in shellfish in 2010-2014 but not before and not after those years. Ecological niches illustrated strong biotic constrains during those years that may have affected *Pseudo-nitzschia* spp. in its access to fresh water inputs. Among environmental drivers, salinity was higher during this period and silicate concentration were limited, probably because of *Pseudo-nitzschia* spp. proliferation.

8.2 Introduction

As primary producers, phytoplankton organisms are essential to the marine food chain and many scientists rely on their biomass and productivity to estimate the food supply available for species of interest among its consumers. However, for certain species, the sudden rise of cells' density is associated with the production of toxins. The latter can be ingested by primary consumers and have consequences on local wildlife and public health, specifically after the consumption of contaminated shellfish (James et al., 2010). The Harmful Algal Blooms (HABs) concern numerous species that are still under study to assess the complex co-effects of various environmental conditions (freshwater input, temperature increase, eutrophication) to either cells' proliferation or toxins production (Bresnan et al., 2020). For instance, climate change is being predicted to worsen eutrophication's impacts on water quality (Nazari-Sharabian et al., 2018) and to accentuate both intensity and frequency of HABs (Griffith & Gobler, 2020; Gobler, 2020). Nevertheless, the past effects of eutrophication are being targeted by regulations measures from the European Union (EU) or at national scales. For example, tools such as the Urban Wastewater Treatment and Nitrates Directives adopted in 1991, then the Water Framework Directive (2000), and later the Marine Strategy Framework Directive (2008) have been showing results in EU member states that could still be improved by more ambitious measures (less derogation, better technologies in water treatment, optimal fertilisation) (Ulén et al., 2007; Tynkkynen et al., 2014; Grizzetti et al., 2021).

Pseudo-nitzschia sp. is an auto-phototrophic diatom that forms long chains of elongated cells. It has been known to produce domoïc acid (DA) and cause shellfish poisoning since 1987, after an outbreak affecting blue mussels (*Mytilus edulis*) in Canada (Bates et al., 1998). The number of species within this genus is constantly increasing ; from 37 identified species in 2012 (Lelong et al., 2012) to at least 63 species currently accepted in AlgaeBase (`www.algaebase.org`, Guiry & Guiry (2021)). However, not all of *Pseudo-nitzschia* sp. are toxic (Lelong et al., 2012). In European waters, *P. australis* is the most widespread cause of Amnesic Shellfish Poisoning (ASP) (Bresnan et al., 2021). It is the consequence of the ingestion of DA-contaminated shellfish, therefore fisheries areas are due to close when the EU regulatory limit of 20 mg DA.kg^{-1} of dry shellfish tissue is reached (EFSA, 2009). Furthermore, studies explored the effects within upper marine trophic levels following fish ingestion (Lefebvre et al., 2012) and reported DA concentrations in sea lions in Monterey Bay (Bargu et al., 2012a) and seals in Scotland (Hall & Frame, 2010), with various neurological residual signs. DA ingestion is also affecting seabirds (Van Hemert et al., 2020). It was revealed that a strange behavioural in those organisms found in California in 1961, which is known to have inspired the famous Hitchcock's movie "The Birds", was no less than the consequence of DA contamination (Bargu et al., 2012b).

Various species are often recorded in the same area, and intra-specific seasonal successions occur on an annual basis (Klein et al., 2010; Lelong et al., 2012; Lefran et al., 2020). The annual distribution is also often described as bimodal with blooms occurring in spring then in autumn (Trainer et al., 2012; Guallar et al., 2021) In their review, Lelong et al. (2012) indicate that overall stress conditions influence DA production (effects vary with the species under study), notably, it could be enhanced by phosphate, silicate and iron limitation or light excess. High concentrations of trace metal like lithium or copper (Maldonado et al., 2002) and the presence of bivalves could also enhance DA production (Sauvey et al., 2021). Additionally, both cells division rates and DA production are greater under high salinity compared to low salinity (Doucette et al., 2008). As an organism totally depending on environmental abiotic resources, the *Pseudo-nitzschia* sp.'s growth is also expected to be influenced by river discharge and runoffs. Indeed, in the Gulf of Mexico, higher *Pseudo-nitzschia* sp. records since the 1950s were linked with eutrophication in the Mississippi river (increase of nitrate flux) (Dortch et al., 1997; Parsons & Dortch, 2002).

Along the north-east Atlantic coast, various past events have caused shellfish fisheries closures. Major outbreaks happened in 2011 and 2012 in various areas (Husson et al., 2016). The first records of DA in shellfish in the Bay of Seine go back to 2004 and were associated with the presence of *P. autralis* and *P. multiseries* (Nezan et al., 2006). However, since 2014, lower DA concentrations occurred and mostly below the sanitary thresholds, except for the Brittany area on the western coastline (Belin & Soudant, 2018; Bresnan et al., 2021). The latter being mapped as a sensitive zone regarding eutrophication issues due to intensive agricultural practises (Gruau et al., 2005). Reaching the Channel in Normandy, the Seine river has the greatest inflow and catchment basin (under urban and agricultural pressures) and largely contribute to the freshwater inputs in the Bay of Seine (Billen et al., 2007). Following European and national regulations for better water quality, Romero et al. (2016) highlighted a slight improvement, with lower ammonium and phosphate content. It suggests that the system has been changing over the past 20 years.

Our study first summarises the results acquired during a sampling campaign in spring 2019 around *Pseudo-nitzschia* sp.'s bloom. It aims at understanding the effect of the Seine river's plume onto the cells' distribution and toxicity both spatially and within the water column. Secondly, the approach investigated the circumstances around the contamination of the local fisheries during the years 2011-2014. It compares both environmental and biotic conditions surrounding *Pseudo-nitzschia* sp. abundance at the Seine river's mouth and the associated toxicity over a 15 years period.

8.3 Material & Methods

Located along the northern coast of France, the Bay of Seine is known to be under major HABs events. Both monthly monitored stations around the Seine's river mouth (Antifer and Cabourg) frequently record high abundance of *Pseudo-nitzschia* sp. in the area (Belin & Soudant, 2018). Our first approach aims at understanding the effects of the Seine river's plume on *Pseudo-nitzschia* sp. distribution during a bloom. Therefore, in order to pinpoint the sampling dates, a close monitoring of Cabourg's flora composition was done.

8.3.1 The *in situ* approach

In 2019, a two steps sampling campaign within the Seine's estuary occurred on the 25th of April then on the 21st of May. The aim was to target both proliferation phases of *Pseudo-nitzschia* sp., pre-bloom situation during the exponential increase, then a post-bloom situation after the cells count was found decreasing. The campaign was organised a week after recording more than 10^4 cells/L^{-1}, an alert threshold previously estimated according to blooms dynamics the previous years. The pre-bloom's *Pseudo-nitzschia* sp. concentration was of 35k cells/L^{-1} on the 17th of April, and up to 260k at the time of the first campaign. The second date correspond to a post-bloom phase with cells concentration down to 8k cells.L^{-1}. According to the French Hydrological bank, the Seine's flow was measured at 169 m^3.s^{-1} (April's average : 324m^3.s^{-1}) and at 244 m^3.s^{-1} (May's average : 285m^3.s^{-1})

respectively during the each sampling. During this period, no fisheries closures were issued due to ASP intoxication.

The protocol was scheduled around high tide (+/- 3 hours). Three transects were established (namely North-Middle-South), each of them were initially composed of 5 sampling coordinates but due to bad weather conditions not all could have been sampled (Figure 8.1). Three boats carried out the sampling simultaneously on each transect, from inner Seine's estuary toward the Bay. The average depth in the area is around 10 meters at high tide. To better apprehend cells' distribution in the water column, four sampling depths (surface, 3m, 6m and bottom) were programmed ; when time (weather) was not permitting, the last point was only sampled at surface, mid-depth and bottom. 5L Niskins were used to collect water samples, 2L were used for domoic acid estimation, 1L for phytoplankton monitoring (later fixed with acid lugol), 250ml for cytometry, and 2*125ml for nutrient concentrations. A CTD was fixed on the Niskin to record depth, water temperature, salinity and dissolved oxygen values. A total of 71 samples were gathered and analysed. PAM (Pulse Amplitude Modulated - PAM-Control, Germany) measurements estimated the maximum quantum efficiency of the photosystem II (F_v/F_m, excitation measured at λ=470 nm and frequency = 0.6 KHz for 8 irradiances between 75 and 1833 µmolphoton.m^{-2}.s^{-1}) which allows to assess the physiological state of the phytoplankton community (Maxwell & Johnson, 2000).

At IFREMER's lab in Port-en-Bessin, *Pseudo-nitzschia* sp. abundance was establish by reverse light microscopy on 10 ml tanks according to the monitoring network REPHY's protocole (Neaud-Masson, 2016). Domoic acid was quantified for both particular (pDA ; limit of quantification = 250 ng.L^{-1}) and dissolved (dDA ; limit of quantification = 250 ng.L^{-1}) content through High Performance Liquid Chromatography (HPLC - Agilent Technologies) following (Einarsson, 1985) and Pocklington et al. (1990). Pigments measurement were aslo done through HPLC following (Van Heukelem & Thomas, 2001). Nutrients concentrations were given by flow spectrophotometry (Bran+Luebbe, AutoAnalyser3) for the ammonium ($[NH_4^+]$), nitrate ($[NO_3^-]$), nitrite ($[NO_2^-]$) and phosphate ($[H_3PO_4]$) content according to Aminot & Kérouel (2004) protocols.

Water samples used for cytometry analysis were taken straight to the labora-

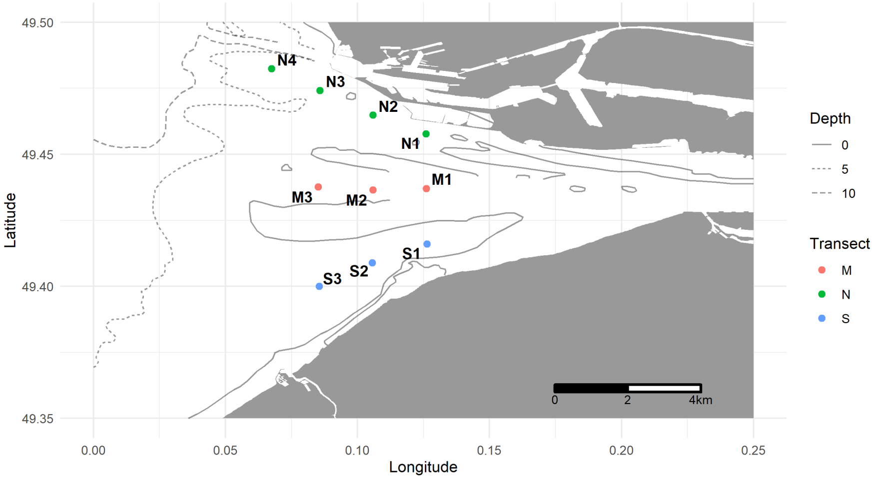


FIGURE 8.1 – Seine's estuary sampling map. Bathymetry lines are based on SHOM's records (Naval Hydrographic and Oceanographic Service, depth in meters).

tory. Flow cytometry analysis were performed using a CytoSense (Cytobuoy, Netherland) equipped with a blue laser (488 nm, 50 mW) and a green laser (552 nm, 50 mW). Each sample was given a concentration of pico- and nano-phytoplankton using cells size and fluorescence (Olson et al., 1989; Thyssen et al., 2014; Serre-Fredj et al., 2021).

The distribution of *Pseudo-nitzschia*'s abundance are first illustrated spatially in 3-dimensions in order to pin point the effects of the river's plume (given by lower salinity). Additionally, Spearman's correlations index are calculated for several parameters to better understand the conditions surrounding the bloom.

8.3.2 Past events and historical context

To better understand *Pseudo-nitzschia* spp.'s dynamic in the Bay of Seine, two coastal monitoring stations ANTifer (latitude 49°39'56.707"N ; longitude 0°7'53.972"E) and CABourg (latitude 49°17'54.261"N ; longitude 0°7'1.209"W) were considered for data acquisition and analysis considering their proximity with the Seine river mouth and plume. For toxins monitoring, the fisheries areas considered are located offshore at proximity of either stations (ANT : Areas 7, 8, 9, 11, 12 ; CAB : 4, 5 ; in Figure 8.2).

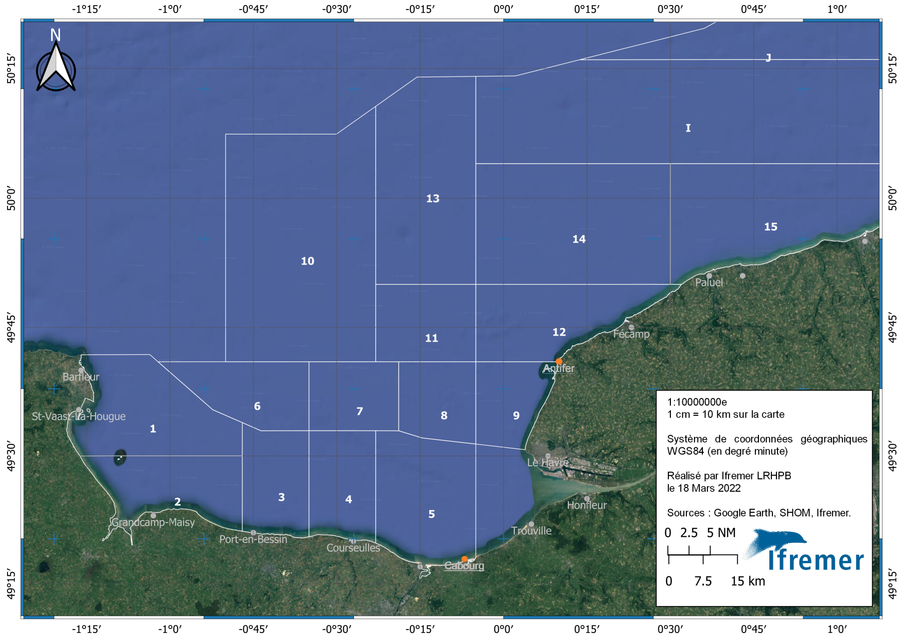


FIGURE 8.2 – Bay of Seine's fisheries map for the King Scallop (*Pecten maximus*). In orange, monitoring stations for micro-phytoplankton community.

Historical data was extracted from the REPHY monitoring program database (REPHY – French Observation And Monitoring Program For Phytoplankton And Hydrology In Coastal Waters, 2021) along with abiotic parameters (nutrient, salinity, temperature, turbidity and dissolved oxygen) from the RHLN (Hydrologic Network for the Normandy Littoral). Additional environmental parameters (wind, rainfalls, daylight duration, flow) were downloaded from weather monitoring stations (Météo France, Hydrological bank). *Pseudo-nitzschia* sp. was grouped into the two complexes that differentiate species according to their width ; the seriata complex (width < 3µm) and the delicatissima complex (width > 3 µm) (Hasle & Syvertsen, 1997).

The toxicity levels found in *Mytilus edulis* and *Pecten maximus* since 2009 were extracted from the REPHYTOX network (REPHYTOX – French Monitoring Program For Phycotoxins In Marine Organisms, 2021) for the Bay of Seine area. However, only values above the sanitary threshold (20 mg DA.kg^{-1}) were kept for analysis, therefore *Mytilus edulis* is not apparent throughout the results. King scallops are mostly collected before and during the harvesting period, roughly from September to April, in open fisheries areas.

Considering that three distinct and continuous time periods (2005-2009, 2010-2014, 2015-2019) were either affected by high DA content or not, mean test (Wilcoxon-Mann-Whitney's test) were performed on data anomalies for each parameters to compare all three periods. First, the overall annual mean obtained from monthly records was compared to the average (2005-2019 period) to define annual anomalies. The final graphical display only present the anomalies and correlations for the month of main abundance and at risk for toxin production by *Pseudo-nitzschia* seriata complex, that is to say from March to September.

Finally, ecological niches using the WitOMI approach (Karasiewicz et al., 2017) were drawn considering abiotic and biotic parameters. The three time-periods (2005-2009, 2010-2014, 2015-2019) were used as subsets (or subniches) for comparison, for each year only the months between March and September were used as *Pseudo-nitzschia* sp. blooms mainly occur within this window. As explained in Karasiewicz et al. (2017), this approach allows to build subniches for a single species (*Pseudo-nitzschia* sp. in this study) taking into account spatial differences. The potential subniche (SP) for *Pseudo-nitzschia* sp. is determined for subset and compared to the realized subniche (SN). Theoretically, if a species does not occupy its full environmental niche, it implies the existence of biotic interaction (SB) (Jackson & Overpeck, 2000). The niche position (marginality) is the distance between the average habitat conditions and the average habitat of the subset. The further from average it is, the most atypical is the habitat. The WitOMIG$_K$ (displayed with an arrow) represents the habitat used by the species of interest. Using this approach to construct ecological subniches will allow to investigate the temporal differences between periods of interest as well as how *Pseudo-nitzschia* sp. interacts with its biotic and abiotic environment.

8.4 Results

8.4.1 Spatial distribution along Seine's river plume

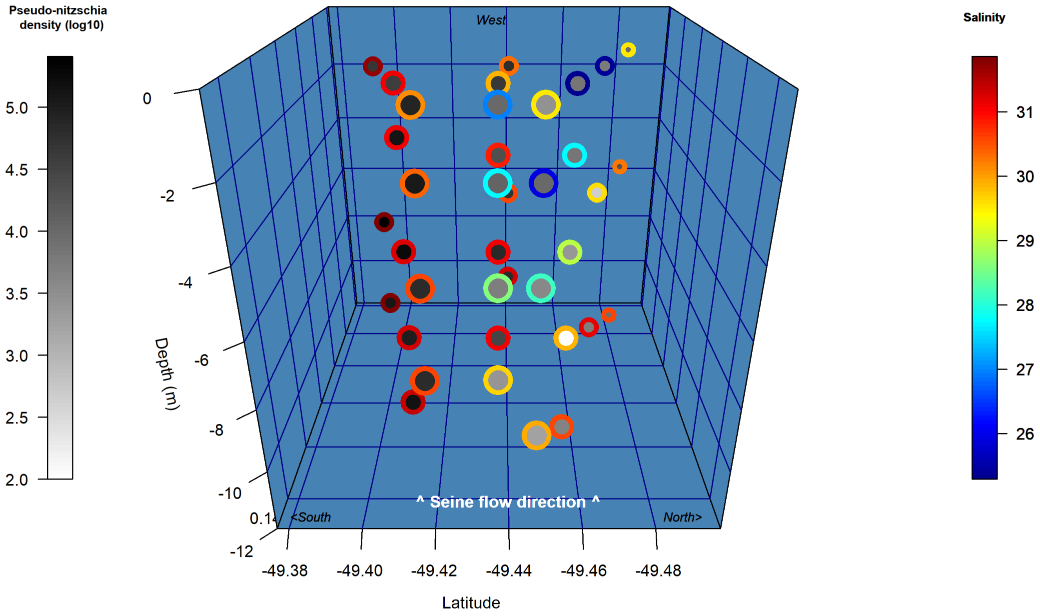
In April 2019, at the bloom's expansion phase, the cells' distribution is first located in high abundance on the southern transect, then in the most saline area of the middle transect (M2 & M3) and finally on the northern transect (Figure 8.3). The distribution is homogeneous in the water column. The spatial representation of salinity indicates that the Seine river's plume was going northward at the time of the first sampling, in April. It also shows that the water was stratified by it with an interface located at 4 meters below the surface.

In May 2019, at bloom's depletion phase, cells' abundance is much lower, the distribution is sporadic and indicates 4 hot-spots around M1 at surface and -6 meters depth, $S_{1:3}$ at -3m depth, $N_{1,2}$ at -3m depth. The Seine river flow covers the whole 3D space, the water is neither stratified, neither under saline influence on a specific transect.

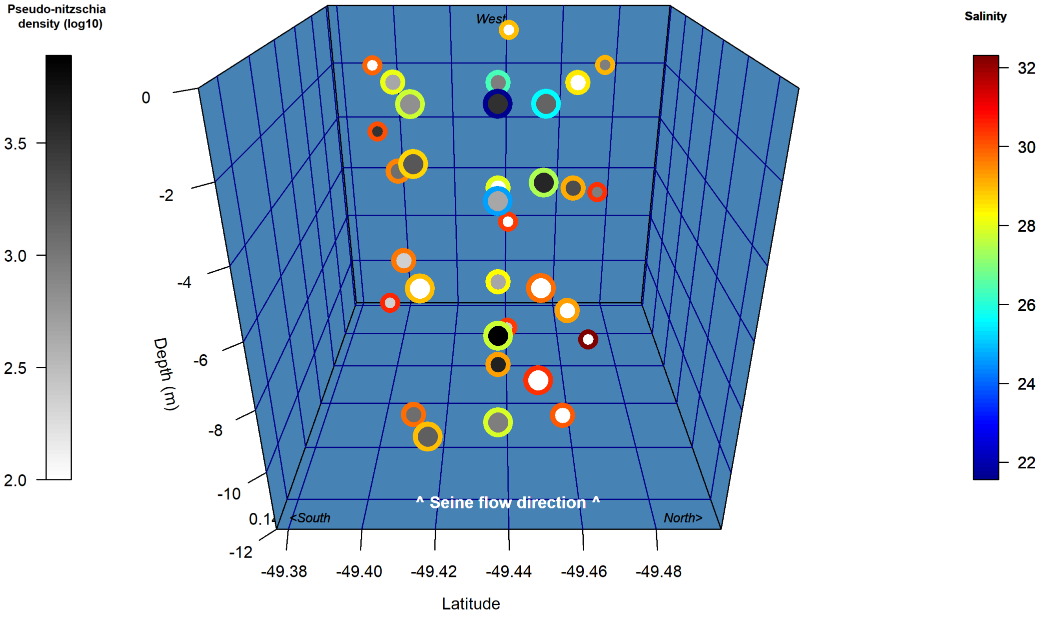
8.4.2 Environmental conditions

During the pre-bloom phase in April, spots showing high densities of *Pseudo-nitzschia* spp. coincide with lower nutrient concentrations (nitrate, phosphate, silicate, ammonium), lower turbidity and lower physiological status (Fv/Fm) compared to spots with lower *Pseudo-nitzschia* spp. densities. They are also located outside the Seine's plume (higher salinity), in areas with higher nitrite concentration and higher N/P ratio. Their presence is associated with higher dissolved oxygen and dDA content (up to 0.5 µgDA.L^{-1}). Additionally, pico-phytoplankton displays the third highest positive correlation (rho= 0.70) with *Pseudo-nitzschia* sp. densities. Spots under high dDA content are naturally associated with the same surrounding conditions, with low nutrient, high dissolved oxygen and pico-phytoplankton concentrations. Despite the low number of values of pDA are above the level of detection, major negative correlation (rho=-0.25) are found deeper in the water column and with low pheophytin concentrations.

During the post-bloom phase in May, even if phytoplankton displayed lower concentrations, results indicate that spots of higher abundance coincide with higher NO2+NO3 nutrient content and are also located in the most marine areas. Dissolved DA content in the water is much lower and the surrounding community displays lower physiological status. On the other hand, pDA is higher compared to the pre-bloom phase, it is correlated with high dissolved oxygen and N/P ratio (rho=0.75), with low nutrient concentration (ammonium, phosphate, nitrate, silicate) and low turbidity. Particulate DA was mainly measured within the southern transect (up to 0.4 µgDA.L^{-1}). Pico and nano-phytoplankton are also less abundant in area under high pDA content.

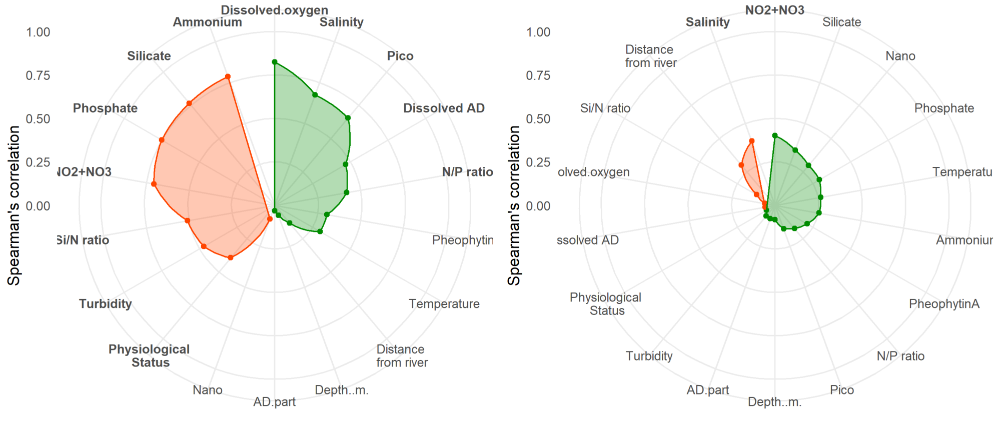


(a) Pre-bloom phase



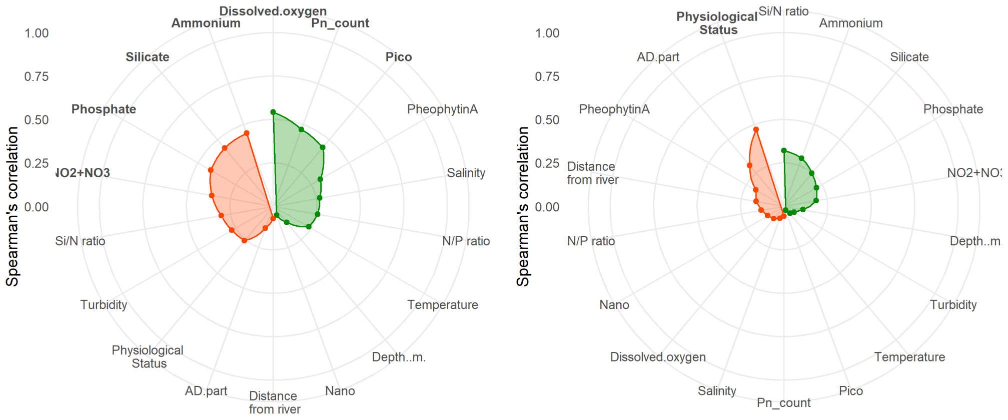
(b) Post-bloom phase

FIGURE 8.3 – 3D representation of *Pseudo-nitzschia* (black-white scale) and salinity (red-blue scale) distribution in the Seine's estuary. The graphical point of vue is from the Seine's river flow, the smaller the dot, the further away it is from the estuary's mouth.



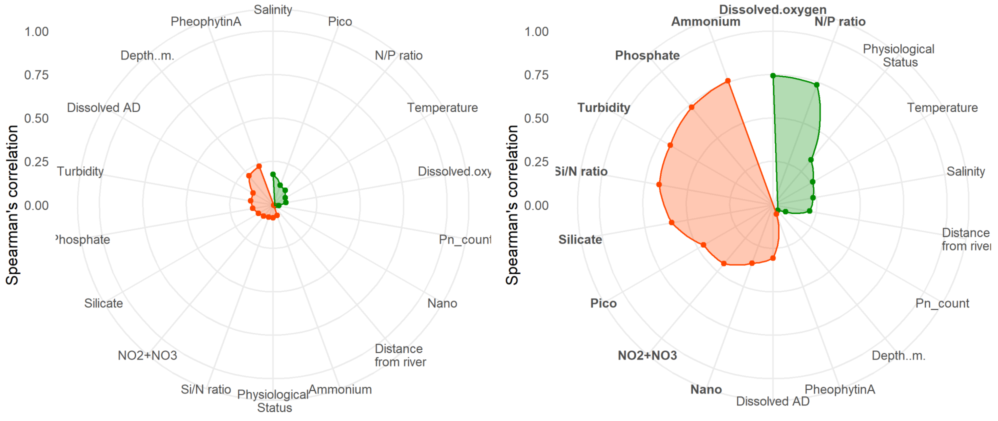
April 25th, 2019 for Pn count

May 21th, 2019 for Pn count



April 25th, 2019 for Dissolved AD

May 21th, 2019 for Dissolved AD



April 25th, 2019 for AD.part

May 21th, 2019 for AD.part

FIGURE 8.4 – Spearman's correlations values displayed for a selection of parameters around *Pseudo-nitschia*'s abundance (up), dissolved (middle) and particulate (bottom) domoïc acid, during pre- (right graphs) and post- (left) bloom phases during spring 2019. In red ; the negative correlations, in green ; the positive ones. **Bold** parameters's correlations are associated with p-values < 0.05.

8.4.3 Knowledge of historical events

Over the past fifteen years, *Pseudo-nitzschia delicatissima* and *Pseudo-nitzschia seriata* complexes have had an average concentration between 10^3 and 10^4 cells.L^{-1}, maximum values reaching a million cells.L^{-1} in CAB (Figure 8.5). Before 2011, the concentration of *Pseudo-nitzschia delicatissima* complex was however lower. The largest blooms are found between 2011 and 2013 and were associated with contaminations and closures in numerous areas in the Bay of Seine. Since 2014, no records of shellfish contamination reached the sanitary threshold although *P. seriata* complex's average density outreached 10^4 cells.L^{-1} in Cabourg. We add that highest abundance are found in spring, with a bloom starting usually around April or May, also depending on the year, a second bloom can happen in August or September.

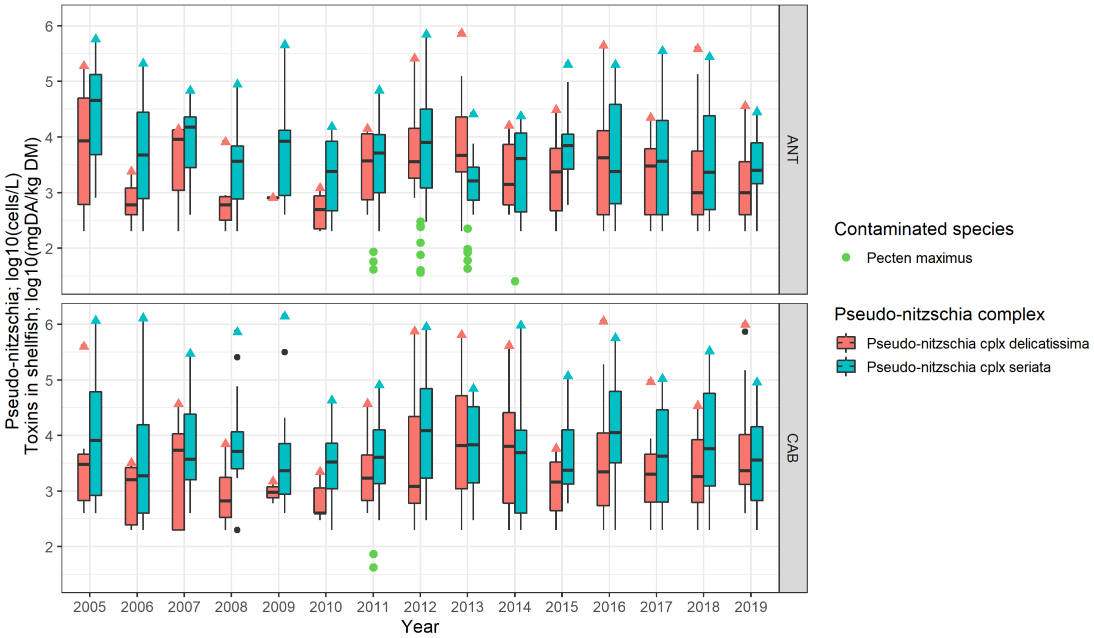


FIGURE 8.5 – Historic of the two *Pseudo-nitzschia* complexes densities (> 100 cells.L^{-1}) over the years at two estuarine locations ANT (Northern coast) and CAB (Southern coast). In green, the fisheries area's maximum toxin contents (when above sanitary limit, >20 mgDA.kg^{-1} of Dry Meat) found in the species *Pecten maximus*

Toxins have been only affecting *Pecten maximus* (slow depurating organisms that can accumulate toxins easily over time) in the Bay of Seine over a precise period from 2011 to 2014, whereas *Pseudo-nitzschia* sp. records remained high. To better understand the ecology of *Pseudo-nitzchia* sp. ecological subniches were drawn for three periods of 5 years of interest, before, while and after major toxicity outbreaks which occurred between 2011-2014. First, the ecological niche is mainly affected (on the x-axis) by temperature *versus* fresh water inputs (64% of the variance is explained along this axis). On the y-axis, the environment is spread between wind influence and silicate concentrations in the water, and both daily light duration and dissolved oxygen. *Pseudo-nitzschia seriata* complex occupies most of the environmental conditions, temperature and daylight duration but also silicate concentrations influence its shape. Regarding the three periods, habitats' marginalities are quite central, typical of the average conditions. *Pseudo-nitzschia*'s marginality is always in-between temperature and daily light duration. The striking observation is during the second period 2010-2014, when toxins were measured in shellfish. The environmental space that could have been used by the complex is not occupied, displaying (in yellow) a vast area under the river flow influence, which is related to biotic interactions (competition, paratism or predation).

The changes in environmental conditions that differentiate the periods were investigated through mean comparison (Figure 8.7). Considering that *Pseudo-nitzschia* spp.'s bloom and toxin release occur over the months from March to September, only parameters measured during those periods were considered. The results show that the period associated with high DA contamination in shellfish (2010-2014) was displaying slightly higher values in daylight duration, and salinity. This period also displayed the lowest values of temperature, river flow and both nitrogen and silicate concentrations. The N/P ratio is significantly increasing throughout the whole time period, driven by phosphate reduction.

8.5 Discussion

Harmful Algal Blooms represent major threats for local activities, from tourism and human health to food economy. While human intoxications are now rare and prevented by monthly to weekly monitoring of biological communities and toxins content in shellfish, the circumstances surrounding blooms are still complicated

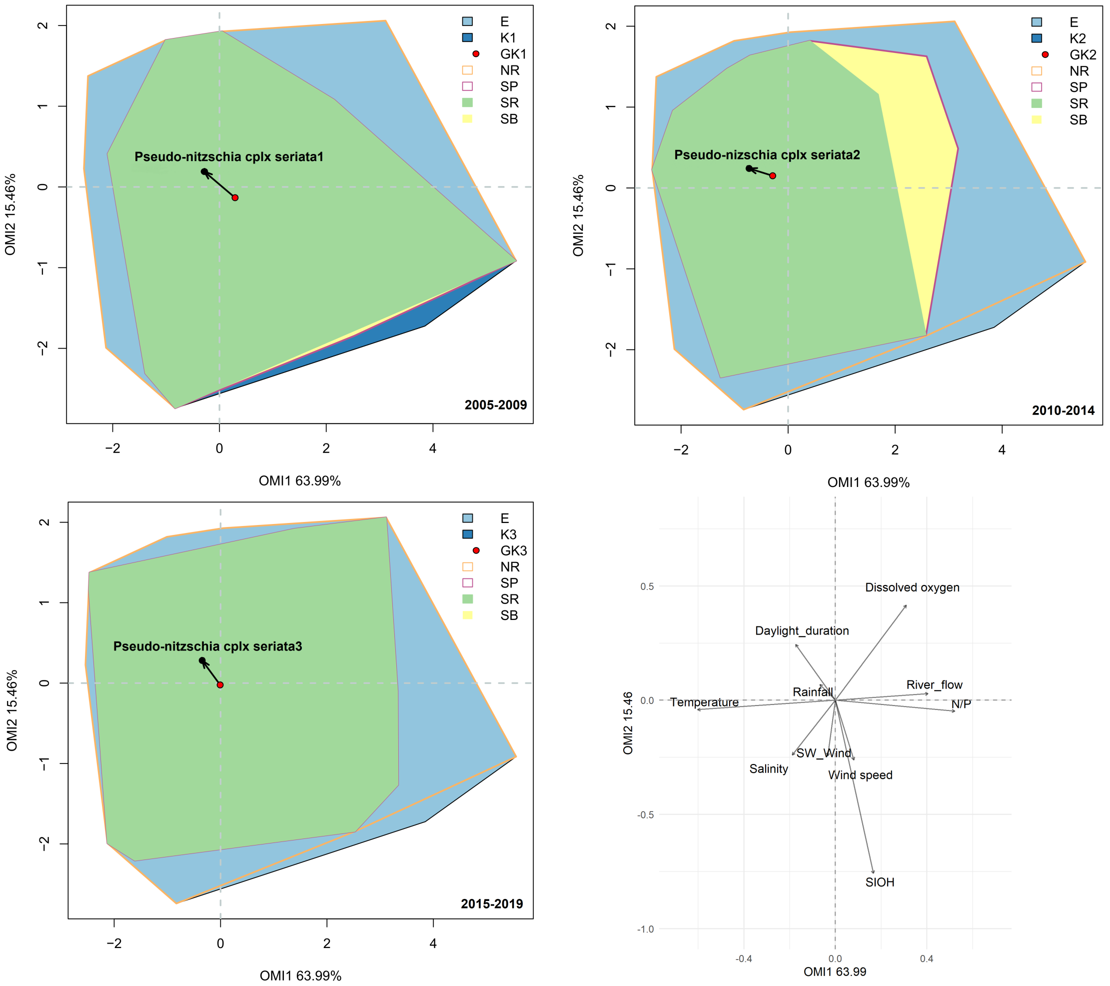


FIGURE 8.6 – Comparison between WitOMI subniches (niche for a selected area within a general environmental space) for three periods of 5 years between 2005 and 2019. The months concerned by blooms and toxicity are selected ; from March to September. E : Environment, K : Station subset, GK : Habitat's marginality within a subset, NR : Realized niche, SP : Potential subniche, SR : Realised subniche, SB : space explained by the influence of biotic interactions. The arrows locate the sub-origin WitOMIGk position for *Pseudo-nitzschia seriata* complex.

and under investigations. *Pseudo-nitzschia* sp. is a cosmopolite genus, records show related ASP events worldwide (Lelong et al., 2012). Domoic acid is also being found to reach predator organisms through the marine trophic network (Lefebvre et al., 2012).

ASP events have decreased over the past few years along the European Atlan-

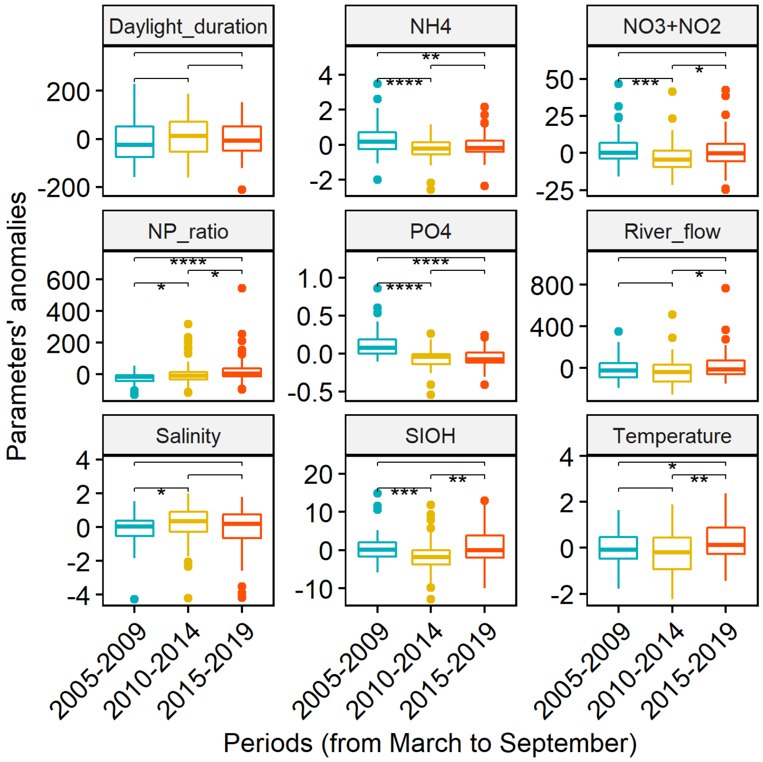


FIGURE 8.7 – Main parameter's anomalies for the three time periods 2005-2009, 2010-2014, 2015-2019. Only the months between March to September were considered for each year. The stars indicate the level of significance given after a Wilcoxon test (significance symbols : "****", "***", "**", "*" are respectively associated with the p-value = 0, 0.0001, 0.001, 0.01, 0.05).

tic margin, at the exception of Brittany area in France, Galicia and the northern coast of Portugal (Bresnan et al., 2021). The authors explain this decrease in Scotland and a selection of other countries by a change in toxin monitoring in *Pecten maximus* following EU Shellfish Directive amendments in 2004. Indeed, scallops depurate slowly from toxin content compared to mussels, and their gonads hold most of DA content, not the muscle (Blanco et al., 2002; Bresnan et al., 2017). Therefore, certain countries avoid closures by performing shucking and toxin estimation in the abductor muscle only, prior its sale (as long as DA levels remain below 4.6 mgDA/kg^{-1} in the muscle, and below 250 mgDA/kg^{-1} in the whole organism) but it has not been the case in France (Bresnan et al., 2021; EFSA Panel on Contaminants in the Food Chain , CONTAM).

8.5.1 *Pseudo-nitzschia*'s bloom distribution at river's plume

Regarding the distribution of *Pseudo-nitzschia* sp. at a river's mouth, our results show a dispersion outside the Seine's plume, in the southern transect. The plume of the river is directed northward following the current given by southwestern winds (Brylinski et al., 1991). It is also characterised by higher turbidity, which could lead to light limitation causing reduced phytoplankton's growth as observed before in the Bay of Seine (Cugier et al., 2005; Tas & Lundholm, 2017; Morelle et al., 2018). Thus, even though the cells' distribution in the Seine's mouth is correlated with salinity, the relationship between salinity and *Pseudo-nitzschia* spp.'s distribution could be indirect as most species are euryhaline (known to develop under a wide range of salinity, mainly between 15-35) (Thessen et al., 2005). However, DA production could be enhanced within higher saline conditions (Doucette et al., 2008; Pednekar et al., 2018). Doucette et al. (2008) hypothesised that the cell's energy used to maintain the osmotic balance at low salinity competed with the energy needed for DA production. Additionally, the rapid proliferation through cells' divisions is permitted at the expense of good physiological status (Fv/Fm) which is also known to be reduced by P limitation (Napoléon et al., 2012). Overall, *Pseudo-nitzschia* sp.'s has a coherent location within the most productive zone, at the interface between light limitation (river's plume turbidity) and nutrients limitation (outer bay area) (Smith & Demaster, 1996).

In our approach, *Pseudo-nitzschia* sp. bloom is joined with a two-steps DA content in the water samples ; first release of dDA at pre-bloom phase then pDA at post-bloom phase. While no precise identification was performed, historical reports suggest that *P. australis* was the main cause of DA production (Klein et al., 2010; Husson et al., 2016; Thorel et al., 2017). At first, dissolved DA was measured during the bloom expansion phase. This form is mostly associated with allelopathy ; affecting grazing rates of zooplankton (Bargu et al., 2006), or even inhibiting the growth other organisms such as cryptophytes (Van Meerssche & Pinckney, 2017; Van Meerssche et al., 2018). Then, particulate DA during bloom's depletion phase, both times the maximum was located on the southern transect outside the river's plume. Similar results on pDA were reported in California Bight where scientists measured the highest pDA content in sediment traps a week after bloom's drastic depletion (Schnetzer et al., 2007). In Scotland, lags of 3 to 6 weeks separate bloom's and DA's maximum in the scallop *Pecten maximus* (Bresnan et al., 2017). Between both dates, models indicate that at high tide the Seine river's plume got larger and affected nearly half of the eastern Bay of Seine, and was not only directed northward (`https://marc.ifremer.fr/resultats/temperature_et_salinite`). Given that the remaining cells were in salinity spots, we could suggest that the change in direction and intensity of the Seine's plume may have led directly or indirectly to dying cells' gathering at these spots, leading to higher pDA concentrations. Afterward, remaining cells and thus pDA are transported through fecal pellets or marine snow aggregation and sink down the water column reaching benthic organisms few days after the bloom's end (Umhau et al., 2018). In the Bay of Seine, we observe that scallops affected by ASP are located within the eastern basin, which is mainly affected by the Seine estuary due to the macrotidal environment and the coastal hydrodynamic system drifting northward (Brylinski et al., 1991; Brunet et al., 1996). The currents originated from the river may push and transport the dying cells and pDA further in the bay as they sink down to the seabed.

In 2019, no toxicity above sanitary levels was measured in shellfish. At the moment, no regular monitoring follow scallops sanitary status on an annual scale, results are mostly issued during the harvesting period, from November to April. Nevertheless, further sampling and monitoring of scallops would enable to link *Pseudo-nitzschia* sp. and other eventual HABs impacts on benthic organisms.

During the bloom's expansion phase, the elevated correlation with picophytoplankton (but not with nanophytoplankton) could not be analysed in-depths at a species level. However, few relationships between *Pseudo-nitzschia* spp. and other organisms were highlighted through the effects of substances produced during a bloom. In a study exploring biofouling, *Pseudo-nitzschia* sp.'s ability to produce transparent exopolymer particles (TEPs) was associated with increased picophytoplankton densities (especially of *Prochlorococcus*), but justified by a decrease in phosphate and nitrogen concentrations (Leterme et al., 2016). In another, TEPs coagulation's properties seem to reduce ciliates' predation on pico-plankton-size particles in bloom circumstances as these organisms tend to colonise TEPs (Mari & Rassoulzadegan, 2004).

8.5.2 Estuaries and *Pseudo-nitzschia* sp. HABs

Within phytoplankton, blooms frequencies and intensities are influenced by the surrounding conditions and result from ideal resources and irradiance circumstances (bottom-up). Co-effects of climate change, eutrophication, pollution but also food web interactions can directly or indirectly play a role in driving phytoplankton's proliferation and therefore HABs' (Glibert et al., 2018). Eutrophication and more generally nutrient enrichment represents a stimulation for harmful algal proliferation. (Parsons & Dortch, 2002; Heisler et al., 2008). For instance, along the Atlantic French coast, *Pseudo-nitzschia* spp. blooms usually happen from April to September and their initiation is mainly due to increases in temperature and irradiance (Husson et al., 2016).

For about the last 30 years, regulations measures have been implemented to improve water quality at a European and national scale. Our results on environmental change regarding nutrient composition are in agreement with the review of Romero et al. (2016) on the Seine's water quality, which indeed had known a considerable decrease in nutrient inputs. Since 2010, nearly 90% of water samples (*versus* 60% between 2000-2010) already displayed phosphate and ammonium concentrations under the "good" status regarding water quality ($< 0.5\text{mg.L}^{-1}$). However, nitrate contents are sill either in "moderate" status ($< 25\text{mg.L}^{-1}$) or "poor" status ($< 50\text{mg.L}^{-1}$), our results even display an increase since 2015 (from March to September). Such changes also affect nutrient ratios, notably an increase of the N/P as illustrated through our 15 years approach between 2005 and 2019. There is a lack of evidence directly linking N/P ratio with HABs (Davidson et al., 2012), however, *Pseudo-nitzschia* spp.'s environmental niche established by Husson et al. (2016) for the Atlantic French coast presented affinities with lower N/Si ratio. Moreover, phytoplankton, through community assemblage, could be directly impacted by such environmental changes.

In accordance with our observations, Husson et al. (2016) did noticed that between 1995 and 2012 and compared to other coastal areas in Brittany, *Pseudo-nitzschia* sp. abundance could regularly reached high values without triggering major ASP outbreak in shellfish in the Bay of Seine. The authors described the latter with lower salinity and chlorophyll-a content but similar range in temperature and irradiance compared to Southern french areas. Moreover, Husson et al. (2016) stated that *Pseudo-nitzschia* sp. bloom initiation was around May in the Bay of Seine compared to the southern areas where blooms were initiated as early as March. Our campaign indicates also that blooms can occur as early as April in the Bay of Seine. Discussed before, salinity could play a role in relation with the toxic potential of *Pseudo-nitzschia* sp.'s harmful bloom. (Boivin-Rioux et al., 2022) explored the dynamics of *P. seriata* in western Atlantic coasts to model HABs dynamics. They highlighted that *Pseudo-nitzschia* spp. blooms were more likely occurring in periods displaying higher salinity and lower temperature, which is in agreement with the characteristics of our 2010-2014 period. Regarding toxicity, domoic acid production is known to be related with *P. australis*, but at the moment no effective approach enabled to monitor closely species succession in the Bay of Seine. Species successions and their drivers (e.g. nutrient ratios, water temperature) can however grandly influence the toxicity potential of certain years and period compared to other (Thorel et al., 2017; Bowers et al., 2018; Delegrange et al., 2018).

Besides direct effects of environmental drivers, abiotic interactions and their potential influence onto diversity are still poorly understood in phytoplankton. Exploring niche distribution along environmental space indicated that the period under toxin pressure was also the period during when *Pseudo-nitzschia*'s niche was reduced due to biotic interaction. As explain by Jackson & Overpeck (2000), the realised niche, if it does not occupy the full potential niche, is under biotic pressures. Looking at past research on biotic relationships between *Pseudo-nitzschia* sp. and its surrounding community, few co-occurences are found with *Chaetoceros socialis*, interaction with bacteria were documented (Lelong et al., 2012). However, there is still a lack of evidence to say that these interaction were inducing DA production.

8.6 Conclusion

Pseudo-nitzschia sp. is now a well-known diatom whose species can produce toxins that lead to HABs worldwide. While cultures enable to better understand the interaction between cells and environment, the field observations are often more complex and the result of multiple vectors. Our study investigated an algal event at a river's plume that did not cause any ASP-related closures in the surrounding shellfish fisheries. The bloom was located at a specific area, outside the river's direct influence at the interface between light and nutrient limitation, pDA was measured at bloom's end and river flow and currents can make the toxins available for benthic organisms. Since major ASP event between 2011 and 2014, DA content did not outreach the EU sanitary limit despite an annual and similar bloom presence. We raise the hypothesis that changes in environmental conditions led to favourable circumstance for DA production during a narrow time period over the last 20 years, more specifically, our results indicates that biotic interactions could be the main difference and cause of *Pseudo-nitzschia*'s restrained niche those years.

9

Discussion Générale

> ”They spoke of [the sea] as a contestant or a place or even an enemy. But the old man always thought of her as feminine and as something that gave or withheld great favours, and if she did wild or wicked things it was because she could not help them.”
>
> Ernest Hemingway, The Old Man and the Sea

Menée durant trois ans et demi, cette thèse s'inscrit au sein du projet européen Interreg S3-EuroHAB qui réunit plusieurs partenaires Britanniques et Français travaillant autour de la Manche. L'objectif de ce projet est de renseigner sur les risques d'efflorescences de phytoplancton nuisible dans les eaux de la Manche, par la mise en place d'un portail de suivi en temps quasi-réel (24-48h), utilisant des données satellites. Il s'adresse aux scientifiques, politiques publiques et utilisateurs de la mer professionnels ou récréatifs. Le portail se base sur des suivis de réflectance satellite (mesures, par capteurs optiques, de la lumière solaire réfléchie par la surface de l'eau) couplés à des circonstances environnementales pour estimer la probabilité de la présence d'un bloom à risque à une localisation géographique donnée. Dans l'élaboration des algorithmes derrières un tel portail, il est important d'assurer l'adéquation entre les observations satellites et la réalité de terrain. Il est également essentiel de comprendre les mécanismes influençant les phénomènes de dispersion et de prolifération des microalgues. C'est dans cet esprit qu'ont été élaborées les thématiques développées durant cette thèse. Les objectifs et possibilités sont ainsi diverses et variées et ont permis d'aborder des sujets allant de l'écologie fonctionnelle des communautés à la variabilité des contenus cellulaires, en passant par l'étude des efflorescences algales nuisibles.

Dans un premier temps, l'étude des communautés (Chapitre 3) permet de mettre en place les connaissances associées à la variabilité spatiale et temporelle des assemblages microphytoplanctoniques le long de sites d'études contrastés de la Manche. Ces dernières montrent que les zones côtières et estuariennes peuvent être dissociées au travers de l'assemblage phytoplanctonique qui les caractérise, notamment de part la différence dans les influences marines/fluviales et de l'hydrodynamisme de ces zones d'interface. A chaque système, en parallèle de la phénologie qui rythme les assemblages taxonomiques saisonniers, une forte stabilité est observée avec des communautés qui gardent une similarité constante, de l'ordre de 35%, avec chacune des communautés des années précédentes (+/- selon la saison estivale/hivernale), sur plus d'une décennie de suivis.

Cette similarité des communautés d'un point de vue taxonomique a conduit au traitement de ces communautés sous un angle différent, celui de l'approche fonctionnelle (Chapitre 4), afin de confirmer ou non les premiers résultats. De plus, l'étude de la diversité fonctionnelle permet de mettre en place une approche innovante dans la compréhension des assemblages phytoplanctoniques. Cette dernière s'articule autour d'un constat de baisse de chl-a des zones de grands estuaires. Temporellement, un changement d'assemblage fonctionnel est observé avec la diminution d'organismes mixotrophes à hétérotrophes de taille faible à moyenne, mais une augmentation de diatomées moyennes à larges et de larges dinoflagellés. Il est également établi que le micro-phytoplancton est dominée par des diatomées coloniales de petites tailles, que les zones estuariennes sont plutôt favorables à des organismes solitaires et que les systèmes marins auraient une plus grande diversité fonctionnelle. Cependant, cette approche, notamment dans la préparation de sa base de traits fonctionnels, aura soulevé divers questionnements ; (i) d'abord, concernant les origines spatiales bibliographiques de ces traits et de leur application dans un milieu littoral réduit, (ii) puis aussi, sur le manque de prise en compte de la plasticité morphologique et physiologique des cellules phytoplanctoniques.

Face au premier cas (i), une approche double (Chapitre 5) associe au groupement fonctionnel un groupe établi par niche écologique afin d'évaluer l'adéquation entre les deux. Il est estimé effectivement que des taxons partageant des traits similaires auraient tendance à également se retrouver dans des conditions environnementales proches. Dans le cas de la plasticité (ii), une approche expérimentale mensuelle sur un cycle annuel (Chapitre 6) fut développée afin de quantifier la variabilité intra-cellulaire des volumes occupés par les lipides et la chl-a (par rapport au biovolume total de la cellule). Une baisse des teneurs lipidiques est observée en période estivale. Elle peut être attribuée à la fois aux nécessités de prolifération (divisions cellulaires rapides) des microalgues à cette période, ou encore au besoin réduit de la capacité de flottabilité assurée par les lipides en cette période riche en apports de lumière. Les acides gras sont également plutôt produits en hiver, afin d'assurer la perméabilité des membranes des cellules à basse température. Parallèlement, les teneurs en chl-a sont plus marquées par une variabilité spatiale avec des teneurs plus importantes en milieu marin, plus turbide, pour faire face à la plus faible pénétration de la lumière dans la colonne d'eau.

Enfin, les efflorescences associées à deux genres potentiellement toxiques ont été étudiées en lien avec les conditions environnementales qui les accompagnent (Chapitre 7 & 8). Chez *Dinophysis* sp., les blooms toxiques affectent les côtes anglaises et françaises et posent des problèmes économiques de plus en plus importants depuis 2015 quant aux contaminations des coquillages. Nos analyses associent ces proliférations au réchauffement estival des eaux (d'abord au sud-ouest de l'Angleterre puis en Baie de Seine un mois plus tard), qui entraîne une stratification du milieu, favorable au développement de *Dinophysis*. Les niches comparées de ces deux environnements sont dissociées, non-superposées, indiquant que les conditions entourant les blooms toxiques sont malgré tout différentes d'un système à l'autre. Chez *Pseudo-nitzschia* sp. les blooms sont récurrents chaque année mais pas forcément associés à une toxicité. On remarque que durant la période 2010-2014, qui fut favorable à une production majeure de toxines dans le milieu, la niche écologique du complexe potentiellement toxique *Pseudo-nitzschia seriata* est contrainte par des interactions biotiques (compétition, parasitisme ou prédation). Cela différencie cette période des 5 années précédentes et suivantes qui, elles, montrent une occupation optimale de la niche par le genre étudié.

La thèse aura donc été caractérisée par une diversité de problématiques, d'approches, et de résultats qui viennent enrichir les connaissances scientifiques actuelles sur les communautés phytoplanctoniques. Ci-dessous, les différents chapitres sont repris et discutés sous la lumière de la problématique qui a lancé ce projet doctoral. Ce sera une place d'échange balayant plus de 3 ans de recherche ayant apportés réponses et questionnements nouveaux. C'est l'occasion de *prendre du recul* et de revenir sur cette expérience, ce qu'elle apporte et ce qu'elle propose.

9.1 Des communautés face à des enjeux écologiques majeurs

9.1.1 L'étude d'un environnement changeant

En 2021, 77% des citoyens du monde estiment avoir reconnu des effets du changement global dans leur région[1]. Ainsi, lorsque l'on évoque un environnement changeant, il est tout d'abord naturel de penser aux actualités mettant en scène le changement global ; de la montée des eaux à l'acidification des océans, en passant par la fonte des glaces, l'augmentation d'évènements extrêmes sévères et de l'eutrophisation des eaux côtières (Allison & Bassett, 2015; Nazari-Sharabian

---

[1] `https://www.ipsos.com/fr-fr/obscop-2021`

et al., 2018). Face à ces constats, des études combinant des données à larges échelles spatiales et temporelles sont nécessaires afin de modéliser les trajectoires futures de l'environnement. Les rapports du GIEC ont pour rôle de combiner et présenter les résultats de telles analyses en prédisant, entre autre, les conséquences environnementales de plusieurs scénarios climatiques (Masson-Delmotte et al., 2021; Pörtner et al., 2022).

Cependant, les changements environnementaux vont également être observables à plus petite échelle. En milieu côtier, un environnement changeant va se traduire dans le statut macro ou mégatidal d'un site. Il se retrouve au sein d'un estuaire qui, selon le fleuve qui lui est associé, va être impacté par des débits variables apportant éléments nutritifs (dont issus des engrais), métaux lourds et polluants divers (pesticides, polychlorobiphényle-PCB, composés pharmaceutiques, etc...) (Berthelsen et al., 2018; Cabral et al., 2019). Des contraintes météorologiques et anthropiques extrêmes peuvent également soumettre l'environnement à une pression soudaine et intense, avec peu de temps pour s'adapter. Cela va être le cas des rejets d'hydrocarbures (Nelson & Grubesic, 2018), ou des intempéries (Garzon & Ferreira, 2016). De manière générale, à chaque pression on peut observer résistance, résilience ou adaptation du milieu (Thrush et al., 2008; Wiltshire et al., 2008). A titre d'exemple, entre 2019 et 2020, un incendie d'ampleur rarement observée a frappé l'Australie, libérant des centaines de millions de tonnes de dioxyde de carbone dans l'air sur 3 mois (van der Velde et al., 2021). En réponse aux retombées cendrées (chargées en particules de fer, d'azote et de phosphore), des efflorescences phytoplanctoniques sans précédent ont suivi durant 4 mois, doublant la production primaire (via la chlorophylle-a) habituellement enregistrée dans cette région plutôt oligotrophe (Tang et al., 2021).

Quelle que soit l'échelle utilisée dans les travaux relatifs aux changements environnementaux, de nombreuses approches scientifiques sont permises grâces aux efforts des multiples réseaux de suivis mis en place. A large échelle spatiale, les campagnes en mer, souvent annuelles ou bi-annuelles, vont avoir pour objectifs de sonder les océans et faire un suivi des populations soumises à la pression de pêche et un suivi hydrobiologique des paramètres biotiques (compartiments primaires, cas du Continuous Plankton Recorder) et abiotiques de l'eau. A échelle locale et régionale, des réseaux de suivi mensuel voire hebdomadaire permettent de suivre parallèlement les producteurs primaires et la qualité de l'eau en milieu côtier. A l'étranger des séries temporelles longues sont d'ores et déjà bien connues ; c'est le cas de L4 au sud de l'Angleterre (Widdicombe & Harbour, 2021), et de Helgoland au Nord de l'Allemagne (Kraberg et al., 2019)). En France, ces suivis regroupent (sans s'y limiter) le REPHY, le RHLN et le SRN (présentés au chapitre 2). Ces derniers sont à l'origine de la majorité des données utilisées dans cette thèse. Ils ont permis, vers la fin des années 80, d'opter pour une stratégie de surveillance des eaux littorales nationales à haute résolution spatio-temporelle. Ces réseaux s'orientent autour du compartiment microphytoplanctonique, qui représente une grande diversité taxonomique ; en Manche elle s'élève en effet à plus d'une centaine de taxons. Face aux enjeux associés à une telle diversité, les réseaux ne cessent de se perfectionner, comme ce fut le cas avec l'implémentation d'évaluations internationales (2016) [2], dont l'objectif est d'évaluer et de réduire le biais observateur des différents laboratoires partenaires. C'est également dans cet objectif qu'à été mis en place le Service National d'Obersvation (SNO) PHYTOBS qui permet une labellisation homogène des unités taxonomiques et permet une utilisation facilitée des bases SOMLIT et REPHY.

Le phytoplancton est par définition "errant", c'est à dire entièrement dépendant de l'environnement marin, étant très limité dans ses déplacements. Ainsi, l'étude de la communauté phytoplanctonique de différents sites contrastés permet d'accéder à une caractérisation de ces derniers, non pas selon leur position géographique, mais selon leur composition spécifique phytoplanctonique. En effet, tout au long des travaux menés, il a été constaté que la taille et le débit d'un estuaire caractérisent et influencent la communauté primaire microphytoplanctonique. A l'échelle des côtes françaises de la Manche, une diversité spatiale est retrouvée dans les assemblages taxonomiques et fonctionnels, dissociant des communautés d'un système dynamique (enrichi en oxygène dissous), d'un système estuarien sous influence de la Seine et des systèmes marin ou intermédiaire (entre marin et estuarien, Chapitre 3). Il est possible d'observer à l'échelle d'une même baie, que deux estuaires vont présenter des communautés primaires différentes, c'est le cas de la Baie des

---

[2] Evaluation IPI ; Inter-Comparaison Internationale, initiée par le Marine Institute de Galway.

Veys (embouchure du canal de Carentan) et de l'estuaire de Seine (Chapitres 3 & 4). Bien que séparés de moins d'une centaine de kilomètres, la diversité spécifique microphytoplanctonique diffère entre ces estuaires. D'un point de vue fonctionnel, la communauté primaire de la Baie des Veys a plus de similarité avec celle du Golf Normand-Breton, séparée pourtant par la pointe du Cotentin (Figure 9.1). De plus, cette variabilité spatiale se fait également au regard des distributions des efflorescences toxiques des genres *Dinophysis* et *Pseudo-nitzschia*. En effet, en Baie de Seine, ces taxons prolifèrent préférentiellement à proximité de l'embouchure de la Seine (Chapitre 7 & 8). Cela se justifie par la forte abondance en éléments nutritifs apportés par les fleuves, notamment en période estivale durant laquelle ces éléments deviennent limitants. Chez *Pseudo-nitzschia* sp., ce système représente aussi une zone d'interface qui conserve une influence marine favorable à la prolifération et croissance de l'organisme. Durant la campagne menée en 2019, *Pseudo-nitzschia* sp. était distribuée en dehors du panache de la Seine, jusqu'à persister dans des spots à salinité plus élevée durant sa phase de déclin. En revanche, les petits estuaires ne sont pas tous favorables au développement de blooms toxiques ; en Baie des Veys, les épisodes toxiques sont plus rares, ce qui peut se justifier par la forte exploitation de cette baie dans l'élevage de mollusques bivalves, principalement les huîtres, qui peuvent exercer une pression "top-down" sur les organismes phytoplanctoniques et éviter les proliférations toxiques (Costil et al., 2005; Ubertini et al., 2012). Il s'agit là d'une forme de service écosystémique. En revanche, l'embouchure de Fowey au sud-ouest de l'Angleterre, petit système estuarien où l'on retrouve des élevages de moules (*Mytilus edulis*), recense régulièrement des épisodes toxiques de type DSP.

Enfin, les changements saisonniers rythmés par les oscillations de température et d'irradiance permettent d'orchestrer des successions d'espèces aux sensibilités environnementales différentes (différentes niches écologiques). Malgré cette sensibilité aux conditions du milieu, la composition taxonomique moyenne de la communauté primaire garde chaque année, et tout au long des 12 années d'études, une similarité de 35% avec la communauté initiale, montrant ainsi une faible déviation communautaire (Chapitre 3). Une telle stabilité avait été retrouvée au sein de lacs alpins (Teubner et al., 2003). De plus, il est ainsi mis en évidence qu'en Manche, la communauté phytoplanctonique en période estivale est structurée de façon similaire chaque année, cela est également observé à la

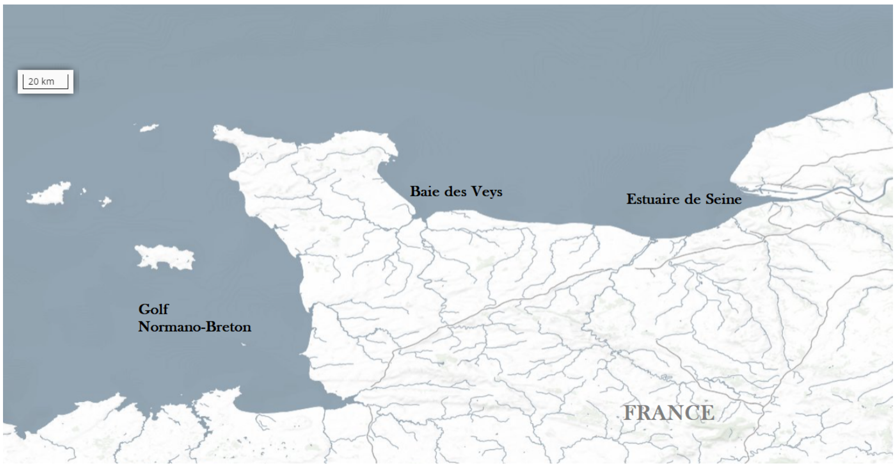


FIGURE 9.1 – Situation des différents environnements étudiés et illustration la division spatiale Est-Ouest par la pointe du Cotentin.

pointe de la Bretagne (Caracciolo et al., 2021b). Cet assemblage est à la fois tiré par les blooms de certains taxons dominants mais également par le mécanisme inébranlable faisant succéder une efflorescence de dinoflagellés en été aux blooms printaniers des diatomées que l'on retrouve dans le principe théorique du Mandala de Margalef datant de 1978 (Figure 9.2). En revanche, la communauté hivernale est moins diversifiée, et les taxons présents sont plus opportunistes face à la plus faible luminosité journalière et aux plus faibles températures. Néanmoins, les augmentations de températures futures seront amenées à perturber ces communautés hivernales (Domingues et al., 2014). Des modifications de la diversité spécifique, l'avancement des périodes des initiations des blooms printaniers pourraient ainsi être observés, le milieu marin en fin d'hiver étant enrichi en nutriments des suites des intempéries automnales et des fontes précoces de glaces selon les localisations (Winder & Schindler, 2004).

9.1.2 Mieux comprendre la relation à l'environnement

Si la succession saisonnière au sein du microphytoplancton est devenue une connaissance établie et acquise pour les milieux tempérés, elle n'est pas hasardeuse

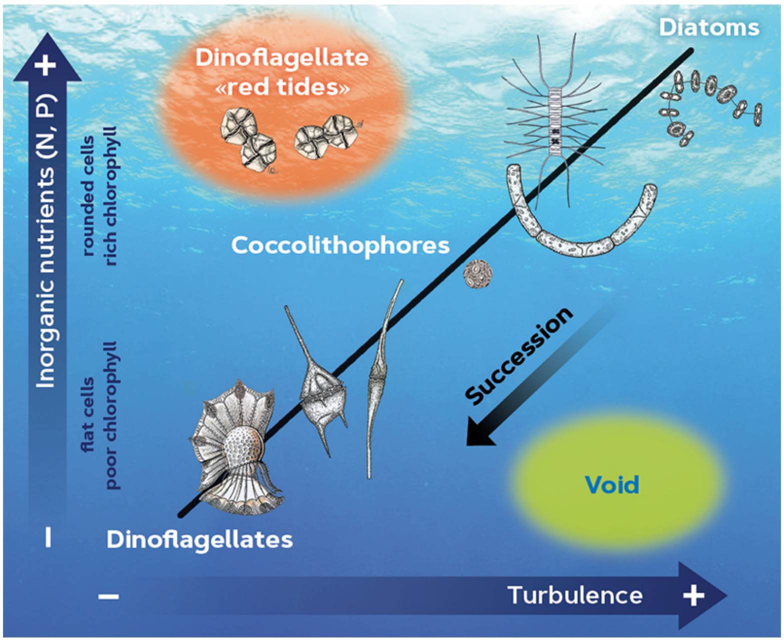


FIGURE 9.2 – Principe du Mandala de Margalef; représentation schématique de la succession saisonnière des principaux groupes phytoplanctonique selon des axes de turbulences ou de concentrations en nutriments (illustration extraite de Villa et al. (2020)).

et résulte d'une division fonctionnelle fondamentale entre les classes de diatomées et dinoflagellés. D'après nos données, ces deux classes rassemblent plus de 90% de la diversité taxonomique en milieu Atlantique Nord-Est. En effet, à travers des recherches bibliographiques sur les traits (morphologiques, physiologiques et comportementaux) de ces organismes, les différences fonctionnelles entre les taxons au sein de chacune des deux classes étaient telles qu'elles ont dues êtres analysées séparément pour faire ressortir les regroupements fonctionnels au sein de chacun (Chapitre 4). En outre, d'un côté les diatomées sont des organismes photo-autotrophes, dépendant des apports lumineux et nutritifs, dont la diversité morphologique constitue le principal axe de différenciation (forme élongée/ronde, aspect coloniale, présence de soies ou d'épines, mobilité en présence d'un raphé). De l'autre côté, les dinoflagellés ont des formes plus homogènes mais vont présenter des capacités vis-à-vis de la nutrition bien particulières (régime phagotrophe; via hétérotrophie stricte ou mixotrophie, possibilité de déplacement grâce aux flagelles). C'est pourquoi, il est difficile d'éviter cette division lorsqu'on étudie le phytoplancton puisqu'après des décennies à étudier ces organismes, aux noms "dinoflagellés" et "diatomées" sont déjà associées des aptitudes environnementales particulières.

Par ailleurs, considérant que la cellule phytoplanctonique va échanger avec l'environnement au travers de l'ensemble de sa surface, il est essentiel de comprendre comment ces échanges ont lieu, et par quels moyens ils peuvent être facilités, afin de mieux appréhender les réponses de la communauté primaire aux changements de l'environnement. L'approche fonctionnelle devient alors au coeur des réflexions puisqu'au travers des caractéristiques cellulaires il est possible d'accéder aux informations relatives à la fitness [3] d'un organisme phytoplanctonique.

Aux travers des recherches menées, le choix des traits caractérisant un genre ou une espèce a nécessité la compréhension de leur intérêt écologique. La taille de la cellule va influencer de nombreux processus physiologiques internes (ex : taux de croissance, d'acquisition et d'utilisation des nutriments et de la lumière, Litchman & Klausmeier (2008); Key et al. (2010); Marañón (2015)). En parallèle, la forme de la cellule conditionne la surface disponible pour absorber le maximum de lumière tout en protégeant la cellule des pressions de prédations (illustrée Figure 9.3) (Naselli-Flores & Barone, 2011; Stanca et al., 2013; Ryabov et al., 2021). De la forme va aussi dépendre le rapport Surface/Volume, qui renseigne sur l'efficacité de la cellule à échanger avec l'environnement. Ensemble, taille et forme vont avoir des effets sur la flottabilité et donc le positionnement dans la colonne d'eau, de même que d'autres teneurs intra-celulaires dont la densité est plus faible que l'eau (ex : lipides; Pančić & Kiørboe (2018), osmolytes; (Boyd & Gradmann, 2002)). Nos résultats vont également mettre en évidence une plus forte présence d'organismes possédant des mécanismes de défense à la prédation (présence de soies) en milieu estuarien. A ces traits s'ajoutent des traits moins ordinaires comme la capacité de prédation et le déplacement associé à la "chasse". Ces traits, propres à la classe des dinoflagellés, ont soulevé une réflexion sur la place d'un organisme hétérotrophe au sein d'une étude phytoplanctonique. *Noctiluca scintillans* [4] fait-elle partie du zooplancton ? Bien souvent les études évitent de

---

[3] Fitness ou valeur sélective; capacité à survivre et se reproduire efficacement.

[4] *Amphidinium, Katodinium, Polykrikos, Protoperidinium + Peridinium, Protoperidinium bipes* et *Torodinium* font également partis de la base de données à traits fonctionnels exploitée.

diviser et les replacent au rang supérieur de "plancton". Leur place dans cette approche se justifie par leur classification parmi les organismes unicellulaires des dinoflagellés, possédant diverses aptitudes vis-à-vis de la nutrition, dont principalement la photoautotrophie (Barton et al., 2013a). L'évolution en réponse aux stress nutritifs aura pu les amener à favoriser un régime entièrement basé sur la prédation. La prédation chez les dinoflagellés va principalement concerner des organismes du nano et pico-phytoplancton (principalement ciliées, cryptophytes). Enfin, l'étude comparative de différents régimes trophiques porte un intérêt tout particulier, la place de l'hétérotrophie dans la communauté enrichie une approche fonctionnelle mettant déjà en avant la photo-autotrophie et la mixotrophie.

Les traits fonctionnels de cette étude (développés au Chapitre 4) ont été choisis pour leur pertinence vis-à-vis de l'écologie et de la relation à l'environnement du phytoplancton et selon leur disponibilité dans la littérature scientifique. Le choix de ne pas prendre certains traits basés sur des calculs de traits connus (taux de fixation de certains éléments nutritifs, taux de croissance, composition élémentaire, etc...) a été fait de part la connaissance au préalable de la forte variabilité et plasticité de ces traits selon l'espèce voire selon l'individu et également selon les conditions environnementales. Néanmoins, cette plasticité au sein du phytoplancton a été illustrée au travers de l'approche expérimentale des taux intra-cellulaires en lipides et chl-*a* par microscopie confocale (Chapitre 6). Une variabilité spatiale et saisonnière a pu être mise en évidence pour la communauté mais également pour certains taxons présents sur une longue période temporelle. Cette variabilité était caractérisée par un plus fort taux de chlorophyll-*a* au sein de sites à faible pénétration lumineuse. De plus, des taux en lipides plus faibles en période estivale par rapport à l'hivernale peuvent s'expliquer tout d'abord par la production plus importante en acides gras insaturés en hiver pour le maintien de la fluidité membranaire (Mortensen et al., 1988), puis par le grand nombre de divisions cellulaires qui ne laisseraient pas le temps aux cellules d'accumuler les lipides en été, et/ou au travers de la flottabilité conférée par les lipides ; plus le taux en lipide est élevé, plus l'espèce accède à la lumière en se rapprochant de la surface lorsque cette dernière est limitante (Pančić & Kiørboe, 2018). Concrètement, ces approches de terrains sont essentielles à la compréhension des mécanismes intra-cellulaires et de leurs variabilités spatiales saisonnières. Il est

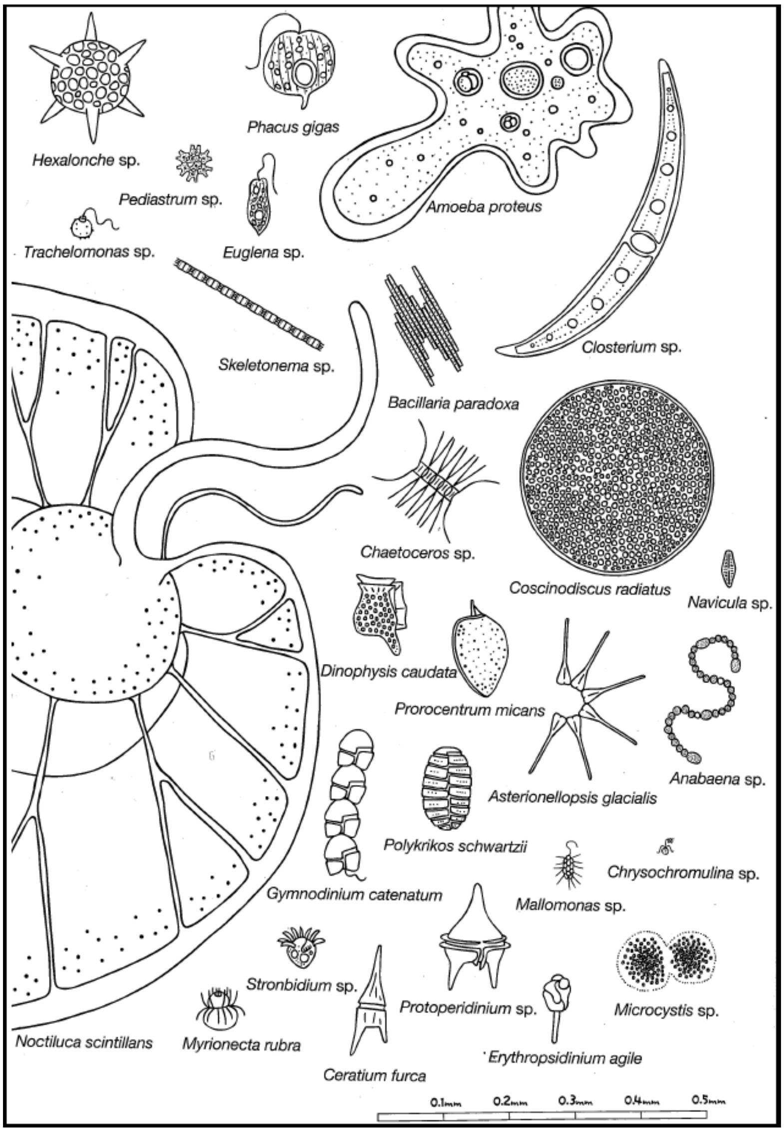


FIGURE 9.3 – Illustration de la diversité morphologique des organismes phytoplanctoniques (illustration tirée et adaptée de Société Japonaise de Plancton (2011)).

néanmoins difficile d'intégrer de telles approches dans un programme de suivi régulier des eaux côtières, un suivi de cet ampleur est extrêmement chronophage et surtout peu accessible encore d'un point de vue matériel. Pour conclure, intégrer des processus physiologiques issus de calculs au sein d'une base de données sur plusieurs dizaines de taxons demanderait de gros efforts d'approximation quant à leur variabilité et la pose d'hypothèses supplémentaires quant au lien entre ces processus et les traits utilisés pour les calculer. Cela rendrait donc l'étude et ses conclusions plus complexes et sans doute moins réalistes ou crédibles, d'autant plus que les traits d'ores et déjà choisis sont déjà soumis à de fortes variabilités. Dans les travaux présentés (Chapitres 4 & 5), l'objectif est de créer une base de traits variés (une dizaine de traits ont été caractérisés), permettant de regrouper une grande quantité de taxons microphytoplanctoniques, déjà connus pour leur diversité (Figure 9.3), selon leurs similarités, tout en évitant des degrés de complexité pouvant nuire à l'intégrité de l'approche.

Par ailleurs, le choix de définir des groupes fonctionnels au travers d'une démarche mathématique reste imparfait. Cela est totalement compréhensible et se voit au travers de la comparaison des dendrogrammes issus des approches fonctionnelles ou écologiques. Il est nécessaire de comprendre qu'un groupement nécessite des compromis, toutes les espèces d'un même groupe fonctionnel ne sont pas identiques en tout point. Les espèces indicatrices présentées dans ces chapitres illustrent ces compromis, et présentent typiquement des traits "classés" comme importants et prioritaires par l'analyse pour faire partis d'un groupe donné. Par exemple un groupe nommé d'après la présence de petites cellules coloniales peut présenter (en minorité) des cellules de taille moyenne ou large, pas coloniale. Cela signifie qu'elles possèdent d'autres traits en commun et que l'analyse, dans son processus de hiérarchisation, a été amenée à classer ces taxons dans ce groupe. Un groupe monospécifique est donc composé d'un taxon isolé présentant de fortes différences fonctionnelles par rapport à l'ensemble des taxons entrés dans l'analyse. Néanmoins, malgré ces limites, l'approche comparée niche-traits (Chapitre 5) met en valeur la proximité fonctionnelle entre deux taxons pouvant être présents côte à côte dans l'arbre hiérarchique mais séparés dans différents groupes fonctionnels après découpage mathématique. Cette proximité est incluse dans le calcul du niveau de mélange (*entanglement*), l'abaissant si ces taxons sont présents dans un même groupe écologique. L'étude comparée niche-traits confirme que, dans la majorité des cas, des taxons présentant des traits similaires et par conséquent partageant un même groupe fonctionnel sont préférentiellement retrouvés dans les mêmes conditions (niches) environnementales. Elle valide par conséquent la pertinence des regroupements par traits fonctionnels ; en effet, si des pressions environnementales bouleversent les niches écologiques de certains taxons phytoplanctoniques, une étude par groupes fonctionnels permet de cibler les organismes qui sont/seront affectés par ces changements et lesquels vont en profiter.

9.1.3 Compétition ou co-existence ; distribution phytoplanctonique observée

Durant le chapitre 5, la question "Le partage de traits fonctionnels communs entraîne-t-il une distribution au sein de niches écologiques similaires ?" dépoussière de nombreuses interrogations empiriques et fondamentales. Il s'agit de principes que l'on attribue sans équivoque à de nombreuses espèces de faunes et de flores, mais qui pourtant ne s'appliquent pas forcément au phytoplancton. C'est une conversation avec des biologistes en halieutique qui a remis à jour l'aspect étrange d'une telle hypothèse d'étude en écologie. En effet, contrairement à la majorité des espèces animales et végétales dont la distribution et l'occupation de l'espace sont soumises au principe d'exclusion compétitive[5], les taxons au sein du microphytoplancton adaptés à un type d'environnement vont le partager, même en conditions nutritives limitantes (Miyazaki et al., 2006). Cette co-existence est à l'origine du Paradoxe du Plancton (Hutchinson, 1961). Afin de répondre à ces interrogations il faut avant tout considérer le plancton à son échelle, de quelques dizaines de micromètres au centimètre et non pas à l'échelle de la mer ou de l'océan. Dans le milieu marin, les organismes peuvent exploiter également l'aspect tri-dimensionnel du milieu ce qui n'est pas toujours facilement accessible par les méthodes d'échantillonnages classiques. C'est une notion que l'on retrouve dans les études de Mitchell et al. (2008), qui montrent qu'il existe des *patches* de phytoplancton de l'ordre d'une dizaine de centimètres et d'une durée de vie d'environ 10 minutes, dans lesquels étaient retrouvés les processus de compétition, de prédation et d'infection.

Par ailleurs, il a été observé au sein du phytoplancton des stratégies de

---

[5] Deux espèces aux mêmes besoins environnementaux et à sensibilité égale, auront une même niche écologique et par conséquent seront en compétition pour les ressources du milieu (Hardin, 1960).

défense afin d'éviter la prédation ou la prolifération d'autres espèces. Notamment, des phénomènes allélopathiques[6] ont été associés à l'acide domoïque produite par le genre *Pseudo-nitzschia* (Van Meerssche & Pinckney, 2017; Van Meerssche et al., 2018). Parallèlement, la production de substance exo-polymère transparente (TEPs) va avoir un effet coagulant pouvant réduire l'effet de prédation sur le picophytoplancton, ils protègent également des attaques virales et concentrent les sels nutritifs (illustrée Figure 9.4, Mari & Rassoulzadegan (2004)).

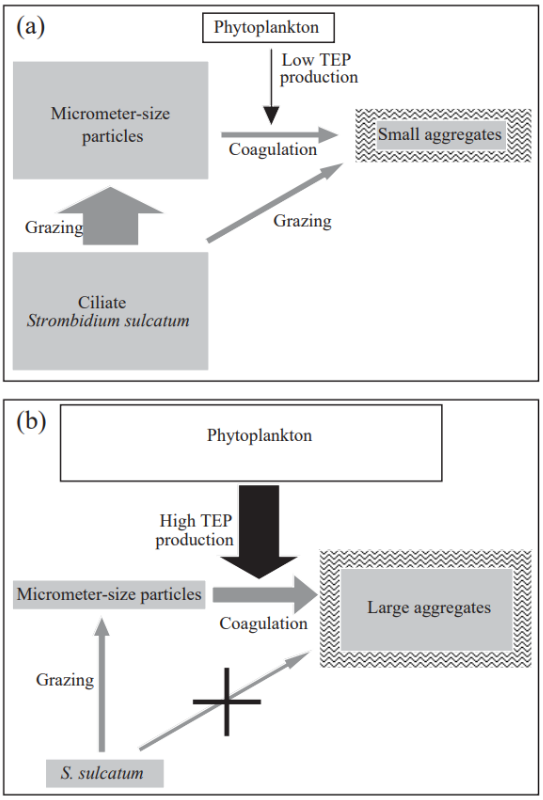


FIGURE 9.4 – Représentation conceptuelle de l'effet d'une (a) faible ou (b) forte concentration en TEPs sur le comportement de prédation de *Strombidium sulcatum* (extrait de Mari & Rassoulzadegan (2004)).

Au cours de nos différentes études, des périodes temporelles ont pu être mises en avant et reliées à des assemblages phytoplanctoniques différents. A l'échelle de la Manche, une baisse notable de la concentration en chl-a a été observée depuis 2008, principalement au niveau des grands estuaires. Notamment, on observe

---

[6] Production de substances biochimiques pouvant influencer la physiologie, la croissance, la survie et la reproduction d'autres organismes.

une diminution de nombreux taxons mixotrophes, hétérotrophes et/ou de petites tailles et une augmentation des organismes benthiques et tychoplanctoniques, ce qui montre entre autre un changement d'hydrodynamisme. De tels changements fonctionnels dans la communauté peuvent avoir des effets à différents niveaux trophiques mais également au sein même du microphytoplancton en modifiant les interactions biotiques. Néanmoins, la diversité est telle qu'il est difficile d'affiner les liens reliant des changements d'assemblages taxonomiques et fonctionnels à d'autres évènements. Ainsi, on a pu observer des augmentations dans les occurrences des contaminations issues des efflorescences du genre *Dinophysis*, qui sont à l'origine d'inquiétudes de plus en plus fortes en Atlantique Nord-Est depuis 2014-2015. De même, le genre *Pseudo-nitzschia* sp. ne cause plus de contaminations depuis 2014-2015, les conditions n'étant plus favorables aux espèces toxiques du genre (notamment *P. australis*). Si des rapprochements environnementaux abiotiques sont plus souvent utilisés pour expliquer ces observations (comme au Chapitre 7), il nous faut considérer les effets des changements au sein même de la communauté phytoplanctonique dont ceux associés aux interactions biotiques, qui sont capables de modifier et réduire les niches écologiques d'autres espèces (Chapitre 8). Il est cependant encore très difficile d'évaluer les interactions des organismes entre eux, des processus de compétition, de prédation, de parasitisme, de symbiose ou encore de commensalisme[7] sont très complexes à évaluer. C'est notamment le cas à l'échelle d'une communauté multi-spécifique d'organismes unicellulaires, extrêmement diversifiés et dont la distribution est la plupart du temps imprévisible car dépendante de très nombreux paramètres et de leurs interactions.

9.2 Absence ou complexité de l'information, les obstacles rencontrés

Tous travaux, quels qu'ils soient, sont limités par les choix imposés dans le but de répondre le plus clairement et exactement possible à une problématique sous contraintes techniques, financières, expérimentales et humaines. Ainsi certaines approches pourraient bénéficier d'apports supplémentaires et leur absence aura

---

[7] Relations entre deux organismes menant à des bénéfices pour l'un sans effet négatif pour l'autre.

pu causer un manque pour l'interprétation des résultats obtenus. Cette partie permet de mettre en lumière les différents obstacles, limites ou remarques qui ont pu être soulevés au fur et à mesure des travaux du doctorat.

En premier lieu, la première difficulté de ces recherches réside dans la disponibilité des données. Aujourd'hui, plus d'une dizaine d'années de données d'abondances microphytoplanctoniques sont disponibles grâce aux réseaux de surveillances locaux et nationaux. La mise en place d'un tel niveau de surveillance, à la fois en terme de fréquence de prélèvements (hebdomadaire à bi-mensuel) et de couverture spatiale est nécessaire pour étudier une communauté dont la période de *turn-over* est estimée à une dizaine de jours. Néanmoins, en amont de cette approche, comme décrit au chapitre méthodologique, un effort d'homogénéisation des compétences est nécessaire. La lecture, l'identification et le comptage des flores planctoniques est un travail laborieux, dont le temps de formation observateur pour pouvoir intégrer le réseau REPHY dans l'identification de flores totales s'élève à 2 ans. Les lecteurs, experts phytoplanctoniques, sont alors amenés à analyser les échantillons issus de quelques sites à leur charge. La stabilité et la fiabilité des données sont assurées par souvent plus d'un lecteur par laboratoire d'observation du littorale, et depuis 2015 par l'exercice de tests internationaux (IPI). L'importance de ces tests est incontestable, ils réduisent le biais observateur autant que possible (`https://www.aquaref.fr/thematique/essai-interlaboratoires`). Initié en 2016, le SNO PHYTOBS (2016) a également permis de labelliser les appellations taxonomiques. Certains outils complémentaires sont également de plus en plus explorés afin de permettre d'augmenter la précision et la rapidité des lectures florales, notamment des approches génétiques (PCR ou ADN environnemental par métabarcoding), ou automatisées (FlowCam, Cytométrie ; Poulton (2016)).

Ces dernières approches permettraient également d'élargir le nombre de dimensions des études. En effet, le terme phytoplancton en milieu naturel est très souvent réduit au compartiment microphytoplanctonique, seul accessible par lecture microscopique classique (via la méthode répandue d'Utermöhl). Les échelons du pico- et nano- phytoplancton sont encore difficilement atteignables, notamment pour une identification taxonomique au genre ou à l'espèce. Les données sont souvent issues de mesures par cytométrie et les abondances sont estimées pour l'ensemble du compartiment (Serre-Fredj et al., 2021). Cependant, ces deux compartiments ne sont pas moins importants, ils participent à une fraction de la chlorophylle-a mesurée *in situ* ou par satellite, proxy de la production primaire réutilisé dans de nombreuses études halieutiques. Ils rassemblent également des organismes proies du micro-plancton (dont dinoflagellées et zooplancton ; larves, copépodes, etc...) et dont les interactions sont encore peu étudiées, mais dont la contribution à l'écosystème est certainement sous-évaluée (Leblanc et al., 2018).

Pour les mêmes raisons, les données renseignant de la diversité zooplanctonique sont souvent limitées à quelques points spatiaux difficilement associables aux points de suivis du phytoplancton. Si les études relatives aux processus de succession phytoplanctonique ne cessent de s'enrichir, celles associées au zooplancton sont encore sporadiques. Un gros travail de suivi devrait être mis en place au même titre que le suivis phytoplanctonique, au travers de la formation de personnels compétents mais également grâce aux identifications automatisées (ZooCam ; `https://wwz.ifremer.fr/L-ocean-pour-tous/Nos-ressources-pedagogiques/Suivez-nos-campagnes/Campagne-EVHOE-2015/Le-ZooCam`). Le zooplancton est pourtant essentiel à la survie des organismes des réseaux trophiques supérieurs, soit parce qu'il constitue un pool de proies initial sur lequel vont dépendre les prédateurs supérieurs, soit parce qu'au sein même du zooplancton des organismes se développent sous forme larvaire (larves de coquillages, de poissons) et rejoindront à l'âge adulte les échelons supérieurs (illustration des interactions entre formes de vie Figure 9.5). C'est donc un maillon intermédiaire entre les producteurs primaires et les autres organismes marins, dont le statut est parfois critique ou associé à des intérêts commerciaux, qui reste encore au stade de boite noire pour de nombreux chercheurs (Aubert et al., 2018; Lomartire et al., 2021).

Au cours de l'approche fonctionnelle, il a été possible de renseigner les caractéristiques de 87 taxons selon une dizaine de traits fonctionnels. Chaque taxon est considéré de façon équitable, la notion d'abondance n'est pas incluse. Néanmoins, des espèces présentant des traits similaires peuvent ne pas avoir la même importance écologique. Nos classifications ne différencient pas les taxons très abondants des taxons rares. Aux chapitres 4 et 5, les résultats de la clusterisation pourraient être approfondis afin de déterminer la distribution de l'abondance et de la place de chaque taxon des groupes fonctionnels dans la communauté. Cela

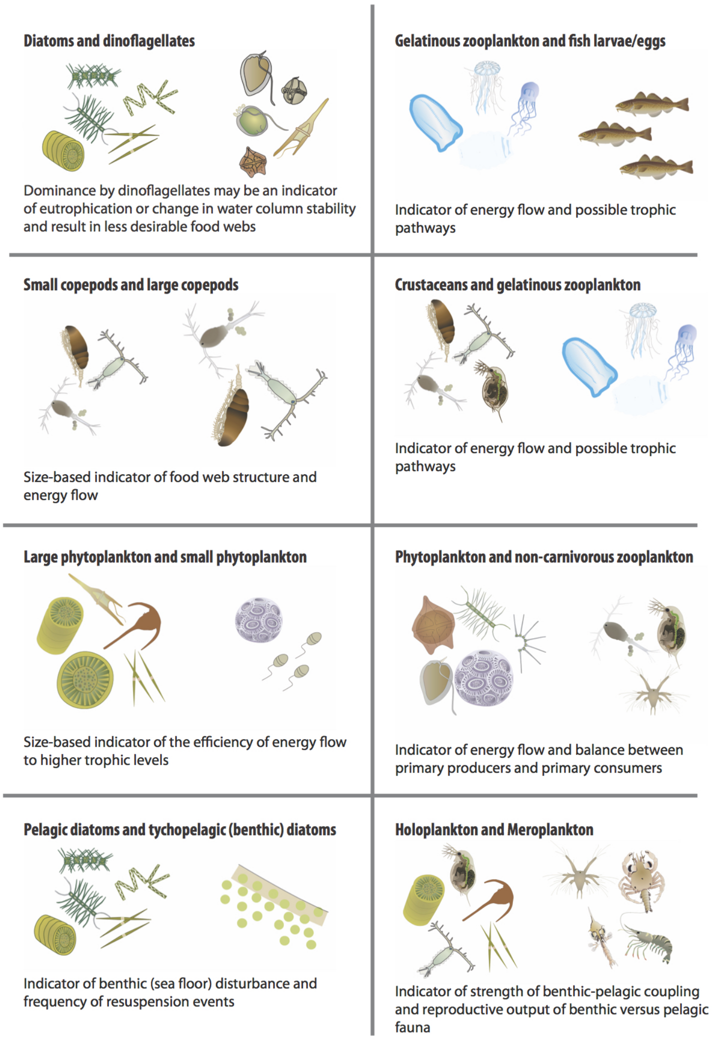


FIGURE 9.5 – Illustration des paires de formes de vies et des stratégies écologiques derrière leur sélection (extrait du rapport OSPAR 2017 ; Changes in Phytoplankton and Zooplankton Communities, décrit dans la publication de McQuatters-Gollop et al. (2019)).

permettrait de déterminer la possible compétition au sein d'un même groupe fonctionnel, notamment chez les diatomées chez lesquelles un groupe fonctionnel est associé à 1 ou 2 environnements préférentiels.

De plus, nous avons discuté plus haut que le choix de ne pas prendre certains traits basés sur des calculs de traits connus (taux de fixation de certains éléments, taux de croissance, etc...) a été fait de part la connaissance au préalable de leur forte variabilité et plasticité selon l'espèce voire selon l'individu. Pourtant, ce n'est pas seulement compliqué à l'échelle de la communauté mais il n'existe surtout pas encore de méthode d'analyse qui pourrait intégrer la variabilité d'un trait selon la phase de développement, la taille, la saison voire même l'intensité lumineuse ou d'autres paramètres biotiques et abiotiques. Cela nécessiterait la mise en place de calculs de modélisation complexes basés sur une description des plus complètes des différents traits et de leur variabilité, et ceux pour un maximum de taxons phytoplanctoniques. S'il serait intéressant d'arriver à ce niveau de précision, il s'agit là de pistes complémentaires pour d'autres travaux d'acquisition de données et de manipulations analytiques.

Après la mise en place d'une campagne de prélèvements et le suivi expérimental de teneurs intra-cellulaires, les limites de ces approches ont pu amener à des choix techniques et des compromis. S'il est, en effet, toujours appréciable de pouvoir répondre à une problématique de la manière la plus complète et riche possible, la réalité est souvent tout autre. La campagne en estuaire de Seine était initialement prévue sur un point supplémentaire et avait été réfléchie de sorte à prendre en compte la présence de métaux traces dans les échantillons, ces derniers pouvant influencer la production de toxines chez *Pseudo-nitzchia* sp. (Maldonado et al., 2002). Cette dernière approche a été rapidement mise de côté au vue de la complexité du prélèvement, à l'échelle du laboratoire et de la réalisation sur le terrain, qui aurait nécessité un outillage particulier qui puisse éviter toute contamination externe de l'échantillon. Les conditions sur le terrain sont également facteurs d'imprévus. Les horaires d'ouvertures portuaires, les exigences liées au nombre de d'échantillons et aux mesures de sondes ainsi que les conditions météorologiques (et les maux associés) ont pu ainsi être limitant. La crise sanitaire puis la faible présence de *Pseudo-nitzschia* sp. les années suivantes n'auront également pas permis de réaliser la campagne en estuaire de Seine sur un autre bloom printanier et d'infirmer ou confirmer nos résultats.

La manipulation expérimentale tri-mensuelle, ayant permis le suivi des teneurs lipidique et chlorophyllienne des cellules microphytoplanctoniques, avait débuté par une expérimentation d'incubation qui s'est avérée peu concluante (problèmes techniques liés à la sédimentation des cellules, la régulation de la température et l'accès à la lumière). Elle aura permis de calibrer et de définir un protocole pour les analyses au microscope confocale. En effet, la manipulation a été réorientée vers un suivi qui n'ajoutait pas de prélèvement mais reprenait des échantillons aux sites d'ores et déjà suivis dans le cadre du REPHY et du RHLN, ce qui assurait à chaque prélèvement d'avoir les paramètres abiotiques d'intérêts associés. La principale limite résidait dans la conservation de l'échantillon, l'impossibilité d'effectuer les analyses cytométriques ni microscopiques sur des échantillons fixés, ce qui amena donc à des analyses en continuité du prélèvement en mer (de 10h à 17h, de Cabourg à Donville). Il est inconcevable que cette approche soit pérennisée au sein d'un suivi régulier. Elle apporte cependant un grand nombre d'information sur la cyclicité saisonnière de teneurs intra-cellulaires chez le phytoplancton ainsi que sur l'utilisation de la microscopie confocale dans ce domaine. Elle saurait donc enrichir des études ponctuelles axées sur des thématiques précises.

Pour finir, ce projet doctoral est représentatif d'une localisation géographique réduite aux zones côtières de la Manche. Nos données de suivis et d'expérimentations se concentrent sur quelques sites préférentiels et ont pu seulement s'étendre au delà des frontières de part les travaux menés en collaboration avec des collègues de Southampton sur *Dinophysis* sp.. Un projet de mobilité en Irlande[8], avait également pour objectif de couper les frontières et d'étudier et comparer les successions spécifiques au sein du genre *Pseudo-nitzschia* sp. via une approche génétique (qPCR). Ainsi, toute approche spatiale est souvent contrainte par des critères matériels, techniques et financiers dans une filière dans laquelle tout se compare et tout s'exporte à large échelle. Si le projet S3-EUROHAB est concentré sur la dynamique de la Manche, les résultats des travaux menés durant le projet doctoral sont cohérents avec des recherches affectant des milieux côtiers à plus larges échelles, des Etat-Unis à la Nouvelle-Zélande. Néanmoins, il serait intéressant que ces travaux, ses approches, résultats et questionnements, soient repris et discutés plus amplement dans d'autres cadres de recherches. Un manque de rencontre sur ces deux dernières années aura amené à un plus faible potentiel d'exportation des travaux de recherches menés. Pourtant, quand cela était possible, ces derniers ont éveillé la curiosité de nombreux collègues aux thématiques

---

[8] Mobilité financée mais compromise des suites de la pandémie Covid19 qui a frappé et forcé des pays d'Europe, et du monde à des isolements plus ou moins strictes, de Mars 2020 à Mars 2022

variées ; bivalves marins et autres espèces halieutiques, démontrant de l'intérêt et du potentiel de ces travaux. Ces études locales se veulent représentatives et indicatrices des changements observables au niveau d'estuaires anthropisés, à large ou faible influence fluviale (*versus* marine), soumis à des réglementations plus ou moins strictes vis-à-vis de l'eutrophisation, et invitent à la réflexion. Les dynamiques variables des efflorescences algales toxiques qui montrent une réduction des contaminations à ASP (*Pseudo-nitzschia* spp.) mais une augmentation des risques liés au DSP (*Dinophysis* spp.) depuis 2015, mériteraient notamment d'être approfondies à d'autres systèmes côtiers, voire d'autres phénomènes relatifs aux HABs. Par exemple, la Rade de Brest, sujette à des efflorescences algales du genre *Alexandrium* sp., montre néanmoins une réduction des occurrences et intensités de ces blooms depuis également 2015, probablement des suites d'un changement dans la composition fonctionnel phytoplanctonique (Chapelle et al., 2021).

9.3 Conclusions et perspectives, les défis pour l'avenir

Tout au long des travaux, plusieurs volets scientifiques ont été explorés. Les approches taxonomiques sur le phytoplancton ont permis d'établir à la fois des différenciations spatiales à l'échelle de la Manche Est et une constance dans l'assemblage de la communauté sur plus d'une décennie. Ces résultats communautaires ont été approfondis par une approche fonctionnelle ayant amené à l'observation d'une réduction de petits organismes (dont ceux à régime mixotrophe ou hétérotrophe) mais une augmentation des diatomées et dinoflagellés de plus grandes tailles. Cette approche par trait a été remise en question et validée d'un point de vue écologique grâce à une approche par niche écologique. Cette dernière a permis de mettre en évidence qu'il existe un lien entre des taxons partageant des traits fonctionnels et leurs préférences environnementales. Pour répondre aux questionnements liés à la notion de plasticité cellulaire, une approche expérimentale a permis d'explorer la variabilité saisonnière des teneurs en lipides et en chl-*a*. Une autre approche aura permis d'échantillonner en 3 dimensions l'embouchure de la Seine durant l'efflorescence d'un genre toxique ; *Pseudo-nitzschia* sp.. Grâce aux données historiques, il aura également été possible de retracer les conditions particulières de son apparition au cours d'une fenêtre temporelle relativement courte à l'échelle de l'étude. Un second genre toxique, *Dinophysis* sp., posant actuellement de plus en plus de problématiques économiques, a également fait l'objet d'une étude comparée trans-Manche, en collaboration avec un laboratoire partenaire dans le cadre du projet S3-EUROHAB.

Néanmoins nos approches par traits et niches (chapitres 4 & 5) utilisent parfois un pas temporel trop large (annuel) pour s'adapter aux contraintes numériques, et bénéficieraient d'une considération à échelle saisonnière afin de mettre en valeur la relation trait-environnement spécifique à ces périodes temporelles. En effet, l'importance de la saisonnalité chez ces organismes amène à des assemblages taxonomiques saisonniers qui répondent à des conditions environnementales données. L'approche fonctionnelle apporte de nombreux bénéfices, elle concrétise des hypothèses et permet une meilleure visualisation des types de changements qui ont lieu au sein de la communauté et ce que cela signifie pour les échelons supérieurs. Associée à une approche par niche adaptée, elle a le potentiel de mettre en avant les mécanismes de sélections derrière les événements saisonniers, les successions spécifiques et les processus de prédation.

Pour autant, les groupes fonctionnels correspondent au meilleur groupement trouvé au vu des traits implémentés dans l'analyse, ils ne sont et ne peuvent être parfaits. Il existe énormément de méthodes afin de former des groupements fonctionnels. Il faut choisir une approche qui réponde aux exigences demandées par la problématique en amont ; soit la sélection des traits est réalisée par le scientifique de sorte à répondre à des contraintes d'études ; ex : la relation bivalves-phytoplancton où les traits comme la capacité à former des colonies et la présence d'épines et de soies sont cruciaux, (David et al., 2012), soit on sélectionne des traits qui caractérisent une communauté sur différents critères pertinent au regard de la fitness, et leur groupement est effectué par un calcul mathématique en fonction des similitudes entre les taxons. Les perceptions et interprétations de l'approche fonctionnelle sont néanmoins différentes et il est fréquent de vouloir retourner à une échelle taxonomique plus *rassurante* pour comprendre les effets observés à l'échelle fonctionnelle.

Comme répandu au sein d'autres échelons biologiques dans l'étude des écosystèmes et des effets du changement global, il serait intéressant de pouvoir identifier des taxons prioritaires, indicateurs de l'état du milieu. Le phytoplancton est souvent étudié soit à l'échelle de l'espèce ou de la souche en laboratoire, soit à l'échelle de la biomasse (chl-a). L'échelle de la communauté, bien que largement étudiée, est plus difficile à appréhender de part l'immense diversité spécifique. C'est pourquoi, l'obtention d'indicateurs taxonomiques est peu aisée compte tenu de la forte variabilité, encore peu comprise, au sein des différents éléments taxonomiques composant le phytoplancton (Domingues et al., 2008). Au sein de la DCE, il existe de nombreux indicateurs permettant d'estimer la qualité de l'eau, près d'un quart d'entre eux concernent le phytoplancton (Birk et al., 2012). Malgré tout, les indicateurs de la composition phytoplanctonique restent compliqués à mettre en place. Le développement d'une méthode pouvant identifier ces marqueurs de l'environnement pourrait donc être tout aussi pertinent, ce qui permettrait de suivre l'apparition ou la disparition de taxons indicateurs dans un milieu et de relier ces changements à l'état environnemental.

Enfin, le phytoplancton est un compartiment majeur au sein des océans, il est représentatif de l'état de ce dernier. Il va permettre d'amortir des phénomènes anthropiques soudains ou progressifs mais cela aura des conséquences sur la sélection des taxons favorisés ou défavorisés dans de telles circonstances. Le phytoplancton n'est pas non plus à considérer seul. Si l'on veut comprendre les effets de changements environnementaux sur le phytoplancton, il faut également comprendre l'effet de ces mêmes changements sur les échelons supérieurs, et comment cela peut altérer les interactions entre les organismes. De plus, comme certaines études commencent à le mettre en avant, le phytoplancton est sujet à des interactions plus complexes et peu connues avec les bactéries et virus de l'océan (Mayali et al., 2018). Une meilleure compréhension des liens entre les organismes biologiques, tout échelon confondu, est au coeur des problématiques de demain. Les changements prédits seront amenés à s'amplifier rapidement pour les milieux marins et aquatiques et leurs effets seront suivis les années à venir. Si les évolutions climatiques et biologiques font parties d'un processus naturel, celles que l'on observe ont des origines anthropiques qu'il est de notre devoir de comprendre et compenser afin de conserver une biodiversité, des fonctions écologiques et un environnement propice à toute vie.

10

Annexes

10.1 Formations et expériences

Au cours des travaux sur le projet doctorale, divers enrichissements ont été possible.

Tout d'abord, au travers de formations doctorales, une centaine d'heures de formations ont permis de développer des connaissances sur différents domaines :

- Structure et fonctionnement de l'Enseignement Supérieur et de la Recherche
- Règles et usages de publication d'un article scientifique
- Mener sa thèse comme un projet
- Intégrité scientifique
- Formations suivies à l'ESPE (Ecoles Supérieures du Professorat et de l'Education) dans le cadre de la préparation à la mission d'enseignement
- Imagerie/Microscopie, Caen
- Microscopie en épifluorescence : théorie et pratique, Port-en-Bessin
- ILICO - Série chronologique, Paris
- MOOC sauvTage : apprendre à sauver une vie à tous les âges, Université de Bretagne Occidentale
- CCAP - Algaculture for Biotechnology, SAMS, Ecosse

Ensuite, dès début 2019 et durant 3 mois, des cours ont été menés en présentiel devant des étudiants de licence 1 à l'Université de Caen. Il s'agissait notamment de 72h de cours, répartis entre travaux dirigés et travaux pratiques autour de l'UE de biologie végétale, sous la tutelle de Mme Isabelle Mussio.

10.2 Productions scientifiques

Le milieu de la recherche s'articule autour de la communication de chacun. Petites pierres à un édifice gigantesque, ce doctorat a fait l'objet de diverses valorisations au travers de publications, réunions de projets, de colloques et d'autres rassemblements scientifiques.

Tout d'abord, le premier chapitre de thèse a fait l'objet d'une publication (extrait donné ci-après) et d'une soumission :

- Lefran, A., Hernandez-Fariñas, T., Gohin, F., & Claquin, P. (2021). Decadal trajectories of phytoplankton communities in contrasted estuarine systems in an epicontinental sea. *Estuarine, Coastal and Shelf Science*, 258, 107409.

• Lefran, A., Hernandez-Fariñas, T. & Claquin, P. (en review), Phytoplankton functional diversity and temporal stability within coastal systems. *Limnology and Oceanography.*

Puis, les évènements ci-dessous ont ainsi fait l'objet de diffusion orales, en présentiel ou par enregistrement video :

• colloque du groupe de travail Phycotox ; du 14 au 16 mai 2019 à Brest (Poster & Oral, intitulé : Insights on the phytoplankton community structure in the Bay of Seine, and the standing of *Pseudo-nitzschia* sp. and *Dinophysis* sp.).

• les Journées Manche-Mer du Nord ; du 17 au 21 décembre 2019, à Lille (Oral, intitulé :)

• colloque CHEERS (global change in estuarine and coastal system functioning) ; du 4 au 8 novembre 2019 à Bordeaux (Oral, intitulé : Resilience and temporal trajectories of micro-phytoplankton communities in the Bay of Seine)

• les Journées REPHY ; les 5 et 6 février 2020, à Nantes (Oral, intitulé : Stability and temporal trajectories of micro-phytoplankton communities in the Bay of Seine)

• colloque de l'ASLO (aquatic science), du 22 au 28 juin 2021, virtuel (Oral, intitulé : Phytoplankton functional diversity representation in contrasted coastal ecosystems facing a changing environment)

• 19$^{\text{ème}}$ conférence internationale de l'ICHA (HABs) (aquatic science), du 9 au 15 septembre 2021, virtuel (Oral, intitulé : Investigating environmental proxies to predict *Dinophysis* spp. blooms along the coasts of the French-English Channel)

• le colloque EVOLECO (évolution des écosystèmes côtiers) ; du 2 au 5 Novembre 2021 à La Rochelle (Oral, intitulé : Diversité fonctionnelle du phytoplancton au sein d'écosystèmes côtiers contrastés, face à un environnement changeant).

• Les Journées des doctorant.e.s et post-doctorant.e.s BOREA 2021, les 2 et 3 décembre à Caen (Oral, intitulé : Etude de la variabilité intra-annuelle des teneurs en lipides et chlorophyll-*a* des cellules phytolanctoniques par microscopie confocale)

Estuarine, Coastal and Shelf Science 258 (2021) 107409

Contents lists available at ScienceDirect

Estuarine, Coastal and Shelf Science

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

Decadal trajectories of phytoplankton communities in contrasted estuarine systems in an epicontinental sea

Angéline Lefran [a,b], Tania Hernández-Fariñas [a], Francis Gohin [c], Pascal Claquin [b,d,*]

[a] IFREMER, Laboratoire Environnement Ressource Normandie, LER/N, Avenue du Général de Gaulle, 14520, Port-en-Bessin, France
[b] Normandie Universités, Université de Caen Normandie, Centre de Recherches en Environnement Côtier (CREC) - Station Marine, BP49, 54, rue du Docteur Charcot, 14530, Luc-sur-Mer, France
[c] IFREMER, Département Dynamiques de l'Environnement Côtier, DYNECO/PELAGOS, Ifremer Brest, BP 70, 29280, Plouzané Brittany, France
[d] Unité Biologie des ORganismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Sorbonne Universités, Muséum National d'Histoire Naturelle, CNRS, Université Pierre et Marie Curie, Université de Caen Normandie, IRD 207, Université des Antilles, Esplanade de la Paix, F-14032, Caen, France

ARTICLE INFO

Keywords:
Phytoplankton
Communities
Estuaries
Coastal
Trajectories
Co-inertia

ABSTRACT

In coastal areas, global changes are known to affect estuaries and their plume leading to water temperature increase and river discharge variations, which are two of the main drivers controlling phytoplankton dynamics. This paper aims at understanding the past 10 years' variations in term of communities' stability and trajectories along with their relationship with the environment. Considering the high environmental variability along coastal areas, we focused our study on six contrasted estuarine systems from the eastern English Channel. Using monthly monitoring from 2008 to 2019, the response of the micro-phytoplankton compartment was investigated through the abundances of a hundred taxa and several abiotic parameters' records. The results indicate an overall stability in community composition with an average of 30–40% similarity between pairs of samples over the study period. The phytoplankton assemblages also display greater spatial heterogeneity during summer in comparison with other seasons. The co-inertia analysis highlighted four separate systems linked to major drivers; a system under strong river and nutrient flows influence, a well-mixed and oxygenized estuary, a system challenged by offshore marine waters, and finally a system under shellfish farms pressure. This structuration is built from the dominance of a handful of species that differs from one place to another, which explains why phytoplankton is mostly site specific. Additionally, the low variations led a by few species' dominance also explains the interannual stability noticed during summer at each area, in spite of the high diversity observed.

1. Introduction

Phytoplankton, as primary producers, are at the base of the marine trophic network and heterotrophic biomass in coastal ecosystems. Understanding phytoplankton dynamics is crucial for explaining variations encountered at higher levels, and eventually leading to changes on an ecosystemic scale (Sumaila et al., 2011). However, there is a high diversity within the phytoplankton compartment, with thousands of species within the world's oceans (Dutkiewicz et al., 2020; Sournia et al., 1991; Tett and Barton, 1995). Physico-chemical environment and biotic pressures (grazers and parasites) are frequently highlighted as major drivers for these communities (Litchman et al., 2010). At the interface between the river's mouth and the sea, estuarine systems are particularly affected by parameters variability and seasonal patterns. River inputs as well as weather events (rainfall, upwelling, heatwaves and turbulences) trigger saline or thermal stratifications of the water column and affect the assemblage of the phytoplankton communities (Cloern and Jassby, 2008; Mallin et al., 1993). These factors vary through temporal and spatial scales, thus defining the seasonal patterns of phytoplankton structure from one ecosystem to another. Therefore, the primary producers' community assemblage, being dependant of long and short-term physical and chemical factors, is also the reflection of the ecosystem's dynamic.

Chlorophyll *a* (Chl-*a* - phytoplankton biomass indicator) in estuarine-coastal ecosystems are mainly due to micro-phytoplankton (cell size $>$ 20 μm) (Carstensen et al., 2015; Wollschläger et al., 2015). Pattern variations within this compartment, such as the decrease of diatoms and the increase of dinoflagellates, have been recorded over

---

[*] Corresponding author. Unité Biologie des ORganismes et Ecosystèmes Aquatiques (BOREA, UMR 7208), Sorbonne Universités, Muséum National d'Histoire Naturelle, CNRS, Université Pierre et Marie Curie, Université de Caen Normandie, IRD 207, Université des Antilles, Esplanade de la Paix, F-14032, Caen, France.
E-mail address: pascal.claquin@unicaen.fr (P. Claquin).

https://doi.org/10.1016/j.ecss.2021.107409
Received 20 November 2020; Received in revised form 5 March 2021; Accepted 10 May 2021

10.3 Tableaux complémentaires aux différents chapitres

Table 10.1 – Tableaux des différents taxons, leur dénomination complète, les abréviations utilisées, leur groupe fonctionnel (GF) et groupe écologique (GE) tels que définis aux chapitres 4 & 5.

Taxon	Abréviation	Classification	Groupe fonctionnel	Groupe écologique
Asterionella formosa	A_formosa	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In dynamic, turibid, colder waters, affected by eastern winds
Asterionellopsis glacialis	A_glacialis	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Akashiwo sanguinea	A_sanguinea	Dinophyceae	NS3 : Mixotrophic, large, round, single, swimming	Under temperature and light duration influence
Actinocyclus	Actinocyclus	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	Generalist, appreciate water runoffs
Alexandrium	Alexandrium	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Need light and freshwater inputs, and N/P ratio
Amphidinium	Amphidinium	Dinophyceae	NS6 : Amphidinium, small, heterotrophic and tychoplanktonic	Under temperature and light duration influence
Brockmanniella brockmannii	B_brockmannii	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	In dynamic, turibid, colder waters, affected by eastern winds
Bacillaria paxillifera	B_paxillifera	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	In dynamic, turibid, colder waters, affected by eastern winds
Bacteriastrum	Bacteriastrum	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	In warm waters with long light exposure, less relations with flows or nutrients
Bellerochea	Bellerochea	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Generalist appreciate water runoffs
Biddulphia	Biddulphia	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	Generalist, appreciate water runoffs
Cylindrotheca closterium + Nitzschia longissima	C_closterium + N_longissima	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	Generalist, appreciate water runoffs
Chaetoceros diadema	C_diadema	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Need long light exposure, with high N/P ratio
Cerataulina pelagica	C_pelagica	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Chaetoceros	Chaetoceros	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Generalist, appreciate water runoffs
Chaetoceros socialis + socialis f. radians	Chaetoceros socialis + socialis f. radians	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	In warm waters with long light exposure, less relations with flows or nutrients
Cochlodinium	Cochlodinium	Dinophyceae	NS4 : Small, high S/V ratio, swimming, mix or autotrophic	Under temperature and light duration influence
Corethron	Corethron	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Need long light exposure, with high N/P ratio
Coscinodiscus + Stellarima	Coscinodiscus + Stellarima	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	Generalist, appreciate water runoffs
Ditylum brightwellii	D_brightwellii	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Generalist, appreciate water runoffs

Continued on next page

Table 10.1 – continued from previous page

Taxon	Shortcut	Classification	GF_Name	GE_name
Dactyliosolen fragilissimus	D_fragilissimus	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Dictyocha	Dictyocha	Dictyochophyceae	S5 : Benthic and mobile, medium sized, single cells	Generalist, appreciate water runoffs
Dinobryon	Dinobryon	Chrysophyceae	NS4 : Small, high S/V ratio, swimming, mix or autotrophic	Appears during west winds in stratified waters
Dinophysis	Dinophysis	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Under temperature and light duration influence
Diploneis	Diploneis	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	In warm waters with long light exposure, less relations with flows or nutrients
Eucampia zodiacus	E_zodiacus	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Diplopsalis + Diplopelta + Diplopsalopsis + Preperidinium + Oblea	e-genus(Diplopsalis)	Dinophyceae	NS3 : Mixotrophic, large, round, single, swimming	Need light and freshwater inputs, and N/P ratio
Navicula + Fallacia + Haslea + Lyrella + Petroneis	e-genus(Navicula)	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	Generalist, appreciate water runoffs
Entomoneis	Entomoneis	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	With marine affinities, high salinities and low N/P ratio
Chaetoceros didymus + protuberans	e-species(C_didymus)	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	In warm waters with long light exposure, less relations with flows or nutrients
Prorocentrum balticum + cordatum	e-species(P_balticum)	Dinophyceae	NS4 : Small, high S/V ratio, swimming, mix or autotrophic	Appears during west winds in stratified waters
Prorocentrum micans + arcuatum + gibbosum + scutellum	e-species(P_micans)	Dinophyceae	NS3 : Mixotrophic, large, round, single, swimming	Appears during west winds in stratified waters
Rhizosolenia imbricata + styliformis	e-species(R_imbricata)	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Rhizosolenia setigera + setigera f. pungens	e-species(R_setigera)	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Thalassiosira levanderi + minima	e-species(T_levanderi)	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	In dynamic, turibid, colder waters, affected by eastern winds
Guinardia delicatula	G_delicatula	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	In warm waters with long light exposure, less relations with flows or nutrients
Guinardia flaccida	G_flaccida	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Gonyaulax spinifera	G_spinifera	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Present with high flows and high N/P ratio
Guinardia striata	G_striata	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Gonyaulax	Gonyaulax	Dinophyceae	NS3 : Mixotrophic, large, round, single, swimming	Need light and freshwater inputs, and N/P ratio
Gymnodinium	Gymnodinium	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Generalist, in-between conditions
Gyrodinium	Gyrodinium	Dinophyceae	NS4 : Small, high S/V ratio, swimming, mix or autotrophic	Generalist, in-between conditions

Continued on next page

Table 10.1 – continued from previous page

Taxon	Shortcut	Classification	GF_Name	GE_name
Heterocapsa triquetra	H_triquetra	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Present with fresh water inputs, dissolved oxygen and high N/P ratio
Helicotheca	Helicotheca	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	Generalist, appreciate water runoffs
Heterocapsa	Heterocapsa	Dinophyceae	NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	Under temperature and light duration influence
Katodinium	Katodinium	Dinophyceae	NS8 : Heterotrophic, elongated, with high S/V ratio	Under temperature and light duration influence
Lepidodinium chlorophorum	L_chlorophorum	Dinophyceae	NS2 : Mixotrophic, medium, round, swimming and toxic	Appears during west winds in stratified waters
Lauderia + Detonula	Lauderia + Detonula	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	Generalist, appreciate water runoffs
Leptocylindrus	Leptocylindrus	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Leptocylindrus, complexe danicus groupe des larges (danicus + curvatus + mediterraneus + aporus + convexus + hargravesii + adriaticus)	Leptocylindrus, complexe danicus	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Leptocylindrus, complexe minimus groupe des fines (L. minimus + Tenuicylindrus belgicus)	Leptocylindrus, cplx minimus	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	In warm waters with long light exposure, less relations with flows or nutrients
Licmophora	Licmophora	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Lithodesmium	Lithodesmium	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	In warm waters with long light exposure, less relations with flows or nutrients
Meuniera membranacea	M_membranacea	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Mesodinium rubrum	M_rubrum	Litostomatea	NS3 : Mixotrophic, large, round, single, swimming	Under temperature and light duration influence
Mediopyxis	Mediopyxis	Khakista incertae sedis	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Need long light exposure, with high N/P ratio
Melosira	Melosira	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Generalist, appreciate water runoffs
Noctiluca scintillans	N_scintillans	Dinophyceae	NS7 : N. scintillans, XXL-size, round and heterotrophic	Under temperature and light duration influence
Odontella sinensis	O_sinensis	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Generalist, appreciate water runoffs
Odontella	Odontella	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In dynamic, turibid, colder waters, affected by eastern winds
Protoperidinium bipes	P_bipes	Dinophyceae	NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	Under temperature and light duration influence
Prorocentrum gracile	P_gracile	Dinophyceae	NS3 : Mixotrophic, large, round, single, swimming	Under temperature and light duration influence
Paralia sulcata	P_sulcata	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Generalist, appreciate water runoffs
Prorocentrum triestinum	P_triestinum	Dinophyceae	NS4 : Small, high S/V ratio, swimming, mix or autotrophic	Appears during west winds in stratified waters

Continued on next page

Table 10.1 – continued from previous page

Taxon	Shortcut	Classification	GF_Name	GE_name
Phaeocystis	Phaeocystis	Prymnesiophyceae	NS1 : Phaeocystis, forming curved colonies	Generalist, in-between conditions
Plagiogramma	Plagiogramma	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	In dynamic, turibid, colder waters, affected by eastern winds
Plagiolemma	Plagiolemma	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	Generalist, appreciate water runoffs
Pleurosigma + Gyrosigma	Pleurosigma + Gyrosigma	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	In warm waters with long light exposure, less relations with flows or nutrients
Polykrikos	Polykrikos	Dinophyceae	NS10 : Large, elongated, with resting stage	Under temperature and light duration influence
Proboscia	Proboscia	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	With marine affinities, high salinities and low N/P ratio
Prorocentrum	Prorocentrum	Dinophyceae	NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	Under temperature and light duration influence
Protoperidinium + Peridinium	Protoperidinium + Peridinium	Dinophyceae	NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	Generalist, in-between conditions
Pseudo-nitzschia	Pseudo-nitzschia	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	Generalist, appreciate water runoffs
Pseudo-nitzschia cplx delicatissima	Pseudo-nitzschia cplx delicatissima	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Pseudo-nitzschia cplx seriata	Pseudo-nitzschia cplx seriata	Bacillariophyceae	S2 : Elongated, Xlarge and chain forming, with low S/Vratio	In warm waters with long light exposure, less relations with flows or nutrients
Pyrocystis	Pyrocystis	Dinophyceae	NS10 : Large, elongated, with resting stage	Present with high flows and high N/P ratio
Rhaphoneis + Delphineis	Rhaphoneis + Delphineis	Bacillariophyceae	S5 : Benthic and mobile, medium sized, single cells	Generalist, appreciate water runoffs
Scenedesmus	Scenedesmus	Chlorophyceae	NS9 : Scenedesmus, chain forming with spines	Present with fresh water inputs, dissolved oxygen and high N/P ratio
Scrippsiella	Scrippsiella	Dinophyceae	NS5 : Mix/heterotrophic round, swimming, low S/V ratio, with resting stage	Generalist, in-between conditions
Skeletonema	Skeletonema	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Generalist, appreciate water runoffs
Striatella	Striatella	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Synedra + Toxarium	Synedra + Toxarium	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	In warm waters with long light exposure, less relations with flows or nutrients
Thalassiosira gravida	T_ gravida	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	Generalist, appreciate water runoffs
Trigonium alternans	T_alternans	Bacillariophyceae	S4 : Tychoplanktonic, medium sized, chain forming	Generalist, appreciate water runoffs
Thalassionema	Thalassionema	Bacillariophyceae	S3 : Large, diverse colonial aspects, low S/V ratio	Generalist, appreciate water runoffs
Thalassiosira + Porosira	Thalassiosira + Porosira	Bacillariophyceae	S1 : Small, round, chain forming, with resting stage	Generalist, appreciate water runoffs
Torodinium	Torodinium	Dinophyceae	NS8 : Heterotrophic, elongated, with high S/V ratio	Generalist, in-between conditions

TABLE 10.2 – Base de traits fonctionnels élaborée et exploitée pour les chapitres 4 & 5.

Shortcut	Tmax.Nordic	S.V_mean	Spine_or_Setae_presence	Cover	Shape	Colony	Motility	Ingestion	Habitat	RestingStage	Substance producer
Bacteriastrum	]50,100]	]0,1]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	No
Chaetoceros	]0,25]	]1,10]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	No
C_diadema	]25,50]	]0,1]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	No
e-species(C_didymus)	]25,50]	]0,1]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	No
Chaetoceros socialis + socialis f. radians	]0,25]	]1,10]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	Harmful
Leptocylindrus, cplx minimus	]25,50]	]1,10]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
Melosira	]0,25]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Tychoplanktonic	1	No
P_sulcata	]100,200]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Tychoplanktonic	1	No
Skeletonema	]0,25]	]1,10]	No	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	1	No
Thalassiosira + Porosira	]100,200]	]0,1]	Setae	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	0	No
e-species(T_levanderi)	]0,25]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	0	No
Bellerochea	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
C_pelagica	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Corethron	]100,200]	]0,1]	Setae	Siliceous	Elongated	None	Floater	Autotrophe	Planktonic	0	No
D_fragilissimus	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
D_brightwellii	]100,200]	]0,1]	Spines	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
G_flaccida	]200,500]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Leptocylindrus	]50,100]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
Leptocylindrus, complexe danicus	]50,100]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
Mediopyxis	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
Odontella	]200,500]	]0,1]	Spines	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
O_sinensis	]200,500]	]0,1]	Spines	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Proboscia	]500,1500]	]0,1]	No	Siliceous	Elongated	None	Floater	Autotrophe	Planktonic	1	No
Pseudo-nitzschia	]100,200]	]1,10]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	Toxic
Pseudo-nitzschia cplx delicatissima	]100,200]	]1,10]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	Toxic
Pseudo-nitzschia cplx seriata	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	Toxic
e-species(R_imbricata)	]500,1500]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
e-species(R_setigera)	]500,1500]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	1	No
Actinocyclus	]50,100]	]0,1]	No	Siliceous	Round	None	Floater	Autotrophe	Planktonic	0	No
A_formosa	]50,100]	]1,10]	No	Siliceous	Elongated	Curved	Floater	Autotrophe	Planktonic	0	No
A_glacialis	]50,100]	]0,1]	Spines	Siliceous	Elongated	Curved	Floater	Autotrophe	Planktonic	0	No
Coscinodiscus + Stellarima	]50,100]	]0,1]	No	Siliceous	Round	None	Floater	Autotrophe	Planktonic	0	Harmful
E_zodiacus	]50,100]	]0,1]	No	Siliceous	Round	Curved	Floater	Autotrophe	Planktonic	0	No
G_striata	]100,200]	]0,1]	No	Siliceous	Elongated	Curved	Floater	Autotrophe	Planktonic	0	No
Lauderia + Detonula	]50,100]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	0	No
Licmophora	]50,100]	]0,1]	No	Siliceous	Elongated	Curved	Floater	Autotrophe	Epiphytic	0	No
M_membranacea	]50,100]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Striatella	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Epiphytic	0	No
Synedra + Toxarium	]50,100]	]1,10]	No	Siliceous	Elongated	None	Floater	Autotrophe	Epiphytic	0	No
Thalassionema	]100,200]	]1,10]	No	Siliceous	Elongated	Curved	Floater	Autotrophe	Planktonic	0	No
B_paxillifera	]100,200]	]0,1]	No	Siliceous	Elongated	Straight	Gliding	Autotrophe	Tychoplanktonic	0	No
B_brockmannii	]25,50]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Tychoplanktonic	0	No
C_closterium + N_longissima	]25,50]	]10,30]	No	Siliceous	Elongated	None	Floater	Autotrophe	Tychoplanktonic	0	Harmful

Continued on next page

Table 10.2 – continued from previous page

Shortcut	Tmax.Nordic	S.V mean	Spine or Setae presence	Cover	Shape	Colony	Motility	Ingestion	Habitat	Resting Stage	Substance producer
G_delicatula	]25,50]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Helicotheca	]100,200]	]10,30]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Planktonic	0	No
Lithodesmium	]25,50]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Tychoplanktonic	0	No
Plagiogramma	]25,50]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Tychoplanktonic	0	No
T_ gravida	]25,50]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Planktonic	0	No
T_alternans	]50,100]	]0,1]	No	Siliceous	Round	Straight	Floater	Autotrophe	Tychoplanktonic	0	No
Biddulphia	]50,100]	]0,1]	No	Siliceous	Elongated	Straight	Floater	Autotrophe	Benthic	0	No
Dictyocha	]25,50]	]0,1]	Spines	Siliceous	Round	None	Swimmer	Autotrophe	Planktonic	0	No
Diploneis	]25,50]	]10,30]	No	Siliceous	Elongated	None	Gliding	Autotrophe	Benthic	0	No
Entomoneis	]25,50]	]30,60]	No	Siliceous	Elongated	None	Gliding	Autotrophe	Benthic	0	No
e-genus(Navicula)	]50,100]	]0,1]	No	Siliceous	Elongated	None	Gliding	Autotrophe	Benthic	0	No
Plagiolemma	]50,100]	]1,10]	No	Siliceous	Round	None	Swimmer	Autotrophe	Benthic	1	No
Pleurosigma + Gyrosigma	]200,500]	]0,1]	No	Siliceous	Elongated	None	Gliding	Autotrophe	Benthic	0	No
Rhaphoneis + Delphineis	]50,100]	]0,1]	No	Siliceous	Elongated	None	Floater	Autotrophe	Benthic	0	No
Phaeocystis	]0,25]	]1,10]	No	Organic	Round	Curved	Swimmer	Autotrophe	Planktonic	0	Harmful
Alexandrium	]25,50]	]10,30]	No	Organic	Round	Straight	Swimmer	Mix	Planktonic	1	Toxic
Dinophysis	]50,100]	]10,30]	No	Organic	Round	None	Swimmer	Mix	Planktonic	0	Toxic
G_spinifera	]25,50]	]0,1]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	1	Toxic
Gymnodinium	]50,100]	]10,30]	No	Naked	Round	Curved	Swimmer	Mix	Planktonic	0	Toxic
H_triquetra	]25,50]	]1,10]	No	Organic	Round	None	Swimmer	Mix	Planktonic	1	Toxic
L_chlorophorum	]25,50]	]10,30]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	0	Toxic
A_sanguinea	]50,100]	]30,60]	No	Naked	Round	None	Swimmer	Mix	Planktonic	0	Harmful
e-genus(Diplopsalis)	]50,100]	]0,1]	No	Organic	Round	None	Swimmer	Mix	Planktonic	1	No
Gonyaulax	]50,100]	]0,1]	No	Organic	Round	None	Swimmer	Mix	Planktonic	1	No
M_rubrum	]50,100]	]0,1]	Setae	Naked	Round	None	Swimmer	Mix	Planktonic	0	No
P_gracile	]50,100]	]30,60]	No	Organic	Round	None	Swimmer	Mix	Planktonic	1	No
e-species(P_micans)	]50,100]	]30,60]	No	Organic	Round	None	Swimmer	Mix	Planktonic	1	No
Cochlodinium	]50,100]	]10,30]	No	Naked	Round	Straight	Swimmer	Mix	Planktonic	1	Harmful
Dinobryon	]0,25]	]10,30]	No	Organic	Elongated	Straight	Swimmer	Mix	Planktonic	1	No
Gyrodinium	]50,100]	]10,30]	No	Naked	Elongated	None	Swimmer	Mix	Planktonic	0	No
e-species(P_balticum)	]0,25]	]0,1]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	0	No
P_triestinum	]0,25]	]10,30]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	0	No
Amphidinium	]25,50]	]10,30]	No	Naked	Elongated	None	Swimmer	Heterotrophe	Tychoplanktonic	0	Toxic
Heterocapsa	]25,50]	]0,1]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	1	No
Prorocentrum	]50,100]	]0,1]	No	Organic	Round	None	Swimmer	Autotrophe	Planktonic	1	No
Protoperidinium + Peridinium	]100,200]	]0,1]	No	Organic	Round	None	Swimmer	Heterotrophe	Planktonic	1	No
P_bipes	]25,50]	]0,1]	No	Organic	Round	None	Swimmer	Heterotrophe	Planktonic	1	No
Scrippsiella	]25,50]	]0,1]	No	Calcareous	Round	None	Swimmer	Mix	Planktonic	1	No
N_scintillans	]500,1500]	]0,1]	No	Naked	Round	None	Floater	Heterotrophe	Planktonic	0	Harmful
Katodinium	]25,50]	]30,60]	No	Organic	Elongated	None	Swimmer	Heterotrophe	Planktonic	0	No
Torodinium	]50,100]	]30,60]	No	Naked	Elongated	None	Floater	Heterotrophe	Planktonic	0	No
Scenedesmus	]0,25]	]10,30]	Spines	Organic	Elongated	Straight	Floater	Mix	Planktonic	0	No
Polykrikos	]100,200]	]0,1]	No	Naked	Elongated	Straight	Swimmer	Heterotrophe	Benthic	1	No
Pyrocystis	]100,200]	]0,1]	No	Organic	Elongated	None	Floater	Autotrophe	Planktonic	1	No

11

Bibliographie

Bibliographie

Abonyi, A., Horváth, Z., & Ptacnik, R. (2018). Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. *Freshwater Biology*, 63(2), 178–186. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/fwb.13051.

Aissa-Grouz, N., Garnier, J., & Billen, G. (2018). Long trend reduction of phosphorus wastewater loading in the Seine : determination of phosphorus speciation and sorption for modeling algal growth. *Environmental Science and Pollution Research*, 25(24), 23515–23528.

Allan, R. P. & Soden, B. J. (2008). Atmospheric Warming and the Amplification of Precipitation Extremes. *Science*, 321(5895), 1481–1484. Publisher : American Association for the Advancement of Science.

Allende, L., Fontanarrosa, M. S., Murno, A., & Sinistro, R. (2019). Phytoplankton functional group classifications as a tool for biomonitoring shallow lakes : a case study. *Knowledge & Management of Aquatic Ecosystems*, (420), 5. Number : 420 Publisher : EDP Sciences.

Allison, E. H. & Bassett, H. R. (2015). Climate change in the oceans : Human impacts and responses. *Science*, 350(6262), 778–782. Publisher : American Association for the Advancement of Science.

Almroth-Rosell, E., Wåhlström, I., Hansson, M., Väli, G., Eilola, K., Andersson, P., Viktorsson, L., Hieronymus, M., & Arneborg, L. (2021). A Regime Shift Toward a More Anoxic Environment in a Eutrophic Sea in Northern Europe. *Frontiers in Marine Science*, 8.

Alpine, A. E. & Cloern, J. E. (1992). Trophic interactions and direct physical effects control phytoplankton biomass and production in an estuary. *Limnology and Oceanography*, 37(5), 946–955. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.1992.37.5.0946.

Alves-de Souza, C., González, M. T., & Iriarte, J. L. (2008). Functional groups in marine phytoplankton assemblages dominated by diatoms in fjords of southern Chile. *Journal of Plankton Research*, 30(11), 1233–1243. Publisher : Oxford University Press.

Alves-de Souza, C., Iriarte, J. L., & Mardones, J. I. (2019). Interannual variability of Dinophysis acuminata and Protoceratium reticulatum in a Chilean Fjord : insights from the realized niche analysis. *Toxins*, 11(1), 19. Number : 1 Publisher : Multidisciplinary Digital Publishing Institute.

Aminot, A. & Kérouel, R. (2004). *Hydrologie des écosystèmes marins : paramètres et analyses*. Editions Quae. Google-Books-ID : dd7qZIWQGb8C.

Anantharaj, K., Govindasamy, C., Natanamurugaraj, G., & Jeyachandran, S. (2011). Effect of heavy metals on marine diatom Amphora coffeaeformis (Agardh. Kutz). *Glob J Environ Res*, 5(3), 112–117.

Anderson, D. (2014). HABs in a changing world : a perspective on harmful algal blooms, their impacts, and research and management in a dynamic era of climactic and environmental change. *Harmful algae 2012 : proceedings of the 15th International Conference on Harmful Algae : October 29 - November 2, 2012, CECO, Changwon, Gyeongnam, Korea / editors, Hak Gyoon Kim, Beatriz Reguera, Gustaaf M. Hallegraeff, Chang Kyu Lee, M.*, 2012, 3–17.

Anderson, D. M. (2009). Approaches to monitoring, control and management of harmful algal blooms (HABs). *Ocean & coastal management*, 52(7), 342.

Anderson, D. M., Alpermann, T. J., Cembella, A. D., Collos, Y., Masseret, E., & Montresor, M. (2012). The globally distributed genus Alexandrium : Multifaceted roles in marine ecosystems and impacts on human health. *Harmful Algae*, 14, 10–35.

Anderson, D. M., Boerlage, S. F., & Dixon, M. B. (2017). Harmful Algal Blooms (HABs) and Desalination : A Guide to Impacts, Monitoring and Management.

Anderson, S. I., Franzè, G., Kling, J. D., Wilburn, P., Kremer, C. T., Menden-Deuer, S., Litchman, E., Hutchins, D. A., & Rynearson, T. A. (2022). The interactive effects of temperature and nutrients on a spring phytoplankton community. *Limnology and Oceanography*, n/a(n/a). _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.12023.

Asch, R. G., Stock, C. A., & Sarmiento, J. L. (2019). Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Global Change Biology*, 25(8), 2544–2559. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/gcb.14650.

Ask, J., Rowe, O., Brugel, S., Strömgren, M., Byström, P., & Andersson, A. (2016). Importance of coastal primary production in the northern Baltic Sea. *Ambio*, 45(6), 635–648.

Aubert, A., Antajan, E., Lynam, C., Pitois, S., Pliru, A., Vaz, S., & Thibault, D. (2018). No more reason for ignoring gelatinous zooplankton in ecosystem assessment and marine management : Concrete cost-effective methodology during routine fishery trawl surveys. *Marine Policy*, 89, 100–108.

Aune, T. & Yndestad, M. (1993). Diarrhetic shellfish poisoning. Pages : 87–104 Publication Title : Algal toxins in seafood and drinking water.

Avdelas, L., Avdic-Mravlje, E., Borges Marques, A. C., Cano, S., Capelle, J. J., Carvalho, N., Cozzolino, M., Dennis, J., Ellis, T., Fernández Polanco, J. M., Guillen, J., Lasner, T., Le Bihan, V., Llorente, I., Mol, A., Nicheva, S., Nielsen, R., van Oostenbrugge, H., Villasante, S., Visnic, S., Zhelev, K., & Asche, F. (2021). The decline of mussel aquaculture in the European Union : causes, economic impacts and opportunities. *Reviews in Aquaculture*, 13(1), 91–118. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/raq.12465.

Bargu, S., Goldstein, T., Roberts, K., Li, C., & Gulland, F. (2012a). Pseudo-nitzschia blooms, domoic acid, and related California sea lion strandings in Monterey Bay, California. *Marine Mammal Science*, 28(2), 237–253. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1748-7692.2011.00480.x.

Bargu, S., Lefebvre, K., & Silver, M. W. (2006). Effect of dissolved domoic acid on the grazing rate of krill Euphausia pacifica. *Marine Ecology Progress Series*, 312, 169–175.

Bargu, S., Silver, M. W., Ohman, M. D., Benitez-Nelson, C. R., & Garrison, D. L. (2012b). Mystery behind Hitchcock's birds. *Nature Geoscience*, 5(1), 2–3. Number : 1 Publisher : Nature Publishing Group.

Barnes, M. K., Tilstone, G. H., Smyth, T. J., Widdicombe, C. E., Gloël, J., Robinson, C., Kaiser, J., & Suggett, D. J. (2015). Drivers and effects of Karenia mikimotoi blooms in the western English Channel. *Progress in Oceanography*, 137, 456–469.

Barton, A. D., Finkel, Z. V., Ward, B. A., Johns, D. G., & Follows, M. J. (2013a). On the roles of cell size and trophic strategy in North Atlantic diatom and dinoflagellate communities. *Limnology and Oceanography*, 58(1), 254–266. Publisher : Wiley Online Library.

Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., Kiørboe, T., & Ward, B. A. (2013b). The biogeography of marine plankton traits. *Ecology letters*, 16(4), 522–534. Publisher : Wiley Online Library.

Bates, S. S., Garrison, D. L., & Horner, R. A. (1998). Bloom dynamics and physiology of domoic-acid-producing Pseudo-nitzschia species. *NATO ASI series G ecological sciences*, 41, 267–292. Publisher : Springer Verlag.

Bazin, P., Jouenne, F., Friedl, T., Deton-Cabanillas, A.-F., Roy, B. L., & Véron, B. (2014). Phytoplankton Diversity and Community Composition along the Estuarine Gradient of a Temperate Macrotidal Ecosystem : Combined Morphological and Molecular Approaches. *PLOS ONE*, 9(4), e94110. Publisher : Public Library of Science.

Beaugrand, G., Conversi, A., Atkinson, A., Cloern, J., Chiba, S., Fonda-Umani, S., Kirby, R. R., Greene, C. H., Goberville, E., Otto, S. A., Reid, P. C., Stemmann, L., & Edwards, M. (2019). Prediction of unprecedented biological shifts in the global ocean. *Nature Climate Change*, 9(3), 237–243. Bandiera_abtest : a Number : 3 Primary_atype : Research Publisher : Nature Publishing Group

Subject_term : Climate-change ecology ;Climate-change impacts ;Ecosystem ecology ;Marine biology Subject_term_id : climate-change-ecology ;climate-change-impacts ;ecosystem-ecology ;marine-biology.

Becker, K. W., Collins, J. R., Durham, B. P., Groussman, R. D., White, A. E., Fredricks, H. F., Ossolinski, J. E., Repeta, D. J., Carini, P., Armbrust, E. V., & Van Mooy, B. A. S. (2018). Daily changes in phytoplankton lipidomes reveal mechanisms of energy storage in the open ocean. *Nature Communications*, 9(1), 5179. Number : 1 Publisher : Nature Publishing Group.

Behrenfeld, M. J. & Falkowski, P. G. (1997). Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography*, 42(1), 1–20. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.1997.42.1.0001.

Behrenfeld, M. J., Halsey, K. H., Boss, E., Karp-Boss, L., Milligan, A. J., & Peers, G. (2021). Thoughts on the evolution and ecological niche of diatoms. *Ecological Monographs*, 91(3), e01457. Publisher : Wiley Online Library.

Behrenfeld, M. J., Halsey, K. H., & Milligan, A. J. (2008). Evolved physiological responses of phytoplankton to their integrated growth environment. *Philosophical Transactions of the Royal Society B : Biological Sciences*, 363(1504), 2687–2703. Publisher : Royal Society.

Behrenfeld, M. J., O'Malley, R. T., Siegel, D. A., McClain, C. R., Sarmiento, J. L., Feldman, G. C., Milligan, A. J., Falkowski, P. G., Letelier, R. M., & Boss, E. S. (2006). Climate-driven trends in contemporary ocean productivity. *Nature*, 444(7120), 752–755.

Beliaeff, B., Gros, P., Belin, C., Raffin, B., Gailhard, I., & Durbec, J.-P. (2001). 'Phytoplankton events' in French coastal waters during 1987–1997. *Oceanologica Acta*, 24(5), 425–433.

Belin, C. & Soudant, D. (2018). *Trente années d'observation des micro-algues et des toxines d'algues sur le littoral.* Quae.

Benedetti, F., Gasparini, S., & Ayata, S.-D. (2016). Identifying copepod functional groups from species functional traits. *Journal of Plankton Research*, 38(1), 159–166.

Benedetti, F., Vogt, M., Righetti, D., Guilhaumon, F., & Ayata, S.-D. (2018). Do functional groups of planktonic copepods differ in their ecological niches ? *Journal of Biogeography*, 45(3), 604–616. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/jbi.13166.

Berges, J. A. & Falkowski, P. G. (1998). Physiological stress and cell death in marine phytoplankton : Induction of proteases in response to nitrogen or light limitation. *Limnology and Oceanography*, 43(1), 129–135. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.1998.43.1.0129.

Bernhardt, J. R. & Leslie, H. M. (2013). Resilience to climate change in coastal marine ecosystems. *Annual review of marine science*, 5, 371–392.

Berthelsen, A., Atalah, J., Clark, D., Goodwin, E., Patterson, M., & Sinner, J. (2018). Relationships between biotic indices, multiple stressors and natural variability in New Zealand estuaries. *Ecological Indicators*, 85, 634–643.

Bertozzini, E., Galluzzi, L., Ricci, F., Penna, A., & Magnani, M. (2013). Neutral Lipid Content and Biomass Production in Skeletonema marinoi (Bacillariophyceae) Culture in Response to Nitrate Limitation. *Applied Biochemistry and Biotechnology*, 170(7), 1624–1636.

Bhunia, A. K. (2018). Fish and Shellfish Toxins. In A. K. Bhunia (Ed.), *Foodborne Microbial Pathogens : Mechanisms and Pathogenesis*, Food Science Text Series (pp. 175–180). New York, NY : Springer New York.

Billen, G., Garnier, J., Némery, J., Sebilo, M., Sferratore, A., Barles, S., Benoit, P., & Benoît, M. (2007). A long-term view of nutrient transfers through the Seine river continuum. *Science of The Total Environment*, 375(1), 80–97.

Birk, S., Bonne, W., Borja, A., Brucet, S., Courrat, A., Poikane, S., Solimini, A., van de Bund, W., Zampoukas, N., & Hering, D. (2012). Three hundred ways to assess Europe's surface waters : An almost complete overview of biological methods to implement the Water Framework Directive. *Ecological Indicators*, 18, 31–41.

Blanco, J., Acosta, C. P., Bermúdez de la Puente, M., & Salgado, C. (2002). Depuration and anatomical distribution of the amnesic shellfish poisoning (ASP) toxin domoic acid in the king scallop Pecten maximus. *Aquatic Toxicology*, 60(1), 111–121.

Blatt, M. R., Weisenseel, M. H., & Haupt, W. (1981). A light-dependent current associated with chloroplast aggregation in the alga Vaucheria sessilis. *Planta*, 152(6), 513–526.

Boatman, T. G., Geider, R. J., & Oxborough, K. (2019). Improving the accuracy of single turnover active fluorometry (STAF) for the estimation of phytoplankton primary productivity (PhytoPP). *Frontiers in Marine Science*, 6, 319. Publisher : Frontiers.

Bode, A., Alvarez-Ossorio, M. T., Cabanas, J. M., Miranda, A., & Varela, M. (2009). Recent trends in plankton and upwelling intensity off Galicia (NW Spain). *Progress in Oceanography*, 83(1), 342–350.

Boivin-Rioux, A., Starr, M., Chassé, J., Scarratt, M., Perrie, W., Long, Z., & Lavoie, D. (2022). Harmful algae and climate change on the Canadian East Coast : Exploring occurrence predictions of Dinophysis acuminata, D. norvegica, and Pseudo-nitzschia seriata. *Harmful Algae*, 112, 102183.

Bolte, S. & Cordelières, F. P. (2006). A guided tour into subcellular colocalization analysis in light microscopy. *Journal of Microscopy*, 224(Pt 3), 213–232.

Bonato, S., Christaki, U., Lefebvre, A., Lizon, F., Thyssen, M., & Artigas, L. F. (2015). High spatial variability of phytoplankton assessed by flow cytometry, in a dynamic productive coastal area, in spring : The eastern English Channel. *Estuarine, Coastal and Shelf Science*, 154, 214–223.

Bonnot-Courtois, C., Walter-Simonnet, A.-V., & Baltzer, A. (2014). The Mont-Saint-Michel Bay : An Exceptional Megatidal Environment Influenced by Natural Evolution and Man-Made Modifications. In M. Fort & M.-F. André (Eds.), *Landscapes and Landforms of France*, World Geomorphological Landscapes (pp. 41–51). Dordrecht : Springer Netherlands.

Bouman, H. A., Platt, T., Doblin, M., Figueiras, F. G., Gudmundsson, K., Gudfinnsson, H. G., Huang, B., Hickman, A., Hiscock, M., Jackson, T., Lutz, V. A., Mélin, F., Rey, F., Pepin, P., Segura, V., Tilstone, G. H., van Dongen-Vogels, V., & Sathyendranath, S. (2018). Photosynthesis–irradiance parameters of marine phytoplankton : synthesis of a global data set. *Earth System Science Data*, 10(1), 251–266. Publisher : Copernicus GmbH.

Bowers, H. A., Ryan, J. P., Hayashi, K., Woods, A. L., Marin III, R., Smith, G. J., Hubbard, K. A., Doucette, G. J., Mikulski, C. M., & Gellene, A. G. (2018). Diversity and toxicity of Pseudo-nitzschia species in Monterey Bay : perspectives from targeted and adaptive sampling. *Harmful Algae*, 78, 129–141. Publisher : Elsevier.

Boyd, C. & Gradmann, D. (2002). Impact of osmolytes on buoyancy of marine phytoplankton. *Marine Biology*, 141(4), 605–618.

Bravo, I., Fernández, M. L., Ramilo, I., & Martínez, A. (2001). Toxin composition of the toxic dinoflagellate Prorocentrum lima isolated from different locations along the Galician coast (NW Spain). *Toxicon : Official Journal of the International Society on Toxinology*, 39(10), 1537–1545.

Bray, J. R. & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs*, 27(4), 325–349. Publisher : Wiley Online Library.

Bresnan, E., Arévalo, F., Belin, C., Branco, M. A. C., Cembella, A. D., Clarke, D., Correa, J., Davidson, K., Dhanji-Rapkova, M., Lozano, R. F., Fernández-Tejedor, M., Gufinnsson, H., Carbonell, D. J., Laza-Martinez, A., Lemoine, M., Lewis, A. M., Menéndez, L. M., Maskrey, B. H., McKinney, A., Pazos, Y., Revilla, M., Siano, R., Silva, A., Swan, S., Turner, A. D., Schweibold, L., Provoost, P., & Enevoldsen, H. (2021). Diversity and regional distribution of harmful algal events along the Atlantic margin of Europe. *Harmful Algae*, 102, 101976.

Bresnan, E., Baker-Austin, C., Campos, C. J. A., Davidson, K., Edwards, M., Hall, A., McKinney, A., & Turner, A. D. (2020). Impacts of climate change on human health, HABs and bathing waters, relevant to the coastal and marine environment around the UK. Publisher : Marine Climate Change Impacts Partnership.

Bresnan, E., Fryer, R. J., Fraser, S., Smith, N., Stobo, L., Brown, N., & Turrell, E. (2017). The relationship between Pseudo-nitzschia (Peragallo) and domoic acid in Scottish shellfish. *Harmful Algae*, 63, 193–202.

Bretherton, L., Hillhouse, J., Kamalanathan, M., Finkel, Z. V., Irwin, A. J., & Quigg, A. (2020). Trait-dependent variability of the response of marine phytoplankton to oil and dispersant exposure. *Marine pollution bulletin*, 153, 110906. Publisher : Elsevier.

Brett, M. & Müller-Navarra, D. (1997). The role of highly unsaturated fatty acids in aquatic foodweb processes. *Freshwater Biology*, 38(3), 483–499. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1365-2427.1997.00220.x.

Broecker, W. S. (1975). Climatic change : are we on the brink of a pronounced global warming ? *Science*, 189(4201), 460–463. Publisher : American Association for the Advancement of Science.

Brun, P., Vogt, M., Payne, M. R., Gruber, N., O'Brien, C. J., Buitenhuis, E. T., Le Quéré, C., Leblanc, K., & Luo, Y.-W. (2015). Ecological niches of open ocean phytoplankton taxa. *Limnology and Oceanography*, 60(3), 1020–1038. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.10074.

Brunet, C., Brylinski, J. M., Bodineau, L., Thoumelin, G., Bentley, D., & Hilde, D. (1996). Phytoplankton dynamics during the spring bloom in the south-eastern English Channel. *Estuarine, Coastal and Shelf Science*, 43(4), 469–483. Publisher : Elsevier.

Brylinski, J. M., Brunet, C., Bentley, D., Thoumelin, G., & Hilde, D. (1996). Hydrography and phytoplankton biomass in the eastern English Channel in spring 1992. *Estuarine, Coastal and Shelf Science*, 43(4), 507–519. Publisher : Elsevier.

Brylinski, J. M., Lagadeuc, Y., Gentilhomme, V., Dupont, J. P., Lafite, R., Dupeuble, P. A., Huault, M. F., & Auger, Y. (1991). Le fleuve côtier : un phénomène hydrologique important en Manche Orientale. Exemple du Pas-de-Calais. *Oceanologica Acta, Special issue.* Publisher : Gauthier-Villars.

Cabral, H., Fonseca, V., Sousa, T., & Costa Leal, M. (2019). Synergistic Effects of Climate Change and Marine Pollution : An Overlooked Interaction in Coastal and Estuarine Areas. *International Journal of Environmental Research and Public Health*, 16(15), 2737. Number : 15 Publisher : Multidisciplinary Digital Publishing Institute.

Cahoon, L. B. (2019). Microphytobenthos. In J. K. Cochran, H. J. Bokuniewicz, & P. L. Yager (Eds.), *Encyclopedia of Ocean Sciences (Third Edition)* (pp. 749–751). Oxford : Academic Press.

Caracciolo, M., Beaugrand, G., Hélaouët, P., Gevaert, F., Edwards, M., Lizon, F., Kléparski, L., & Goberville, E. (2021a). Annual phytoplankton succession results from niche-environment interaction. *Journal of Plankton Research*, 43(1), 85–102.

Caracciolo, M., Rigaut-Jalabert, F., Romac, S., Mahé, F., Forsans, S., Gac, J.-P., Arsenieff, L., Manno, M., Chaffron, S., Cariou, T., Hoebeke, M., Bozec, Y., Goberville, E., Gall, F. L., Guilloux, L., Baudoux, A.-C., Vargas, C. d., Not, F., Thiébaut, E., Henry, N., & Simon, N. (2021b). Seasonal temporal dynamics of marine protists communities in tidally mixed coastal waters. (pp. 2021.09.15.460302). Section : New Results Type : article.

Cariou, T., Dubroca, L., Vogel, C., & Bez, N. (2021). Comparison of the spatiotemporal distribution of three flatfish species in the Seine estuary nursery grounds. *Estuarine, Coastal and Shelf Science*, 259, 107471.

Carstensen, J., Klais, R., & Cloern, J. E. (2015). Phytoplankton blooms in estuarine and coastal waters : Seasonal patterns and key species. *Estuarine, Coastal and Shelf Science*, 162, 98–109.

Cavalcanti, L. F., Azevedo-Cutrim, A. C. G., Oliveira, A. L. L., Furtado, J. A., Araújo, B. d. O., Sá, A. K. D.-d.-S., Ferreira, F. S., Santos, N. G. R., Dias, F. J. S., & Cutrim, M. V. J. (2018). Structure of microphytoplankton community and environmental variables in a macrotidal estuarine complex, São Marcos Bay, Maranhão - Brazil. *Brazilian Journal of Oceanography*, 66, 283–300. Publisher : Universidade de São Paulo, Instituto Oceanográfico.

Cañavate, J.-P., van Bergeijk, S., Giráldez, I., González-Ortegón, E., & Vílas, C. (2019). Fatty Acids to Quantify Phytoplankton Functional Groups and Their Spatiotemporal Dynamics in a Highly Turbid Estuary. *Estuaries and Coasts*, 42(8), 1971–1990.

Chakraborty, S., Cadier, M., Visser, A. W., Bruggeman, J., & Andersen, K. H. (2020). Latitudinal Variation in Plankton Traits and Ecosystem Function. *Global Biogeochemical Cycles*, 34(8), e2020GB006564. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1029/2020GB006564.

Chansawang, N., Obara, B., Geider, R. J., & Laissue, P. P. (2016). Three-Dimensional Visualisation and Quantification of Lipids in Microalgae Using Confocal Laser Scanning Microscopy. In T. J. McGenity, K. N. Timmis, & B. Nogales (Eds.), *Hydrocarbon and Lipid Microbiology Protocols : Ultrastructure and Imaging*, Springer Protocols Handbooks (pp. 145–161). Berlin, Heidelberg : Springer.

Chapelle, A., Sourisseau, M., & Plus, M. (2021). Rapport Alex Breizh. Impact des contrôles environnementaux sur la dynamique des efflorescences de l'algue toxique Alexandrium minutum en Rade de Brest. Modélisation en compétition interspécifique.

Charrad, M., Ghazzali, N., Boiteau, V., & Niknafs, A. (2014). NbClust : an R package for determining the relevant number of clusters in a data set. *Journal of statistical software*, 61, 1–36.

Cheng, J., Jacquin, J., Conan, P., Pujo-Pay, M., Barbe, V., George, M., Fabre, P., Bruzaud, S., Ter Halle, A., Meistertzheim, A.-L., & Ghiglione, J.-F. (2021). Relative Influence of Plastic Debris Size and Shape, Chemical Composition and Phytoplankton-Bacteria Interactions in Driving Seawater Plastisphere Abundance, Diversity and Activity. *Frontiers in Microbiology*, 11, 3430.

Chessel, D., Dufour, A. B., & Thioulouse, J. (2004). The ade4 package-I-One-table methods. *R news*, 4(1), 5–10.

Cibic, T., Cerino, F., Karuza, A., Fornasaro, D., Comici, C., & Cabrini, M. (2018). Structural and functional response of phytoplankton to reduced river inputs and anomalous physical-chemical conditions in the Gulf of Trieste (northern Adriatic Sea). *Science of The Total Environment*, 636, 838–853.

Clement, A. C. & Peterson, L. C. (2008). Mechanisms of abrupt climate change of the last glacial period. *Reviews of Geophysics*, 46(4). _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1029/2006RG000204.

Cloern, J. E. (2001). Our evolving conceptual model of the coastal eutrophication problem. *Marine ecology progress series*, 210, 223–253.

Cloern, J. E. & Dufford, R. (2005). Phytoplankton community ecology : principles applied in San Francisco Bay. *Marine Ecology Progress Series*, 285, 11–28.

Cloern, J. E. & Jassby, A. D. (2008). Complex seasonal patterns of primary producers at the land–sea interface. *Ecology Letters*, 11(12), 1294–1303.

Cloern, J. E. & Jassby, A. D. (2010). Patterns and Scales of Phytoplankton Variability in Estuarine–Coastal Ecosystems. *Estuaries and Coasts*, 33(2), 230–241.

Costil, K., Royer, J., Ropert, M., Soletchnik, P., & Mathieu, M. (2005). Spatio-temporal variations in biological performances and summer mortality of the Pacific oyster Crassostrea gigas in Normandy (France). *Helgoland Marine Research*, 59(4), 286–300. Publisher : Springer.

Cotonnec, G., Brunet, C., Sautour, B., & Thoumelin, G. (2001). Nutritive Value and Selection of Food Particles by Copepods During a Spring Bloom of Phaeocystis sp. in the English Channel, as Determined by Pigment and Fatty Acid Analyses. *Journal of Plankton Research*, 23(7), 693–703.

Cugier, P., Billen, G., Guillaud, J. F., Garnier, J., & Ménesguen, A. (2005). Modelling the eutrophication of the Seine Bight (France) under historical, present and future riverine nutrient loading. *Journal of Hydrology*, 304, 381–396.

Cugier, P. & Le Hir, P. (2002). Development of a 3D Hydrodynamic Model for Coastal Ecosystem Modelling. Application to the Plume of the Seine River (France). *Estuarine, Coastal and Shelf Science*, 55(5), 673–695.

Cugier, P., Struski, C., Blanchard, M., Mazurié, J., Pouvreau, S., Olivier, F., Trigui, J. R., & Thiébaut, E. (2010). Assessing the role of benthic filter feeders on phytoplankton production in a shellfish farming site : Mont Saint Michel Bay, France. *Journal of Marine Systems*, 82(1), 21–34.

Côté, B. & Platt, T. (1983). Day-to-day variations in the spring-summer photosynthetic parameters of coastal marine phytoplankton. *Limnology and Oceanography*, 28(2), 320–344. Publisher : Wiley Online Library.

Dauvin, J.-C. (2012). Are the eastern and western basins of the English Channel two separate ecosystems ? *Marine Pollution Bulletin*, 64(3), 463–471.

Dauvin, J.-C. (2019). Chapter 6 - The English Channel : La Manche. In C. Sheppard (Ed.), *World Seas : an Environmental Evaluation (Second Edition)* (pp. 153–188). Academic Press.

Dauvin, J.-C., Desroy, N., Denis, L., & Ruellet, T. (2008). Does the Phaeocystis bloom affect the diel migration of the suprabenthos community ? *Marine pollution bulletin*, 56(1), 77–87. Publisher : Elsevier.

David, V., Ryckaert, M., Karpytchev, M., Bacher, C., Arnaudeau, V., Vidal, N., Maurer, D., & Niquil, N. (2012). Spatial and long-term changes in the functional and structural phytoplankton communities along the French Atlantic coast. *Estuarine, Coastal and Shelf Science*, 108, 37–51.

Davidson, K., Gowen, R. J., Tett, P., Bresnan, E., Harrison, P. J., McKinney, A., Milligan, S., Mills, D. K., Silke, J., & Crooks, A.-M. (2012). Harmful algal blooms : How strong is the evidence that nutrient ratios and forms influence their occurrence ? *Estuarine, Coastal and Shelf Science*, 115, 399–413.

De Caceres, M., Font, X., & Olivia, F. (2010). The management of vegetation classifications with fuzzy clustering. Journal of Vegetation Science.

De Cáceres, M., Coll, L., Legendre, P., Allen, R. B., Wiser, S. K., Fortin, M.-J., Condit, R., & Hubbell, S. (2019). Trajectory analysis in community ecology. *Ecological Monographs*, 89(2).

de Raús Maúre, E., Terauchi, G., Ishizaka, J., Clinton, N., & DeWitt, M. (2021). Globally consistent assessment of coastal eutrophication. *Nature Communications*, 12(1), 6142. Number : 1 Publisher : Nature Publishing Group.

De Senerpont Domis, L. N., Van de Waal, D. B., Helmsing, N. R., Van Donk, E., & Mooij, W. M. (2014). Community stoichiometry in a changing world : combined effects of warming and eutrophication on phytoplankton dynamics. *Ecology*, 95(6), 1485–1495. Publisher : John Wiley & Sons, Ltd.

Dedman, C. J., Christie-Oleza, J. A., Fernández-Juárez, V., & Echeveste, P. (2022). Cell size matters : Nano- and micro-plastics preferentially drive declines of large marine phytoplankton due to co-aggregation. *Journal of Hazardous Materials*, 424, 127488.

Delavenne, J., Marchal, P., & Vaz, S. (2013). Defining a pelagic typology of the eastern English Channel. *Continental Shelf Research*, 52, 87–96.

D'Elbée, J. (2016). *Memento de planctonologie marine*. Editions Quae.

Delegrange, A., Lefebvre, A., Gohin, F., Courcot, L., & Vincent, D. (2018). Pseudo-nitzschia sp. diversity and seasonality in the southern North Sea, domoic acid levels and associated phytoplankton communities. *Estuarine, Coastal and Shelf Science*, 214, 194–206.

Desmit, X., Thieu, V., Billen, G., Campuzano, F., Dulière, V., Garnier, J., Lassaletta, L., Ménesguen, A., Neves, R., Pinto, L., Silvestre, M., Sobrinho, J. L., & Lacroix, G. (2018). Reducing marine eutrophication may require a paradigmatic change. *Science of The Total Environment*, 635, 1444–1466.

Dijkman, N. A. & Kromkamp, J. C. (2006). Phospholipid-derived fatty acids as chemotaxonomic markers for phytoplankton : application for inferring phytoplankton composition. *Marine Ecology Progress Series*, 324, 113–125.

Dijksterhuis, G. B. & Gower, J. C. (1991). The interpretation of generalized procrustes analysis and allied methods. *Food Quality and Preference*, 3(2), 67–87. Publisher : Elsevier.

Dolédec, S., Chessel, D., & Gimaret-Carpentier, C. (2000). Niche separation in community analysis : a new method. *Ecology*, 81(10), 2914–2927. Publisher : Wiley Online Library.

Domingues, R. B., Barbosa, A., & Galvão, H. (2008). Constraints on the use of phytoplankton as a biological quality element within the Water Framework Directive in Portuguese waters. *Marine Pollution Bulletin*, 56(8), 1389–1395.

Domingues, R. B., Guerra, C. C., Barbosa, A. B., Brotas, V., & Galvão, H. M. (2014). Effects of ultraviolet radiation and CO2 increase on winter phytoplankton assemblages in a temperate coastal lagoon. *Journal of Plankton Research*, 36(3), 672–684.

Dorrell, R. G. & Howe, C. J. (2015). Integration of plastids with their hosts : Lessons learned from dinoflagellates. *PNAS*.

Dortch, Q., Robichaux, R., Pool, Milsted, D., Mire, G., Rabalais, N., Soniat, T., Fryxell, G., Turner, R., & Parsons, M. (1997). Abundance and vertical flux of Pseudo-nitzschia in the northern Gulf of Mexico. *Marine Ecology Progress Series*, 146, 249–264.

Doucette, G. J., King, K. L., Thessen, A. E., & Dortch, Q. (2008). The effect of salinity on domoic acid production by the diatom Pseudo-nitzschia multiseries. *Nova Hedwigia*, 133(31), 1439–0485.

Dray, S., Dufour, A. B., & Chessel, D. (2007). The ade4 package-II : Two-table and K-table methods. *R news*, 7(2), 47–52.

Dubinsky, Z. & Stambler, N. (2009). Photoacclimation processes in phytoplankton : Mechanisms, consequences, and applications. *Aquatic Microbial Ecology*, 56(2-3), 163–176. Number : 2-3.

Dubois, A. (2012). *Caractéristique et état écologique Manche - Mer du Nord. Etat physique et chimique : Caractéristiques physiques - débits fluviaux.* Technical report.

Dubois, F., Bénard, M., Jean-Jacques, B., Schapman, D., Roberge, H., Lebon, A., Goux, D., Monterroso, B., Elie, N., Komuro, H., Bazille, C., Levallet, J., Bergot, E., Levallet, G., & Galas, L. (2020). Investigating Tunneling Nanotubes in Cancer Cells : Guidelines for Structural and Functional Studies through Cell Imaging. *BioMed Research International*, 2020, e2701345. Publisher : Hindawi.

Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., & Ward, B. A. (2020). Dimensions of marine phytoplankton diversity. *Biogeosciences*, 17(3), 609–634. Publisher : Copernicus GmbH.

Dutkiewicz, S., Morris, J. J., Follows, M. J., Scott, J., Levitan, O., Dyhrman, S. T., & Berman-Frank, I. (2015). Impact of ocean acidification on the structure of future phytoplankton communities. *Nature Climate Change*, 5(11), 1002–1006.

Décamps, H. (2007). Les systèmes écologiques face au changement climatique. *Responsabilité & Environnement*, (47), 43–48.

Edwards, K. F., Litchman, E., & Klausmeier, C. A. (2013). Functional traits explain phytoplankton community structure and seasonal dynamics in a marine ecosystem. *Ecology Letters*, 16(1), 56–63. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/ele.12012.

Edwards, K. F., Litchman, E., & Klausmeier, C. A. (2016). Functional traits explain phytoplankton responses to environmental gradients across lakes of the United States. Publisher : Wiley.

Edwards, K. F., Thomas, M. K., Klausmeier, C. A., & Litchman, E. (2012). Allometric scaling and taxonomic variation in nutrient utilization traits and maximum growth rate of phytoplankton. *Limnology and Oceanography*, 57(2), 554–566. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2012.57.2.0554.

EFSA (2009). Marine biotoxins in shellfish – Summary on regulated marine biotoxins. *European Food Safety Authority Journal*, 7(8), 1306.

EFSA Panel on Animal Health and Welfare (AHAW) (2015). Oyster mortality. *EFSA Journal*, 13(6), 4122. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.2903/j.efsa.2015.4122.

EFSA Panel on Contaminants in the Food Chain (CONTAM), ., Schrenk, D., Bignami, M., Bodin, L., del Mazo, J., Grasl-Kraupp, B., Hogstrand, C., Chipman,

K. J., Leblanc, J.-C., Nebbia, C. S., Nielsen, E., Ntzani, E., Petersen, A., Sand, S., Schwerdtle, T., Vleminckx, C., Wallace, H., Martinez, A. G., Gerssen, A., Tubaro, A., Cascio, C., Abrahantes, J. C., Steinkellner, H., & Hoogenboom, L. R. (2021). Evaluation of the shucking of certain species of scallops contaminated with domoic acid with a view to the production of edible parts meeting the safety requirements foreseen in the Union legislation. *EFSA Journal*, 19(8), e06809. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.2903/j.efsa.2021.6809.

Eilertsen, H. C., Sandberg, S., & Tøllefsen, H. (1995). Photoperiodic control of diatom spore growth : a theory to explain the onset of phytoplankton blooms. *Marine ecology progress series. Oldendorf*, 116(1), 303–307.

Einarsson, S. (1985). Selective determination of secondary amino acids using precolumn derivatization with 9-fluorenylmethylchloroformate and reversed-phase high-performance liquid chromatography. *Journal of Chromatography A*, 348, 213–220. Publisher : Elsevier.

Elbrächter, M. (2003). Dinophyte reproduction : progress and conflicts. *Journal of Phycology*, 39(4), 629–632. Publisher : Wiley Online Library.

Falk-Petersen, S., Sargent, J. R., Henderson, J., Hegseth, E. N., Hop, H., & Okolodkov, Y. B. (1998). Lipids and fatty acids in ice algae and phytoplankton from the Marginal Ice Zone in the Barents Sea. *Polar Biology*, 20(1), 41–47.

FAO, . (2021). FAO Yearbook. Fishery and Aquaculture Statistics 2019/FAO annuaire. Statistiques des pêches et de l'aquaculture 2019/FAO anuario. Estadísticas de pesca y acuicultura 2019.

Feely, R. A., Sabine, C. L., Lee, K., Berelson, W., Kleypas, J., Fabry, V. J., & Millero, F. J. (2004). Impact of Anthropogenic CO2 on the CaCO3 System in the Oceans. *Science*, 305(5682), 362–366. Publisher : American Association for the Advancement of Science.

Felpeto, A. B., Roy, S., & Vasconcelos, V. M. (2018). Allelopathy prevents competitive exclusion and promotes phytoplankton biodiversity. *Oikos*, 127(1), 85–98. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/oik.04046.

Fensome, R., Taylor, F., Norris, G., Sarjeant, W., Wharton, D., & Williams, G. (1993). A classification of living and fossil dinoflagellates. *Micropaleontology*, 39(2), 192–526. Publisher : The Micropaleontology Project, Inc.

Fidalgo, J. P., Cid, A., Torres, E., Sukenik, A., & Herrero, C. (1998). Effects of nitrogen source and growth phase on proximate biochemical composition, lipid classes and fatty acid profile of the marine microalga Isochrysis galbana. *Aquaculture*, 166(1), 105–116.

Field, C. B., Behrenfeld, M. J., Randerson, J. T., & Falkowski, P. (1998). Primary production of the biosphere : integrating terrestrial and oceanic components. *science*, 281(5374), 237–240.

Finkel, Z. V., Beardall, J., Flynn, K. J., Quigg, A., Rees, T. A. V., & Raven, J. A. (2010). Phytoplankton in a changing world : cell size and elemental stoichiometry. *Journal of Plankton Research*, 32(1), 119–137.

Fleming, L. E., Broad, K., Clement, A., Dewailly, E., Elmir, S., Knap, A., Pomponi, S. A., Smith, S., Solo Gabriele, H., & Walsh, P. (2006). Oceans and human health : Emerging public health risks in the marine environment. *Marine Pollution Bulletin*, 53(10), 545–560.

Fraisse, S., Bormans, M., & Lagadeuc, Y. (2015). Turbulence effects on phytoplankton morphofunctional traits selection. *Limnology and Oceanography*, 60(3), 872–884. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.10066.

Friebele, E. S., Correll, D. L., & Faust, M. A. (1978). Relationship between phytoplankton cell size and the rate of orthophosphate uptake : in situ observations of an estuarine population. *Marine Biology*, 45(1), 39–52. Publisher : Springer.

Frölicher, T. L., Fischer, E. M., & Gruber, N. (2018). Marine heatwaves under global warming. *Nature*, 560(7718), 360–364.

Frölicher, T. L. & Laufkötter, C. (2018). Emerging risks from marine heat waves. *Nature Communications*, 9(1).

Füssy, Z. & Oborník, M. (2018). Complex Endosymbioses I : From Primary to Complex Plastids, Multiple Independent Events. In E. Maréchal (Ed.), *Plastids :*

Methods and Protocols, Methods in Molecular Biology (pp. 17–35). New York, NY : Springer US.

Galili, T. (2015). dendextend : an R package for visualizing, adjusting and comparing trees of hierarchical clustering. *Bioinformatics*, 31(22), 3718–3720. Publisher : Oxford University Press.

Gallardi, D. (2014). Effects of Bivalve Aquaculture on the Environment and Their Possible Mitigation : A Review. *Fisheries and Aquaculture Journal*, 05(03).

Galloway, A. W. E. & Winder, M. (2015). Partitioning the Relative Importance of Phylogeny and Environmental Conditions on Phytoplankton Fatty Acids. *PLOS ONE*, 10(6), e0130053. Publisher : Public Library of Science.

Gardes, T., Debret, M., Copard, Y., Coynel, A., Deloffre, J., Fournier, M., Revillon, S., Nizou, J., Develle, A.-L., Sabatier, P., Marcotte, S., Patault, E., Faivre, Q., & Portet-Koltalo, F. (2020). Flux estimation, temporal trends and source determination of trace metal contamination in a major tributary of the Seine estuary, France. *Science of The Total Environment*, 724, 138249.

Garnier, J., Riou, P., Le Gendre, R., Ramarson, A., Billen, G., Cugier, P., Schapira, M., Théry, S., Thieu, V., & Ménesguen, A. (2019). Managing the Agri-Food System of Watersheds to Combat Coastal Eutrophication : A Land-to-Sea Modelling Approach to the French Coastal English Channel. *Geosciences*, 9(10), 441. Number : 10 Publisher : Multidisciplinary Digital Publishing Institute.

Garzon, J. L. & Ferreira, C. M. (2016). Storm surge modeling in large estuaries : sensitivity analyses to parameters and physical processes in the Chesapeake Bay. *Journal of Marine Science and Engineering*, 4(3), 45. Publisher : Multidisciplinary Digital Publishing Institute.

Gemmell, B. J., Oh, G., Buskey, E. J., & Villareal, T. A. (2016). Dynamic sinking behaviour in marine phytoplankton : rapid changes in buoyancy may aid in nutrient uptake. *Proceedings of the Royal Society B : Biological Sciences*, 283(1840), 20161126. Publisher : Royal Society.

Genty, B., Briantais, J.-M., & Baker, N. R. (1989). The relationship between the quantum yield of photosynthetic electron transport and quenching of chlorophyll fluorescence. *Biochimica et Biophysica Acta (BBA) - General Subjects*, 990(1), 87–92.

Gessner, B. D. & Middaugh, J. P. (1995). Paralytic Shellfish Poisoning in Alaska : A 20-Year Retrospective Analysis. *American Journal of Epidemiology*, 141(8), 766–770.

Gladyshev, M. I. & Gubelit, Y. I. (2019). Green Tides : New Consequences of the Eutrophication of Natural Waters (Invited Review). *Contemporary Problems of Ecology*, 12(2), 109–125.

Glibert, P. M. (2016). Margalef revisited : A new phytoplankton mandala incorporating twelve dimensions, including nutritional physiology. *Harmful Algae*, 55, 25–30.

Glibert, P. M., Al-Azri, A., Icarus Allen, J., Bouwman, A. F., Beusen, A. H. W., Burford, M. A., Harrison, P. J., & Zhou, M. (2018). Key Questions and Recent Research Advances on Harmful Algal Blooms in Relation to Nutrients and Eutrophication. In P. M. Glibert, E. Berdalet, M. A. Burford, G. C. Pitcher, & M. Zhou (Eds.), *Global Ecology and Oceanography of Harmful Algal Blooms*, Ecological Studies (pp. 229–259). Cham : Springer International Publishing.

Gobler, C. J. (2020). Climate Change and Harmful Algal Blooms : Insights and perspective. *Harmful Algae*, 91, 101731.

Gohin, F., Bryère, P., & Griffiths, J. W. (2015). The exceptional surface turbidity of the North-West European shelf seas during the stormy 2013–2014 winter : Consequences for the initiation of the phytoplankton blooms ? *Journal of Marine Systems*, 148, 70–85.

Gohin, F., Van der Zande, D., Tilstone, G., Eleveld, M. A., Lefebvre, A., Andrieux-Loyer, F., Blauw, A. N., Bryère, P., Devreker, D., Garnesson, P., Hernández Fariñas, T., Lamaury, Y., Lampert, L., Lavigne, H., Menet-Nedelec, F., Pardo, S., & Saulquin, B. (2019). Twenty years of satellite and in situ observations of surface chlorophyll-a from the northern Bay of Biscay to the eastern English Channel. Is the water quality improving ? *Remote Sensing of Environment*, 233, 111343.

Gomes, V. H. F., Vieira, I. C. G., Salomão, R. P., & ter Steege, H. (2019). Amazonian tree species threatened by deforestation and climate change. *Nature Climate Change*, 9(7), 547–553. Number : 7 Publisher : Nature Publishing Group.

Govender, T., Ramanna, L., Rawat, I., & Bux, F. (2012). BODIPY staining, an alternative to the Nile Red fluorescence method for the evaluation of intracellular lipids in microalgae. *Bioresource Technology*, 114, 507–511.

Gower, J. C. (1975). Generalized procrustes analysis. *Psychometrika*, 40(1), 33–51. Publisher : Springer.

Graco-Roza, C., Soininen, J., Corrêa, G., Pacheco, F. S., Miranda, M., Domingos, P., & Marinho, M. M. (2021). Functional rather than taxonomic diversity reveals changes in the phytoplankton community of a large dammed river. *Ecological Indicators*, 121, 107048.

Grangeré, K., Lefebvre, S., Bacher, C., Cugier, P., & Ménesguen, A. (2010). Modelling the spatial heterogeneity of ecological processes in an intertidal estuarine bay : dynamic interactions between bivalves and phytoplankton. *Marine Ecology Progress Series*, 415, 141–158.

Grant, J. & Pastres, R. (2019). Ecosystem Models of Bivalve Aquaculture : Implications for Supporting Goods and Services. In A. C. Smaal, J. G. Ferreira, J. Grant, J. K. Petersen, & Strand (Eds.), *Goods and Services of Marine Bivalves* (pp. 507–525). Cham : Springer International Publishing.

Granéli, E. & Flynn, K. (2006). Chemical and Physical Factors Influencing Toxin Content. *Ecology of Harmful Algae*, (pp. 229–241). Publisher : Springer.

Grattan, L. M., Holobaugh, S., & Morris, J. G. (2016). Harmful algal blooms and public health. *Harmful Algae*, 57, 2–8.

Greenspan, P. & Fowler, S. D. (1985). Spectrofluorometric studies of the lipid probe, nile red. *Journal of lipid research*, 26(7), 781–789. Publisher : Elsevier.

Greve, W., Reiners, F., Nast, J., & Hoffmann, S. (2004). Helgoland Roads meso- and macrozooplankton time-series 1974 to 2004 : lessons from 30 years of single spot, high frequency sampling at the only off-shore island of the North Sea. *Helgoland Marine Research*, 58(4), 274–288. Publisher : Springer.

Griffith, A. W. & Gobler, C. J. (2020). Harmful algal blooms : A climate change co-stressor in marine and freshwater ecosystems. *Harmful Algae*, 91, 101590.

Grinnell, J. (1917). The Niche-Relationships of the California Thrasher. *The Auk*, 34(4), 427–433. Publisher : American Ornithological Society.

Grizzetti, B., Vigiak, O., Udias, A., Aloe, A., Zanni, M., Bouraoui, F., Pistocchi, A., Dorati, C., Friedland, R., De Roo, A., Benitez Sanz, C., Leip, A., & Bielza, M. (2021). How EU policies could reduce nutrient pollution in European inland and coastal waters. *Global Environmental Change*, 69, 102281.

Groß, E., Boersma, M., & Meunier, C. L. (2021). Environmental impacts on single-cell variation within a ubiquitous diatom : The role of growth rate. *PLOS ONE*, 16(5), e0251213. Publisher : Public Library of Science.

Gruau, G., Legeas, M., Riou, C., Gallacier, E., Martineau, F., & Hénin, O. (2005). The oxygen isotope composition of dissolved anthropogenic phosphates : a new tool for eutrophication research ? *Water Research*, 39(1), 232–238.

Gruber, N. (2011). Warming up, turning sour, losing breath : ocean biogeochemistry under global change. *Philosophical Transaction of The Royal Society*, (369), 1980–1996.

Guallar, C., Chapelle, A., & Bacher, C. (2021). Realised niche and suitability index highlight spatial and temporal distribution of toxic phytoplankton species. *Marine Ecology Progress Series*, 662, 15–34.

Guillen, J., Asche, F., Carvalho, N., Fernández Polanco, J. M., Llorente, I., Nielsen, R., Nielsen, M., & Villasante, S. (2019). Aquaculture subsidies in the European Union : Evolution, impact and future potential for growth. *Marine Policy*, 104, 19–28.

Guilloux, L., Rigaut-Jalabert, F., Jouenne, F., Ristori, S., Viprey, M., Not, F., Vaulot, D., & Simon, N. (2013). An annotated checklist of Marine Phytoplankton taxa at the SOMLIT-Astan time series off Roscoff (Western English Channel, France) : data collected from 2000 to 2010. *Cah. Biol. Mar*, 54, 247–256. Publisher : Citeseer.

Guiry, M. & Guiry, G. (2021). AlgaeBase. World-wide electronic publication, National University of Ireland, Galway.

Gómez, F. (2007). On the consortium of the tintinnid Eutintinnus and the diatom Chaetoceros in the Pacific Ocean. *Marine Biology*, 151(5), 1899–1906.

Hall, A. J. & Frame, E. (2010). Evidence of domoic acid exposure in harbour seals from Scotland : A potential factor in the decline in abundance ? *Harmful Algae*, 9(5), 489–493.

Hallegraeff, G. M. (2010). Ocean climate change, phytoplankton community responses, and harmful algal blooms : a formidable predictive challenge1. *Journal of phycology*, 46(2), 220–235.

Halpern, B. S., Selkoe, K. A., Micheli, F., & Kappel, C. V. (2007). Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats. *Conservation Biology*, 21(5), 1301–1315. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1523-1739.2007.00752.x.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., Bruno, J. F., Casey, K. S., Ebert, C., Fox, H. E., Fujita, R., Heinemann, D., Lenihan, H. S., Madin, E. M. P., Perry, M. T., Selig, E. R., Spalding, M., Steneck, R., & Watson, R. (2008). A Global Map of Human Impact on Marine Ecosystems. *Science*, 319(5865), 948–952. Publisher : American Association for the Advancement of Science.

Hardin, G. (1960). The Competitive Exclusion Principle : An idea that took a century to be born has implications in ecology, economics, and genetics. *science*, 131(3409), 1292–1297. Publisher : American Association for the Advancement of Science.

Harris, G. (1986). Phytoplankton ecology-Structure, function and fluctuation.

Hasle, G. R. & Syvertsen, E. E. (1997). Marine Diatoms. In *Identifying Marine Phytoplankton* (pp. 5–385). Academic Press - Elsevier, tomas carmelo r. edition.

Hattenrath-Lehmann, T. K., Marcoval, M. A., Berry, D. L., Fire, S., Wang, Z., Morton, S. L., & Gobler, C. J. (2013). The emergence of Dinophysis acuminata blooms and DSP toxins in shellfish in New York waters. *Harmful Algae*, 26, 33–44. Publisher : Elsevier.

He, Q. & Silliman, B. R. (2019). Climate Change, Human Impacts, and Coastal Ecosystems in the Anthropocene. *Current Biology*, 29(19), R1021–R1035.

Heisler, J., Glibert, P. M., Burkholder, J. M., Anderson, D. M., Cochlan, W., Dennison, W. C., Dortch, Q., Gobler, C. J., Heil, C. A., Humphries, E., Lewitus, A., Magnien, R., Marshall, H. G., Sellner, K., Stockwell, D. A., Stoecker, D. K., & Suddleson, M. (2008). Eutrophication and harmful algal blooms : A scientific consensus. *Harmful Algae*, 8(1), 3–13.

Hellessey, N., Johnson, R., Ericson, J. A., Nichols, P. D., Kawaguchi, S., Nicol, S., Hoem, N., & Virtue, P. (2020). Antarctic Krill Lipid and Fatty acid Content Variability is Associated to Satellite Derived Chlorophyll a and Sea Surface Temperatures. *Scientific Reports*, 10(1), 6060. Bandiera_abtest : a Cc_license_type : cc_by Cg_type : Nature Research Journals Number : 1 Primary_atype : Research Publisher : Nature Publishing Group Subject_term : Environmental monitoring ;Lipidomics ;Marine biology ;Marine chemistry Subject_term_id : environmental-monitoring ;lipidomics ;marine-biology ;marine-chemistry.

Henson, S. A., Cael, B. B., Allen, S. R., & Dutkiewicz, S. (2021). Future phytoplankton diversity in a changing climate. *Nature Communications*, 12(1), 5372. Bandiera_abtest : a Cc_license_type : cc_by Cg_type : Nature Research Journals Number : 1 Primary_atype : Research Publisher : Nature Publishing Group Subject_term : Biooceanography ;Marine biology Subject_term_id : biooceanography ;marine-biology.

Henson, S. A., Cole, H. S., Hopkins, J., Martin, A. P., & Yool, A. (2018). Detection of climate change-driven trends in phytoplankton phenology. *Global change biology*, 24(1), e101–e111.

Hernandez-Farinas, T., Soudant, D., Barillé, L., Belin, C., Lefebvre, A., & Bacher, C. (2013). Temporal changes in the phytoplankton community along the French coast of the eastern English Channel and the southern Bight of the North Sea. *ICES Journal of marine science*, 71(4), 821–833.

Hernández Fariñas, T., Ribeiro, L., Soudant, D., Belin, C., Bacher, C., Lampert, L., & Barillé, L. (2017). Contribution of benthic microalgae to the temporal variation in phytoplankton assemblages in a macrotidal system. *Journal of Phycology - Wiley Online Library*, 53, 1020–1034.

Hernández-Urcera, J., Rial, P., García-Portela, M., Lourés, P., Kilcoyne, J., Rodríguez, F., Fernández-Villamarín, A., & Reguera, B. (2018). Notes on the Cultivation of Two Mixotrophic Dinophysis Species and Their Ciliate Prey Mesodinium rubrum. *Toxins*, 10(12), 505. Number : 12 Publisher : Multidisciplinary Digital Publishing Institute.

Hinder, S. L., Hays, G. C., Edwards, M., Roberts, E. C., Walne, A. W., & Gravenor, M. B. (2012). Changes in marine dinoflagellate and diatom abundance under climate change. *Nature Climate Change*, 2(4), 271–275. Publisher : Nature Publishing Group.

Hofmann, M., Worm, B., Rahmstorf, S., & Schellnhuber, H. J. (2011). Declining ocean chlorophyll under unabated anthropogenic CO 2 emissions. *Environmental Research Letters*, 6(3), 034035. Publisher : IOP Publishing.

Hofmann, P., Chatzinotas, A., Harpole, W. S., & Dunker, S. (2019). Temperature and stoichiometric dependence of phytoplankton traits. *Ecology*, 100(12), e02875. _eprint : https ://esajournals.onlinelibrary.wiley.com/doi/pdf/10.1002/ecy.2875.

Hoppenrath, M., Elbrächter, M., & Drebes, G. (2009). Marine phytoplankton. Publisher : Schweizerbart'sche Verlagsbuchhandlung.

Hughes, T. P., Kerry, J. T., Álvarez Noriega, M., Álvarez Romero, J. G., Anderson, K. D., Baird, A. H., Babcock, R. C., Beger, M., Bellwood, D. R., Berkelmans, R., Bridge, T. C., Butler, I. R., Byrne, M., Cantin, N. E., Comeau, S., Connolly, S. R., Cumming, G. S., Dalton, S. J., Diaz-Pulido, G., Eakin, C. M., Figueira, W. F., Gilmour, J. P., Harrison, H. B., Heron, S. F., Hoey, A. S., Hobbs, J.-P. A., Hoogenboom, M. O., Kennedy, E. V., Kuo, C.-y., Lough, J. M., Lowe, R. J., Liu, G., McCulloch, M. T., Malcolm, H. A., McWilliam, M. J., Pandolfi, J. M., Pears, R. J., Pratchett, M. S., Schoepf, V., Simpson, T., Skirving, W. J., Sommer, B., Torda, G., Wachenfeld, D. R., Willis, B. L., & Wilson, S. K. (2017). Global warming and recurrent mass bleaching of corals. *Nature*, 543(7645), 373–377. Number : 7645 Publisher : Nature Publishing Group.

Huot, Y., Babin, M., Bruyant, F., Grob, C., Twardowski, M. S., & Claustre, H. (2007). Does chlorophyll a provide the best index of phytoplankton biomass for primary productivity studies ? *Biogeosciences Discussions*, 4(2), 707.

Hurd, C. L., Lenton, A., Tilbrook, B., & Boyd, P. W. (2018). Current understanding and challenges for oceans in a higher-CO2 world. *Nature Climate Change*, 8(8), 686–694. Number : 8 Publisher : Nature Publishing Group.

Hurrell, J. (2020). NAO Index Data, provided by the Climate Analysis Section, NCAR, Boulder, USA.

Husson, B., Hernández-Fariñas, T., Le Gendre, R., Schapira, M., & Chapelle, A. (2016). Two decades of Pseudo-nitzschia spp. blooms and king scallop (Pecten maximus) contamination by domoic acid along the French Atlantic and English Channel coasts : Seasonal dynamics, spatial heterogeneity and interannual variability. *Harmful Algae*, 51, 26–39.

Hutchinson, G. E. (1957). Population studies-animal ecology and demography-concluding remarks. In *Cold Spring Harbor symposia on quantitative biology*, volume 22 (pp. 415–427). : COLD SPRING HARBOR LAB PRESS, PUBLICATIONS DEPT 1 BUNGTOWN RD, COLD SPRING ….

Hutchinson, G. E. (1961). The Paradox of the Plankton. *The American Naturalist*, 95(882), 137–145.

Iriarte, A. & Purdie, D. A. (2004). Factors controlling the timing of major spring bloom events in an UK south coast estuary. *Estuarine, Coastal and Shelf Science*, 61(4), 679–690.

Irwin, A. J., Nelles, A. M., & Finkel, Z. V. (2012). Phytoplankton niches estimated from field data. *Limnology and Oceanography*, 57(3), 787–797. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2012.57.3.0787.

Jackson, S. T. & Overpeck, J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology*, 26(S4), 194–220. Publisher : Cambridge University Press.

James, K. J., Carey, B., O'halloran, J., van Pelt, F. N. A. M., & Škrabáková, Z. (2010). Shellfish toxicity : human health implications of marine algal toxins. *Epidemiology & Infection*, 138(7), 927–940. Publisher : Cambridge University Press.

Johansson, L., Jalkanen, J.-P., Kalli, J., & Kukkonen, J. (2013). The evolution of shipping emissions and the costs of regulation changes in the northern EU area. *Atmospheric Chemistry and Physics*, 13(22), 11375–11389. Publisher : Copernicus GmbH.

Jouenne, F., Lefebvre, S., Véron, B., & Lagadeuc, Y. (2007). Phytoplankton community structure and primary production in small intertidal estuarine-bay ecosystem (eastern English Channel, France). *Marine Biology*, 151(3), 805–825.

Jónasdóttir, S. H. (2019). Fatty Acid Profiles and Production in Marine Phytoplankton. *Marine Drugs*, 17(3), E151.

Karasiewicz, S., Breton, E., Lefebvre, A., Fariñas, T. H., & Lefebvre, S. (2018). Realized niche analysis of phytoplankton communities involving HAB : Phaeocystis spp. as a case study. *Harmful algae*, 72, 1–13. Publisher : Elsevier.

Karasiewicz, S., Dolédec, S., & Lefebvre, S. (2017). Within outlying mean indexes : refining the OMI analysis for the realized niche decomposition. *PeerJ*, 5, e3364. Publisher : PeerJ Inc.

Kassambara, A. & Mundt, F. (2017). Package 'factoextra'. *Extract and visualize the results of multivariate data analyses*, 76.

Keeling, P. J. & Burki, F. (2019). Progress towards the Tree of Eukaryotes. *Current Biology*, 29(16), R808–R817.

Key, T., McCarthy, A., Campbell, D. A., Six, C., Roy, S., & Finkel, Z. V. (2010). Cell size trade-offs govern light exploitation strategies in marine phytoplankton. *Environmental Microbiology*, 12(1), 95–104. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1462-2920.2009.02046.x.

Kim, M., Nam, S. W., Shin, W., Coats, D. W., & Park, M. G. (2012). Dinophysis Caudata (dinophyceae) Sequesters and Retains Plastids from the

Mixotrophic Ciliate Prey Mesodinium Rubrum1. *Journal of Phycology*, 48(3), 569–579. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1529-8817.2012.01150.x.

Kimor, B. (1992). The impact of eutrophication on phytoplankton composition in coastal marine ecosystems. *Marine Coastal Eutrophication*, (pp. 871–878).

Kirkpatrick, B., Fleming, L. E., Squicciarini, D., Backer, L. C., Clark, R., Abraham, W., Benson, J., Cheng, Y. S., Johnson, D., Pierce, R., Zaias, J., Bossart, G. D., & Baden, D. G. (2004). Literature Review of Florida Red Tide : Implications for Human Health Effects. *Harmful algae*, 3(2), 99–115.

Klein, C., Claquin, P., Bouchart, V., Le Roy, B., & Véron, B. (2010). Dynamics of Pseudo-nitzschia spp. and domoic acid production in a macrotidal ecosystem of the Eastern English Channel (Normandy, France). *Harmful Algae*, 9(2), 218–226.

Kouakou, C. R. C. & Poder, T. G. (2019). Economic impact of harmful algal blooms on human health : a systematic review. *Journal of Water and Health*, 17(4), 499–516.

Kraberg, A., Kieb, U., Peters, S., & Wiltshire, K. H. (2019). An updated phytoplankton check-list for the Helgoland Roads time series station with eleven new records of diatoms and dinoflagellates. *Helgoland Marine Research*, 73(1), 9.

Kruk, C., Devercelli, M., & Huszar, V. L. (2021). Reynolds Functional Groups : a trait-based pathway from patterns to predictions. *Hydrobiologia*, 848(1), 113–129.

Kruk, C. & Segura, A. M. (2012). The habitat template of phytoplankton morphology-based functional groups. *Hydrobiologia*, 698(1), 191–202.

Kumar, K., Kumar, S., & Nair, A. (2009). Risk assessment of the amnesic shellfish poison, domoic acid, on animals and humans. *Journal of environmental biology / Academy of Environmental Biology, India*, 30, 319–25.

Laliberté, E., Legendre, P., Shipley, B., & Laliberté, M. E. (2014). Package 'FD'. *Measuring functional diversity from multiple traits, and other tools for functional ecology.*

Lamont, T., Barlow, R. G., & Brewin, R. J. W. (2019). Long-Term Trends in Phytoplankton Chlorophyll a and Size Structure in the Benguela Upwelling System. *Journal of Geophysical Research : Oceans*, 124(2), 1170–1195. _eprint : https ://agupubs.onlinelibrary.wiley.com/doi/pdf/10.1029/2018JC014334.

Lamy, D., Artigas, L. F., Jauzein, C., Lizon, F., & Cornille, V. (2006). Coastal bacterial viability and production in the eastern English Channel : a case study during a Phaeocystis globosa bloom. *Journal of Sea Research*, 56(3), 227–238. Publisher : Elsevier.

Landschützer, P., Gruber, N., Bakker, D. C. E., Stemmler, I., & Six, K. D. (2018). Strengthening seasonal marine CO 2 variations due to increasing atmospheric CO 2. *Nature Climate Change*, 8(2), 146.

Laplace-Treyture, C., Derot, J., Prévost, E., Le Mat, A., & Jamoneau, A. (2021). Phytoplankton morpho-functional trait dataset from French water-bodies. *Scientific Data*, 8(1), 40. Number : 1 Publisher : Nature Publishing Group.

Larkum, A. W. D. & Vesk, M. (2003). Algal Plastids : Their Fine Structure and Properties. In A. W. D. Larkum, S. E. Douglas, & J. A. Raven (Eds.), *Photosynthesis in Algae* (pp. 11–28). Dordrecht : Springer Netherlands.

Lassus, P., Chomérat, N., Hess, P., & Nézan, E. (2016). *Toxic and harmful microalgae of the world ocean*. UNESCO.

Lassus, P., Maggi, P., Proniewski, F., Truquet, P., & Nizard, G. (1991). Distribution verticale de Dinophysis spp au cours d'un cycle de 48 heures dans le port d'Antifer (Normandie).

Leblanc, K., Quéguiner, B., Diaz, F., Cornet, V., Michel-Rodriguez, M., Durrieu de Madron, X., Bowler, C., Malviya, S., Thyssen, M., Grégori, G., Rembauville, M., Grosso, O., Poulain, J., de Vargas, C., Pujo-Pay, M., & Conan, P. (2018). Nanoplanktonic diatoms are globally overlooked but play a role in spring blooms and carbon export. *Nature Communications*, 9(1), 953. Number : 1 Publisher : Nature Publishing Group.

Lefebvre, A. & Dezécache, C. (2020). Trajectories of Changes in Phytoplankton Biomass, Phaeocystis globosa and Diatom (incl. Pseudo-nitzschia sp.) Abundances Related to Nutrient Pressures in the Eastern English Channel, Southern North Sea. *Journal of Marine Science and Engineering*, 8(6), 401. Number : 6 Publisher : Multidisciplinary Digital Publishing Institute.

Lefebvre, K. A., Frame, E. R., & Kendrick, P. S. (2012). Domoic acid and fish behavior : A review. *Harmful Algae*, 13, 126–130.

Lefran, A., Hernández-Fariñas, T., Gohin, F., & Claquin, P. (2021). Decadal trajectories of phytoplankton communities in contrasted estuarine systems in an epicontinental sea. *Estuarine, Coastal and Shelf Science*, 258, 107409.

Lefran, A., Siemering, B., Cusack, C., Clarke, D., Silke, J., & Salas, R. (2020). Pseudo-nitzschia biogeography combining Real-Time PCR analysis and oceanographic models to investigate 13 years trends of ASP toxicity, 2020. In Hess, Ph. (Ed) Proceedings of the 18th International Conference on Harmful Algae, Nantes, International Society for the Study of Harmful Algae. (pp. 214).

Legendre, L., Demers, S., Therriault, J.-C., & Boudreau, C.-A. (1985). Tidal variations in the photosynthesis of estuarine phytoplankton isolated in a tank. *Marine Biology*, 88(3), 301–309. Publisher : Springer.

Legendre, P. & Legendre, L. (2012). *Numerical ecology*. Elsevier.

Lelong, A., Hegaret, H., Soudant, P., & Bates, S. S. (2012). Pseudo-nitzschia (Bacillariophyceae) species, domoic acid and amnesic shellfish poisoning : revisiting previous paradigms. *Phycologia*, 51(2), 168–216. Publisher : Taylor & Francis.

Leterme, S. C., Edwards, M., Seuront, L., Attrill, M. J., Reid, P. C., & John, A. W. G. (2005). Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. *Limnology and Oceanography*, 50(4), 1244–1253.

Leterme, S. C., Le Lan, C., Hemraj, D. A., & Ellis, A. V. (2016). The impact of diatoms on the biofouling of seawater reverse osmosis membranes in a model cross-flow system. *Desalination*, 392, 8–13.

Lewis, K. & Allen, J. I. (2009). Validation of a hydrodynamic-ecosystem model simulation with time-series data collected in the western English Channel. *Journal of Marine Systems*, 77(3), 296–311.

Lindegren, M., Checkley, D. M., Ohman, M. D., Koslow, J. A., & Goericke, R. (2016). Resilience and stability of a pelagic marine ecosystem. *Proceedings of the Royal Society B : Biological Sciences*, 283(1822), 20151931. Publisher : Royal Society.

Litchman, E., de Tezanos Pinto, P., Klausmeier, C. A., Thomas, M. K., & Yoshiyama, K. (2010). Linking traits to species diversity and community structure in phytoplankton. In L. Naselli-Flores & G. Rossetti (Eds.), *Fifty years after the "Homage to Santa Rosalia" : Old and new paradigms on biodiversity in aquatic ecosystems*, Developments in Hydrobiology 213 (pp. 15–28). Dordrecht : Springer Netherlands.

Litchman, E., Edwards, K., Klausmeier, C., & Thomas, M. (2012). Phytoplankton niches, traits and eco-evolutionary responses to global environmental change. *Marine Ecology Progress Series*, 470, 235–248.

Litchman, E. & Klausmeier, C. A. (2008). Trait-based community ecology of phytoplankton. *Annual review of ecology, evolution, and systematics*, 39, 615–639.

Litchman, E., Klausmeier, C. A., Schofield, O. M., & Falkowski, P. G. (2007). The role of functional traits and trade-offs in structuring phytoplankton communities : scaling from cellular to ecosystem level. *Ecology letters*, 10(12), 1170–1181.

Liénart, C., Savoye, N., Bozec, Y., Breton, E., Conan, P., David, V., Feunteun, E., Grangeré, K., Kerhervé, P., Lebreton, B., Lefebvre, S., L'Helguen, S., Mousseau, L., Raimbault, P., Richard, P., Riera, P., Sauriau, P.-G., Schaal, G., Aubert, F., Aubin, S., Bichon, S., Boinet, C., Bourasseau, L., Bréret, M., Caparros, J., Cariou, T., Charlier, K., Claquin, P., Cornille, V., Corre, A.-M., Costes, L., Crispi, O., Crouvoisier, M., Czamanski, M., Del Amo, Y., Derriennic, H., Dindinaud, F., Durozier, M., Hanquiez, V., Nowaczyk, A., Devesa, J., Ferreira, S., Fornier, M., Garcia, F., Garcia, N., Geslin, S., Grossteffan, E., Gueux, A., Guillaudeau, J., Guillou, G., Joly, O., Lachaussée, N., Lafont, M., Lamoureux, J., Lecuyer, E., Lehodey, J.-P., Lemeille, D., Leroux, C., Macé, E., Maria, E., Pineau, P., Petit, F., Pujo-Pay, M., Rimelin-Maury, P., & Sultan, E. (2017). Dynamics of particulate organic matter composition in coastal systems : A spatio-temporal study at multi-systems scale. *Progress in Oceanography*, 156, 221–239.

Loewen, C. J. G., Vinebrooke, R. D., & Zurawell, R. W. (2021). Quantifying seasonal succession of phytoplankton trait-environment associations in human-altered landscapes. *Limnology and Oceanography*, 66(4), 1409–1423. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.11694.

Loir, M. (2004). *Guide des diatomées*. Delachaux et Niestlé.

Lomartire, S., Marques, J. C., & Gonçalves, A. M. M. (2021). The key role of zooplankton in ecosystem services : A perspective of interaction between zooplankton and fish recruitment. *Ecological Indicators*, 129, 107867.

Lopes, V. M., Rosa, R., & Costa, P. R. (2018). Presence and persistence of the amnesic shellfish poisoning toxin, domoic acid, in octopus and cuttlefish brains. *Marine Environmental Research*, 133, 45–48.

Louchart, A., Lizon, F., Lefebvre, A., Didry, M., Schmitt, F. G., & Artigas, L. F. (2020). Phytoplankton distribution from Western to Central English Channel, revealed by automated flow cytometry during the summer-fall transition. *Continental Shelf Research*, 195, 104056.

Luypaert, T., Hagan, J. G., McCarthy, M. L., & Poti, M. (2020). Status of Marine Biodiversity in the Anthropocene. In S. Jungblut, V. Liebich, & M. Bode-Dalby (Eds.), *YOUMARES 9 - The Oceans : Our Research, Our Future : Proceedings of the 2018 conference for YOUng MArine RESearcher in Oldenburg, Germany* (pp. 57–82). Cham : Springer International Publishing.

Lê, S., Josse, J., & Husson, F. (2008). FactoMineR : an R package for multivariate analysis. *Journal of statistical software*, 25, 1–18.

Lürling, M. (2021). Grazing resistance in phytoplankton. *Hydrobiologia*, 848(1), 237–249.

Mackey, K., Mioni, C., Ryan, J., & Paytan, A. (2012). Phosphorus Cycling in the Red Tide Incubator Region of Monterey Bay in Response to Upwelling. *Frontiers in Microbiology*, 3.

MacRae, R. A., Fensome, R. A., & Williams, G. L. (1996). Fossil dinoflagellate diversity, originations, and extinctions and their significance. *Canadian Journal of Botany*, 74(11), 1687–1694. Publisher : NRC Research Press.

Madariaga, I. d. & Joint, I. (1992). A comparative study of phytoplankton physiological indicators. *Journal of Experimental Marine Biology and Ecology*, 158(2), 149–165.

Maddock, L., Boalch, G. T., & Harbour, D. S. (1981). Populations of phytoplankton in the western English Channel between 1964 and 1974. *Journal of the Marine Biological Association of the United Kingdom*, 61(3), 565–583. Publisher : Cambridge University Press.

Maillard, F., Elie, N., Villain-Naud, N., Lepoittevin, M., Martinez, A.-S., & Lelong, C. (2021). Male triploid oysters of Crassostrea gigas exhibit defects in mitosis and meiosis during early spermatogenesis. *FEBS Open Bio*, n/a(n/a). _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/2211-5463.13356.

Maldonado, M. T., Hughes, M. P., Rue, E. L., & Wells, M. L. (2002). The effect of Fe and Cu on growth and domoic acid production by Pseudo-nitzschia multiseries and Pseudo-nitzschia australis. *Limnology and Oceanography*, 47(2), 515–526. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2002.47.2.0515.

Mallin, M. A., Paerl, H. W., Rudek, J., & Bates, P. W. (1993). Regulation of estuarine primary production by watershed rainfall and river flow. *Marine Ecology-Progress Series*, 93, 199–199. Publisher : INTER RESEARCH.

Mammola, S. & Cardoso, P. (2020). Functional diversity metrics using kernel density n-dimensional hypervolumes. *Methods in Ecology and Evolution*, 11(8), 986–995. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/2041-210X.13424.

Mandal, S., Smith, S. L., Priyadarshi, A., & Yamazaki, H. (2019). Micro-Scale Variability Impacts the Outcome of Competition Between Different Modeled Size Classes of Phytoplankton. *Frontiers in Marine Science*, 6.

Marañón, E. (2015). Cell Size as a Key Determinant of Phytoplankton Metabolism and Community Structure. *Annual Review of Marine Science*, 7(1), 241–264. _eprint : https ://doi.org/10.1146/annurev-marine-010814-015955.

Margalef, R. (1978). Life-form of phytoplankton as survival alternatives in an unstable environment. *Oceanologica acta*, 1, 493–509.

Mari, X. & Rassoulzadegan, F. (2004). Role of TEP in the microbial food web structure. I. Grazing behavior of a bacterivorous pelagic ciliate. *Marine Ecology Progress Series*, 279, 13–22.

Martino, S., Gianella, F., & Davidson, K. (2020). An approach for evaluating the economic impacts of harmful algal blooms : The effects of blooms of toxic Dinophysis spp. on the productivity of Scottish shellfish farms. *Harmful Algae*, 99, 101912. Publisher : Elsevier.

María Trigueros, J. & Orive, E. (2001). Seasonal variations of diatoms and dinoflagellates in a shallow, temperate estuary, with emphasis on neritic assemblages. *Hydrobiologia*, 444(1), 119–133.

Masson-Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M. I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, , Yu, R., & Zhou, B., Eds. (2021). *Climate Change 2021 : The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press.

Maxwell, K. & Johnson, G. N. (2000). Chlorophyll fluorescence—a practical guide. *Journal of Experimental Botany*, 51(345), 659–668.

Mayali, X., Dyhrman, S., & Francis, C. (2018). *Metabolic Interactions Between Bacteria and Phytoplankton*, volume 9. Frontiers in Microbiology and Frontiers in Marine Science.

Mazzocchi, M. G., Dubroca, L., García-Comas, C., Di Capua, I., & d'Alcalà, M. R. (2012). Stability and resilience in coastal copepod assemblages : the case of the Mediterranean long-term ecological research at Station MC (LTER-MC). *Progress in Oceanography*, 97, 135–151. Publisher : Elsevier.

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21(4), 178–185.

McGrath, C. (2020). Highlight : The Colorful History of Plastids.

McLeod, A. I. (2011). *Kendall rank correlation and Mann-Kendall trend test. R package version 2.2.*

Mcnair, H., Hammond, C. N., & Menden-Deuer, S. (2021). Phytoplankton carbon and nitrogen biomass estimates are robust to volume measurement method and growth environment. *Journal of Plankton Research*, 43(2), 103–112. Publisher : Oxford University Press.

McQuatters-Gollop, A., Atkinson, A., Aubert, A., Bedford, J., Best, M., Bresnan, E., Cook, K., Devlin, M., Gowen, R., Johns, D. G., Machairopoulou, M., McKinney, A., Mellor, A., Ostle, C., Scherer, C., & Tett, P. (2019). Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy. *Ecological Indicators*, 101, 913–925.

McQuoid, M. R. & Godhe, A. (2004). Recruitment of coastal planktonic diatoms from benthic versus pelagic cells : Variations in bloom development and species composition. *Limnology and oceanography*, 49(4), 1123–1133. Publisher : Wiley Online Library.

Medlin, L. K. (2016). Evolution of the diatoms : major steps in their evolution and a review of the supporting molecular and morphological evidence. *Phycologia*, 55(1), 79–103. Publisher : Taylor & Francis.

Medlin, L. K. (2018). Mini review : Diatom species as seen through a molecular window. *Brazilian Journal of Botany*, 41(2), 457–469. Publisher : Springer.

Meier, K. J. S., Young, J. R., Kirsch, M., & Feist-Burkhardt, S. (2007). Evolution of different life-cycle strategies in oceanic calcareous dinoflagellates. *European Journal of Phycology*, 42(1), 81–89. Publisher : Taylor & Francis _eprint : https ://doi.org/10.1080/09670260600937833.

Melo-Merino, S. M., Reyes-Bonilla, H., & Lira-Noriega, A. (2020). Ecological niche models and species distribution models in marine environments : A literature review and spatial analysis of evidence. *Ecological Modelling*, 415, 108837.

Meyers, M. T., Cochlan, W. P., Carpenter, E. J., & Kimmerer, W. J. (2019). Effect of ocean acidification on the nutritional quality of marine phytoplankton for copepod reproduction. *PLOS ONE*, 14(5), e0217047. Publisher : Public Library of Science.

Mills, K., Pershing, A., Brown, C., Chen, Y., Chiang, F.-S., Holland, D., Lehuta, S., Nye, J., Sun, J., Thomas, A., & Wahle, R. (2013). Fisheries Management in a Changing Climate : Lessons From the 2012 Ocean Heat Wave in the Northwest Atlantic. *Oceanography*, 26(2).

Millward, G. E., Jha, A. N., Minier, C., Pope, N. D., & Langston, W. J. (2015). The English Channel and its catchments : Status and responses to contaminants. *Marine Pollution Bulletin*, 95(2), 523–528.

Mitchell, J. G., Yamazaki, H., Seuront, L., Wolk, F., & Li, H. (2008). Phytoplankton patch patterns : Seascape anatomy in a turbulent ocean. *Journal of Marine Systems*, 69(3), 247–253.

Miyazaki, T., Tainaka, K.-i., Togashi, T., Suzuki, T., & Yoshimura, J. (2006). Spatial coexistence of phytoplankton species in ecological timescale. *Population Ecology*, 48(2), 107–112. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1007/s10144-006-0256-1.

Moita, M. T., Pazos, Y., Rocha, C., Nolasco, R., & Oliveira, P. B. (2016). Toward predicting Dinophysis blooms off NW Iberia : A decade of events. *Harmful Algae*, 53, 17–32.

Morelle, J., Claquin, P., & Orvain, F. (2020). Evidence for better microphytobenthos dynamics in mixed sand/mud zones than in pure sand or mud intertidal flats (Seine estuary, Normandy, France). *PLOS ONE*, 15(8), e0237211. Publisher : Public Library of Science.

Morelle, J., Schapira, M., Orvain, F., Riou, P., Lopez, P. J., Pierre-Duplessix, O., Rabiller, E., Maheux, F., Simon, B., & Claquin, P. (2018). Annual Phytoplankton Primary Production Estimation in a Temperate Estuary by Coupling PAM and Carbon Incorporation Methods. *Estuaries and Coasts*, 41(5), 1337–1355.

Mortensen, S. H., Børsheim, K. Y., Rainuzzo, J., & Knutsen, G. (1988). Fatty acid and elemental composition of the marine diatom Chaetoceros gracilis Schütt. Effects of silicate deprivation, temperature and light intensity. *Journal of Experimental Marine Biology and Ecology*, 122(2), 173–185.

Moss, B., Jeppesen, E., Søndergaard, M., Lauridsen, T. L., & Liu, Z. (2013). Nitrogen, macrophytes, shallow lakes and nutrient limitation : resolution of a current controversy ? *Hydrobiologia*, 710(1), 3–21.

Muylaert, K., Sabbe, K., & Vyverman, W. (2009). Changes in phytoplankton diversity and community composition along the salinity gradient of the Schelde estuary (Belgium/The Netherlands). *Estuarine, Coastal and Shelf Science*, 82(2), 335–340.

Ménesguen, A., Dussauze, M., Dumas, F., Thouvenin, B., Garnier, V., Lecornu, F., & Répécaud, M. (2019). Ecological model of the Bay of Biscay and English Channel shelf for environmental status assessment part 1 : Nutrients, phytoplankton and oxygen. *Ocean Modelling*, 133, 56–78.

Ménesguen, A. & Gohin, F. (2006). Observation and modelling of natural retention structures in the English Channel. *Journal of Marine Systems*, 63(3), 244–256.

Naik, R. K., Naik, M. M., D'Costa, P. M., & Shaikh, F. (2019). Microplastics in ballast water as an emerging source and vector for harmful chemicals, antibiotics, metals, bacterial pathogens and HAB species : A potential risk to the marine environment and human health. *Marine Pollution Bulletin*, 149, 110525.

Napoléon, C., Fiant, L., Raimbault, V., Riou, P., & Claquin, P. (2014). Dynamics of phytoplankton diversity structure and primary productivity in the English Channel. *Marine Ecology Progress Series*, 505, 49–64.

Napoléon, C., Raimbault, V., Fiant, L., Riou, P., Lefebvre, S., Lampert, L., & Claquin, P. (2012). Spatiotemporal dynamics of physicochemical and photosynthetic parameters in the central English Channel. *Journal of Sea Research*, 69, 43–52.

Naselli-Flores, L. & Barone, R. (2011). Invited Review - Fight on Plankton ! or, Phytoplankton Shape and Size as Adaptive Tools to Get Ahead in the Struggle for Life. *Cryptogamie, Algologie*, 32(2), 157–204. Publisher : Muséum national d'Histoire naturelle, Paris.

Nazari-Sharabian, M., Ahmad, S., & Karakouzian, M. (2018). Climate Change and Eutrophication : A Short Review. *Engineering, Technology and Applied Science Research*, 8(6), 3668–3672.

Neaud-Masson, N. (2016). Observation et dénombrement du phytoplancton marin par microscopie optique photonique-Spécifications techniques et méthodologiques appliquées au REPHY. *Document de méthode.*

Nelson, J. R. & Grubesic, T. H. (2018). Oil spill modeling : Risk, spatial vulnerability, and impact assessment. *Progress in Physical Geography : Earth and Environment*, 42(1), 112–127. Publisher : SAGE Publications Ltd.

Nezan, E., Antoine, E., Fiant, L., Amzil, Z., & Billard, C. (2006). Identification of Pseudonitzschia australis and P. multiseries in the Bay of Seine. Was there a relation to presence of domoic acid in king scallops in autumn 2004. *Harmful Algae News*, 31, 1–3.

Nohe, A., Goffin, A., Tyberghein, L., Lagring, R., De Cauwer, K., Vyverman, W., & Sabbe, K. (2020). Marked changes in diatom and dinoflagellate biomass, composition and seasonality in the Belgian Part of the North Sea between the 1970s and 2000s. *Science of The Total Environment*, 716, 136316.

Not, F., Siano, R., Kooistra, W. H., Simon, N., Vaulot, D., & Probert, I. (2012). Diversity and ecology of eukaryotic marine phytoplankton. In *Advances in Botanical Research*, volume 64 (pp. 1–53). Elsevier.

Nwaneshiudu, A., Kuschal, C., Sakamoto, F. H., Rox Anderson, R., Schwarzenberger, K., & Young, R. C. (2012). Introduction to confocal microscopy. *Journal of Investigative Dermatology*, 132(12), 1–5.

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2018). vegan : Community Ecology Package. R package version 2.5-3.

Olson, R. J., Zettler, E. R., & Anderson, O. K. (1989). Discrimination of eukaryotic phytoplankton cell types from light scatter and autofluorescence properties measured by flow cytometry. *Cytometry*, 10(5), 636–643. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/cyto.990100520.

Ostle, C., Paxman, K., Graves, C. A., Arnold, M., Artigas, L. F., Atkinson, A., Aubert, A., Baptie, M., Bear, B., Bedford, J., Best, M., Bresnan, E., Brittain, R., Broughton, D., Budria, A., Cook, K., Devlin, M., Graham, G., Halliday, N., Hélaouët, P., Johansen, M., Johns, D. G., Lear, D., Machairopoulou, M., McKinney, A., Mellor, A., Milligan, A., Pitois, S., Rombouts, I., Scherer, C., Tett, P., Widdicombe, C., & McQuatters-Gollop, A. (2021). The Plankton Lifeform Extraction Tool : a digital tool to increase the discoverability and usability of plankton time-series data. *Earth System Science Data*, 13(12), 5617–5642. Publisher : Copernicus GmbH.

Oxborough, K., Moore, C. M., Suggett, D. J., Lawson, T., Chan, H. G., & Geider, R. J. (2012). Direct estimation of functional PSII reaction center concentration and PSII electron flux on a volume basis : a new approach to the analysis of Fast Repetition Rate fluorometry (FRRf) data. *Limnology and Oceanography : Methods*, 10(3), 142–154. Publisher : Wiley Online Library.

Paasche, E. (2001). A review of the coccolithophorid Emiliania huxleyi (Prymnesiophyceae), with particular reference to growth, coccolith formation, and calcification-photosynthesis interactions. *Phycologia ; Lawrence*, 40(6), 503–529.

Paerl, H. W., Valdes, L. M., Pinckney, J. L., Piehler, M. F., Dyble, J., & Moisander, P. H. (2003). Phytoplankton Photopigments as Indicators of Estuarine and Coastal Eutrophication. *BioScience*, 53(10), 953–964.

Pannard, A., Claquin, P., Klein, C., Le Roy, B., & Véron, B. (2008). Short-term variability of the phytoplankton community in coastal ecosystem in response to physical and chemical conditions' changes. *Estuarine, Coastal and Shelf Science*, 80(2), 212–224.

Panton, A. & Purdie, D. A. (2022). Dinophysis spp. abundance and toxicity events in South Cornwall, U.K. : Interannual variability and environmental drivers at three coastal sites. *Harmful Algae*, 112, 102169.

Pančić, M. & Kiørboe, T. (2018). Phytoplankton defence mechanisms : traits and trade-offs. *Biological Reviews*, 93(2), 1269–1303. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/brv.12395.

Park, M. G., Kim, S., Kim, H. S., Myung, G., Kang, Y. G., & Yih, W. (2006). First successful culture of the marine dinoflagellate Dinophysis acuminata. *Aquatic Microbial Ecology*, 45(2), 101–106.

Parsons, M. L. & Dortch, Q. (2002). Sedimentological evidence of an increase in Pseudo-nitzschia (Bacillariophyceae)abundance in response to coastal eutrophication. *Limnology and Oceanography*, 47(2), 551–558. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2002.47.2.0551.

Pednekar, S. M., Bates, S. S., Kerkar, V., & Matondkar, S. G. P. (2018). Environmental Factors Affecting the Distribution of Pseudo-nitzschia in Two Monsoonal Estuaries of Western India and Effects of Salinity on Growth and Domoic Acid Production by P. pungens. *Estuaries and Coasts*, 41(5), 1448–1462.

Peperzak, L., Snoeijer, G. J., Dijkema, R., Gieskes, W. W. C., Joordens, J., Peeters, J. C. H., Schol, C., Vrieling, E. G., & Zevenboom, W. (1996). DEVELOPMENT OF A DINOPHYSIS ACUMINATA BLOOM IN THE RIVER RifiNE PLUME (NORTH SEA).

Perrot, T., Rossi, N., Ménesguen, A., & Dumas, F. (2014). Modelling green macroalgal blooms on the coasts of Brittany, France to enhance water quality management. *Journal of Marine Systems*, 132, 38–53.

Petchey, O. L. & Gaston, K. J. (2006). Functional diversity : back to basics and looking forward. *Ecology Letters*, 9(6), 741–758. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1461-0248.2006.00924.x.

Pezy, J.-P., Raoux, A., & Dauvin, J.-C. (2020). An ecosystem approach for studying the impact of offshore wind farms : a French case study. *ICES Journal of Marine Science*, 77(3), 1238–1246. Publisher : Oxford University Press.

Piet, G. J., Pfisterer, A. B., & Rijnsdorp, A. D. (1998). On factors structuring the flatfish assemblage in the southern North Sea. *Journal of Sea Research*, 40(1), 143–152.

Pirani, M., Panton, A., Purdie, D. A., & Sahu, S. K. (2016). Modelling macronutrient dynamics in the Hampshire Avon river : A Bayesian approach to estimate seasonal variability and total flux. *Science of The Total Environment*, 572, 1449–1460.

Pocklington, R., Milley, J. E., Bates, S. S., Bird, C. J., De Freitas, A. S. W., & Quilliam, M. A. (1990). Trace determination of domoic acid in sea water and phytoplankton by high-performance liquid chromatography of the fluorenylmethoxycarbonyl (FMOC) derivative. *International Journal of Environmental Analytical Chemistry*, 38(3), 351–368. Publisher : Taylor & Francis.

Poulton, N. (2016). FlowCam : Quantification and Classification of Phytoplankton by Imaging Flow Cytometry. *Methods in molecular biology.*

Pörtner, H. O., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E., Begum, R. A., Betts, R., Kerr, R. B., Biesbroek, R., Birkmann, J., Bowen, K., Castellanos, E., Cissé, G., Constable, A., Cramer, W., Dodman, D., Eriksen, S. H., Fischlin, A., Garschagen, M., Glavovic, B., Gilmore, E., Haasnoot, M., Harper, S., Hasegawa, T., Hayward, B., Hirabayashi, Y., Howden, M., Kalaba, K., Kiessling, W., Lasco, R., Lawrence, J., Lemos, M. F., Lempert, R., Ley, D., Lissner, T., Lluch-Cota, S., Loeschke, S., Lucatello, S., Luo, Y., Mackey, B., Maharaj, S., Mendaz, C., Mintenbeck, K., Vale, M. M., Morecroft, M. D., Mukherji, A., Mycoo, M., Mustonen, T., Nalau, J., Okem, A., Ometto, J. P., Parmesan, C., Pelling, M., Pinho, P., Poloczanska, E., Racault, M.-F., Reckien, D., Pereira, J., Revi, A., Rose, S., Sanchez-Rodriguez, R., Schipper, E. L. F., Schmidt, D., Schoeman, D., Shaw, R., Singh, C., Solecki, W., Stringer, L., Thomas, A., Totin, E., Trisos, C., Aalst, M. v., Viner, D., Wairiu, M., Warren, R., Yanda, P., & Ibrahim, Z. Z. (2022). *Climate change 2022 : impacts, adaptation and vulnerability.* Publisher : IPCC.

Püttker, T., Crouzeilles, R., Almeida-Gomes, M., Schmoeller, M., Maurenza, D., Alves-Pinto, H., Pardini, R., Vieira, M. V., Banks-Leite, C., Fonseca, C. R., Metzger, J. P., Accacio, G. M., Alexandrino, E. R., Barros, C. S., Bogoni, J. A., Boscolo, D., Brancalion, P. H. S., Bueno, A. A., Cambui, E. C. B., Canale, G. R., Cerqueira, R., Cesar, R. G., Colletta, G. D., Delciellos, A. C., Dixo, M., Estavillo, C., Esteves, C. F., Falcão, F., Farah, F. T., Faria, D., Ferraz, K. M. P. M. B., Ferraz, S. F. B., Ferreira, P. A., Graipel, M. E., Grelle, C. E. V., Hernández, M. I. M., Ivanauskas, N., Laps, R. R., Leal, I. R., Lima, M. M., Lion, M. B., Magioli, M., Magnago, L. F. S., Mangueira, J. R. A. S., Marciano-Jr, E., Mariano-Neto, E., Marques, M. C. M., Martins, S. V., Matos, M. A., Matos, F. A. R., Miachir, J. I., Morante-Filho, J. M., Olifiers, N., Oliveira-Santos, L. G. R., Paciencia, M. L. B., Paglia, A. P., Passamani, M., Peres, C. A., Pinto Leite, C. M., Porto, T. J., Querido, L. C. A., Reis, L. C., Rezende, A. A., Rigueira, D. M. G., Rocha, P. L. B., Rocha-Santos, L., Rodrigues, R. R., Santos, R. A. S., Santos, J. S., Silveira, M. S., Simonelli, M., Tabarelli, M., Vasconcelos, R. N., Viana, B. F., Vieira, E. M., & Prevedello, J. A. (2020). Indirect effects of habitat loss via habitat fragmentation : A cross-taxa analysis of forest-dependent species. *Biological Conservation*, 241, 108368.

R Core Team, . (2018). R : A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria. URL https ://www.R-project.org/.

R Core Team, . (2021). R : A language and environment for statistical computing.R Foundation for Statistical Computing, Vienna, Austria. URL https ://www.R-project.org/.

Rabalais, N. N., Cai, W.-J., Cartensen, J., Conley, D. J., FRY, B., Hu, X., Quiñones-Rivera, Z., Rosenberg, R., Slomp, C. P., Turner, R. E., Voss, M., Wissel, B., & Zhang, J. (2014). Eutrophication-Driven Deoxygenation in the Coastal Ocean. *Oceanography*, 27(1), 172–183. Publisher : Oceanography Society.

Rabalais, N. N., Turner, R. E., Díaz, R. J., & Justić, D. (2009). Global change and eutrophication of coastal waters. *ICES Journal of Marine Science*, 66(7), 1528–1537. Publisher : Oxford Academic.

Radach, G., Berg, J., & Hagmeier, E. (1990). Long-term changes of the annual cycles of meteorological, hydrographic, nutrient and phytoplankton time series at Helgoland and at LV ELBE 1 in the German Bight. *Continental Shelf Research*, 10(4), 305–328.

Raine, R. (2014). A review of the biophysical interactions relevant to the promotion of HABs in stratified systems : The case study of Ireland. *Deep Sea Research Part II : Topical Studies in Oceanography*, 101, 21–31.

Raine, R., Cosgrove, S., Fennell, S., Gregory, C., Bernett, M., & Purdie, D. (2016). Origins of Dinophysis blooms which impact Irish aquaculture. In *Proceedings of the 17th International Conference of Harmful Algae, eds LAO Proença and GM Hallegraeff (Florianópolis : International Society for the Study of Harmful Algae)* (pp. 46–49).

Ramond, P., Siano, R., & Sourisseau, M. (2018). Functional traits of marine protists. Type : dataset.

Raoux, A., Lassalle, G., Pezy, J.-P., Tecchio, S., Safi, G., Ernande, B., Mazé, C., Loc'h, F. L., Lequesne, J., Girardin, V., Dauvin, J.-C., & Niquil, N. (2019). Measuring sensitivity of two OSPAR indicators for a coastal food web model under offshore wind farm construction. *Ecological Indicators*, 96, 728–738.

Rasband, W. (2018). ImageJ,U. S. National Institutes of Health, Bethesda, Maryland, USA, https ://imagej.nih.gov/ij/, 1997-2018.

Rault, J., Le Bris, H., Robert, M., Pawlowski, L., Denamiel, M., & Kopp, D. (2017). Diets and trophic niches of the main commercial fish species from the Celtic Sea. *Journal of Fish Biology*, 91(5), 1449–1474. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/jfb.13470.

Regan, T., Bean, T. P., Ellis, T., Davie, A., Carboni, S., Migaud, H., & Houston, R. D. (2021). Genetic improvement technologies to support the sustainable growth of UK aquaculture. *Reviews in Aquaculture*, 13(4), 1958–1985. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/raq.12553.

Reguera, B., Velo-Suárez, L., Raine, R., & Park, M. G. (2012). Harmful Dinophysis species : A review. *Harmful Algae*, 14, 87–106.

REPHY – French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters, . (2019). REPHY dataset - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters. 1987-2018 Metropolitan data.

REPHY – French Observation And Monitoring Program For Phytoplankton And Hydrology In Coastal Waters, . (2021). REPHY dataset - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters. Metropolitan data. Type : dataset.

REPHYTOX – French Monitoring Program For Phycotoxins In Marine Organisms, . (2021). REPHYTOX dataset. French Monitoring program for Phycotoxins in marine organisms. Data since 1987. Type : dataset.

Reynolds, C. S. (1984). Phytoplankton periodicity : the interactions of form, function and environmental variability. *Freshwater Biology*, 14(2), 111–142. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-2427.1984.tb00027.x.

Reynolds, C. S. (2006). *The Ecology of Phytoplankton.* Cambridge University Press. Google-Books-ID : gDz5jGsPWZYC.

Reynolds, C. S., Huszar, V., Kruk, C., Naselli-Flores, L., & Melo, S. (2002). Towards a functional classification of the freshwater phytoplankton. *Journal of Plankton Research*, 24(5), 417–428.

Rhee, G.-Y. (1982). Effects of Environmental Factors and Their Interactions on Phytoplankton Growth. In K. C. Marshall (Ed.), *Advances in Microbial Ecology : Volume 6*, Advances in Microbial Ecology (pp. 33–74). Boston, MA : Springer US.

Riemann, B., Simonsen, P., & Stensgaard, L. (1989). The carbon and chlorophyll content of phytoplankton from various nutrient regimes. *Journal of Plankton Research*, 11(5), 1037–1045. Publisher : Oxford University Press.

Riisgaard, K. & Hansen, P. J. (2009). Role of food uptake for photosynthesis, growth and survival of the mixotrophic dinoflagellate Dinophysis acuminata. *Marine Ecology Progress Series*, 381, 51–62.

Romero, E., Garnier, J., Billen, G., Ramarson, A., Riou, P., & Gendre, R. L. (2019). Modeling the biogeochemical functioning of the Seine estuary and its coastal zone : Export, retention, and transformations. *Limnology and Oceanography*, 64(3), 895–912.

Romero, E., Garnier, J., Lassaletta, L., Billen, G., Le Gendre, R., Riou, P., & Cugier, P. (2013). Large-scale patterns of river inputs in southwestern Europe : seasonal and interannual variations and potential eutrophication effects at the coastal zone. *Biogeochemistry*, 113(1), 481–505.

Romero, E., Le Gendre, R., Garnier, J., Billen, G., Fisson, C., Silvestre, M., & Riou, P. (2016). Long-term water quality in the lower Seine : Lessons learned over 4 decades of monitoring. *Environmental Science & Policy*, 58, 141–154.

Roselli, L., Litchman, E., Stanca, E., Cozzoli, F., & Basset, A. (2017). Individual trait variation in phytoplankton communities across multiple spatial scales. *Journal of Plankton Research*, 39(3), 577–588. Publisher : Oxford University Press.

Roselli, L., Paparella, F., Stanca, E., & Basset, A. (2015). New data-driven method from 3D confocal microscopy for calculating phytoplankton cell biovolume. *Journal of Microscopy*, 258(3), 200–211. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/jmi.12233.

Roselli, L., Stanca, E., Paparella, F., Mastrolia, A., & Basset, A. (2013). Determination of Coscinodiscus cf. granii biovolume by confocal microscopy : comparison of calculation models. *Journal of Plankton Research*, 35(1), 135–145.

Ross Brown, A., Lilley, M. K. S., Shutler, J., Widdicombe, C., Rooks, P., McEvoy, A., Torres, R., Artioli, Y., Rawle, G., Homyard, J., Tyler, C. R., & Lowe, C. (2022). Harmful Algal Blooms and their impacts on shellfish mariculture follow regionally distinct patterns of water circulation in the western English Channel during the 2018 heatwave. *Harmful Algae*, 111, 102166.

Roy, S. & Chattopadhyay, J. (2007). Toxin-allelopathy among phytoplankton species prevents competitive exclusion. *Journal of Biological Systems*, 15(01), 73–93. Publisher : World Scientific Publishing Co.

Roy, S., Llewellyn, C. A., Egeland, E. S., & Johnsen, G. (2011). *Phytoplankton Pigments : Characterization, Chemotaxonomy and Applications in Oceanography*. Cambridge University Press. Google-Books-ID : K_2AJHmdvxgC.

Ryabov, A., Kerimoglu, O., Litchman, E., Olenina, I., Roselli, L., Basset, A., Stanca, E., & Blasius, B. (2021). Shape matters : the relationship between cell geometry and diversity in phytoplankton. *Ecology letters*, 24(4), 847–861. Publisher : Wiley Online Library.

Safi, K. A. (2003). Microalgal populations of three New Zealand coastal locations : forcing functions and benthic-pelagic links. *Marine Ecology Progress Series*, 259, 67–78.

Salas, R. & Clarke, D. (2019). Review of DSP Toxicity in Ireland : Long-Term Trend Impacts, Biodiversity and Toxin Profiles from a Monitoring Perspective. *Toxins*, 11(2), 61. Number : 2 Publisher : Multidisciplinary Digital Publishing Institute.

Salmaso, N., Naselli-Flores, L., & Padisák, J. (2015). Functional classifications and their application in phytoplankton ecology. *Freshwater Biology*, 60(4), 603–619. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/fwb.12520.

Sanseverino, I., Conduto, D., Pozzoli, L., Dobricic, S., & Lettieri, T. (2016). Algal bloom and its economic impact. *European Commission, Joint Research Centre Institute for Environment and Sustainability*.

Sauterey, B. & Ward, B. A. (2022). Environmental control of marine phytoplankton stoichiometry in the North Atlantic Ocean. *Proceedings of the National Academy of Sciences*, 119(1), e2114602118. Publisher : Proceedings of the National Academy of Sciences.

Sauvey, A., Denis, F., Hégaret, H., Le Roy, B., Lelong, C., Jolly, O., Pavie, M., & Fauchot, J. (2021). Interactions between Filter-Feeding Bivalves and Toxic Diatoms : Influence on the Feeding Behavior of Crassostrea gigas and Pecten maximus and on Toxin Production by Pseudo-nitzschia. *Toxins*, 13(8), 577. Number : 8 Publisher : Multidisciplinary Digital Publishing Institute.

Schapira, M., Courtay, G., & Francoise, S. (2017). Détection des risques de contamination des Coquilles Saint Jacques en Baie de Seine - DISCCO - Rapport Final.

Schlesinger, W. H. & Bernhardt, E. S. (2013). *Biogeochemistry : An Analysis of Global Change*. Academic Press.

Schneck, F., Schwarzbold, A., Rodrigues, S. C., & Melo, A. S. (2011). Environmental variability drives phytoplankton assemblage persistence in a subtropical reservoir. *Austral Ecology*, 36(7), 839–848. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1442-9993.2010.02224.x.

Schnetzer, A., Miller, P. E., Schaffner, R. A., Stauffer, B. A., Jones, B. H., Weisberg, S. B., DiGiacomo, P. M., Berelson, W. M., & Caron, D. A. (2007). Blooms of Pseudo-nitzschia and domoic acid in the San Pedro Channel and Los Angeles harbor areas of the Southern California Bight, 2003–2004. *Harmful Algae*, 6(3), 372–387.

Schoemann, V., Becquevort, S., Stefels, J., Rousseau, V., & Lancelot, C. (2005). Phaeocystis blooms in the global ocean and their controlling mechanisms : a review. *Journal of Sea Research*, 53(1), 43–66.

Schreyers, L., van Emmerik, T., Biermann, L., & Le Lay, Y.-F. (2021). Spotting Green Tides over Brittany from Space : Three Decades of Monitoring with Landsat Imagery. *Remote Sensing*, 13(8), 1408. Number : 8 Publisher : Multidisciplinary Digital Publishing Institute.

Schwenk, D., Seppälä, J., Spilling, K., Virkki, A., Tamminen, T., Oksman-Caldentey, K.-M., & Rischer, H. (2013). Lipid content in 19 brackish and marine microalgae : influence of growth phase, salinity and temperature. *Aquatic Ecology*, 47(4), 415–424.

Segarra, A., Pépin, J. F., Arzul, I., Morga, B., Faury, N., & Renault, T. (2010). Detection and description of a particular Ostreid herpesvirus 1 genotype associated with massive mortality outbreaks of Pacific oysters, Crassostrea gigas, in France in 2008. *Virus Research*, 153(1), 92–99.

Sengupta, A., Dhar, J., Danza, F., Ghoshal, A., Müller, S., & Kakavand, N. (2021). *Active reconfiguration of cytoplasmic lipid droplets governs migration of nutrient-limited phytoplankton.* Technical report, bioRxiv. Section : New Results Type : article.

Serre-Fredj, L., Jacqueline, F., Navon, M., Izabel, G., Chasselin, L., Jolly, O., Repecaud, M., & Claquin, P. (2021). Coupling high frequency monitoring and bioassay experiments to investigate a harmful algal bloom in the Bay of Seine (French-English Channel). *Marine Pollution Bulletin*, 168, 112387.

Shifrin, N. S. & Chisholm, S. W. (1981). Phytoplankton Lipids : Interspecific Differences and Effects of Nitrate, Silicate and Light-Dark Cycles1. *Journal of Phycology*, 17(4), 374–384. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1529-8817.1981.tb00865.x.

Shim, J.-B., Klochkova, T. A., Han, J.-W., Kim, G.-H., Yoo, Y.-D., & Jeong, H.-J. (2011). Comparative proteomics of the mixotrophic dinoflagellate Prorocentrum micans growing in different trophic modes. *Algae*, 26(1), 87–96. Publisher : The Korean Society of Phycology.

Sibbald, S. J. & Archibald, J. M. (2020). Genomic insights into plastid evolution. *Genome biology and evolution*, 12(7), 978–990. Publisher : Oxford University Press.

Simon, N., Cras, A.-L., Foulon, E., & Lemée, R. (2009). Diversity and evolution of marine phytoplankton. *Comptes rendus biologies*, 332(2-3), 159–170.

Slimani, N., Guilbert, E., El Ayni, F., Jrad, A., Boumaiza, M., & Thioulouse, J. (2017). The use of STATICO and COSTATIS, two exploratory three-ways analysis methods : an application to the ecology of aquatic heteroptera in the Medjerda watershed (Tunisia). *Environmental and Ecological Statistics*, 24(2), 269–295. Publisher : Springer.

Small, H. J., Shields, J. D., Reece, K. S., Bateman, K., & Stentiford, G. D. (2012). Morphological and Molecular Characterization of Hematodinium perezi (Dinophyceae : Syndiniales), a Dinoflagellate Parasite of the Harbour Crab, Liocarcinus depurator. *Journal of Eukaryotic Microbiology*, 59(1), 54–66. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1550-7408.2011.00592.x.

Smayda, T. J. & Reynolds, C. S. (2001). Community Assembly in Marine Phytoplankton : Application of Recent Models to Harmful Dinoflagellate Blooms. *Journal of Plankton Research*, 23(5), 447–461.

Smith, W. O. & Demaster, D. J. (1996). Phytoplankton biomass and productivity in the Amazon River plume : correlation with seasonal river discharge. *Continental Shelf Research*, 16(3), 291–319.

Smyth, T., Fishwick, J., Al-Moosawi, L., Cummings, D., Harris, C., Kitidis, V., Rees, A., Martinez-Vicente, V., & Woodward, E. (2010). A broad spatio-temporal view of the western English Channel observatory.

Soberón, J. & Peterson, A. T. (2005). Interpretation of models of fundamental ecological niches and species' distributional areas. Publisher : University of Kansas.

Société Japonaise de Plancton, . (2011). *Encyclopédie Illustrée Le Plancton*. Editions de la station biologique de roscoff edition.

Soudant, D., Beliaeff, B., & Thomas, G. (1997). Explaining Dinophysis cf. acuminata abundance in Antifer (Normandy, France) using dynamic linear regression. *Marine Ecology Progress Series*, 156, 67–74.

Sournia, A., Chrdtiennot-Dinet, M.-J., & Ricard, M. (1991). Marine phytoplankton : how many species in the world ocean ? *Journal of Plankton Research*, 13(5), 1093–1099. Publisher : Oxford Academic.

South, A. (2020). rnaturalearthhires : High Resolution World Vector Map Data from Natural Earth used in rnaturalearth.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine Ecoregions of the World : A Bioregionalization of Coastal and Shelf Areas. *BioScience*, 57(7), 573–583.

Spatharis, S., Tsirtsis, G., Danielidis, D. B., Chi, T. D., & Mouillot, D. (2007). Effects of pulsed nutrient inputs on phytoplankton assemblage structure and blooms in an enclosed coastal area. *Estuarine, Coastal and Shelf Science*, 73(3), 807–815.

Spilling, K., Olli, K., Lehtoranta, J., Kremp, A., Tedesco, L., Tamelander, T., Klais, R., Peltonen, H., & Tamminen, T. (2018). Shifting Diatom—Dinoflagellate Dominance During Spring Bloom in the Baltic Sea and its Potential Effects on Biogeochemical Cycling. *Frontiers in Marine Science*, 5.

SRN Regional Observation and Monitoring program for Phytoplankton and Hydrology in the eastern English Channel, . (2017). SRN dataset - Regional Observation and Monitoring Program for Phytoplankton and Hydrology in the eastern English Channel. 1992-2016. *SEANOE*.

Stanca, E., Cellamare, M., & Basset, A. (2013). Geometric shape as a trait to study phytoplankton distributions in aquatic ecosystems. *Hydrobiologia*, 701(1), 99–116. Publisher : Springer.

Stanca, E. & Parsons, M. L. (2017). Phytoplankton diversity along spatial and temporal gradients in the Florida Keys. *Journal of Plankton Research*, 39(3), 531–549. Publisher : Oxford University Press.

Steidinger, K. A. & Tangen, K. (1997). Dinoflagellates. In *Identifying Marine Phytoplankton* (pp. 387–584). Academic Press - Elsevier, tomas carmelo r. edition.

Stiller, D., Ottinger, M., & Leinenkugel, P. (2019). Spatio-temporal patterns of coastal aquaculture derived from Sentinel-1 time series data and the full Landsat archive. *Remote sensing*, 11(14), 1707. Publisher : Multidisciplinary Digital Publishing Institute.

Stoecker, D. K., Hansen, P. J., Caron, D. A., & Mitra, A. (2017). Mixotrophy in the Marine Plankton. *Annual Review of Marine Science*, 9(1), 311–335. _eprint : https ://doi.org/10.1146/annurev-marine-010816-060617.

Stæhr, P. A., Markager, S., & Sand-Jensen, K. (2004). Pigment specific in vivo light absorption of phytoplankton from estuarine, coastal and oceanic waters. *Marine Ecology Progress Series*, 275, 115–128.

Suddleson, M. & Hoagland, P. (2021). Proceedings of the Workshop on the Socio-economic Effects of Harmful Algal Blooms in the United States.

Suggett, D. J., Warner, M. E., & Leggat, W. (2017). Symbiotic Dinoflagellate Functional Diversity Mediates Coral Survival under Ecological Crisis. *Trends in Ecology & Evolution*, 32(10), 735–745.

Sumaila, U. R., Cheung, W. W. L., Lam, V. W. Y., Pauly, D., & Herrick, S. (2011). Climate change impacts on the biophysics and economics of world fisheries. *Nature Climate Change*, 1(9), 449–456.

Swann, A. L. S., Longo, M., Knox, R. G., Lee, E., & Moorcroft, P. R. (2015). Future deforestation in the Amazon and consequences for South American climate. *Agricultural and Forest Meteorology*, 214-215, 12–24.

Séchet, V., Sibat, M., Billien, G., Carpentier, L., Rovillon, G.-A., Raimbault, V., Malo, F., Gaillard, S., Perrière-Rumebe, M., Hess, P., & Chomérat, N. (2021). Characterization of toxin-producing strains of Dinophysis spp. (Dinophyceae) isolated from French coastal waters, with a particular focus on the D. acuminata-complex. *Harmful Algae*, 107, 101974.

Tang, W., Llort, J., Weis, J., Perron, M. M. G., Basart, S., Li, Z., Sathyendranath, S., Jackson, T., Sanz Rodriguez, E., Proemse, B. C., Bowie, A. R., Schallenberg, C., Strutton, P. G., Matear, R., & Cassar, N. (2021). Widespread phytoplankton blooms triggered by 2019–2020 Australian wildfires. *Nature*, 597(7876), 370–375. Number : 7876 Publisher : Nature Publishing Group.

Tas, S. & Hernández-Becerril, D. U. (2017). Diversity and distribution of the planktonic diatom genus Chaetoceros (Bacillariophyceae) in the Golden Horn Estuary (Sea of Marmara). *Diatom Research*, 32(3), 309–323. Publisher : Taylor & Francis _eprint : https ://doi.org/10.1080/0269249X.2017.1360800.

Tas, S. & Lundholm, N. (2017). Temporal and spatial variability of the potentially toxic Pseudo-nitzschia spp. in a eutrophic estuary (Sea of Marmara). *Journal of the Marine Biological Association of the United Kingdom*, 97(7), 1483–1494. Publisher : Cambridge University Press.

Taylor, F. J. R., Hoppenrath, M., & Saldarriaga, J. F. (2008). Dinoflagellate diversity and distribution. *Biodiversity and conservation*, 17(2), 407–418. Publisher : Springer.

Tett, P. & Barton, E. D. (1995). Why are there about 5000 species of phytoplankton in the sea ? *Journal of Plankton Research*, 17(8), 1693–1704. Publisher : Oxford Academic.

Teubner, K., Tolotti, M., Greisberger, S., Morscheid, H., Dokulil, M. T., & Morscheid, H. (2003). Steady state phytoplankton in a deep pre-alpine lake : species and pigments of epilimnetic versus metalimnetic assemblages. In L. Naselli-Flores, J. Padisák, & M. T. Dokulil (Eds.), *Phytoplankton and Equilibrium Concept : The Ecology of Steady-State Assemblages*, Developments in Hydrobiology (pp. 49–64). Dordrecht : Springer Netherlands.

Thessen, A. E., Dortch, Q., Parsons, M. L., & Morrison, W. (2005). Effect of Salinity on Pseudo-Nitzschia Species (bacillariophyceae) Growth and Distribution1. *Journal of Phycology*, 41(1), 21–29. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1529-8817.2005.04077.x.

Thieu, V., Billen, G., & Garnier, J. (2009). Nutrient transfer in three contrasting NW European watersheds : the Seine, Somme, and Scheldt Rivers. A comparative application of the Seneque/Riverstrahler model. *Water research*, 43(6), 1740–1754. Publisher : Elsevier.

Thioulouse, J. (2011). Simultaneous analysis of a sequence of paired ecological tables : A comparison of several methods. *The Annals of Applied Statistics*, 5(4), 2300–2325. Publisher : Institute of Mathematical Statistics.

Thomas, Y., Cassou, C., Gernez, P., & Pouvreau, S. (2018). Oysters as sentinels of climate variability and climate change in coastal ecosystems. *Environmental Research Letters*, 13(10), 104009. Publisher : IOP Publishing.

Thorel, M., Claquin, P., Schapira, M., Le Gendre, R., Riou, P., Goux, D., Le Roy, B., Raimbault, V., Deton-Cabanillas, A.-F., & Bazin, P. (2017). Nutrient ratios influence variability in Pseudo-nitzschia species diversity and particulate domoic acid production in the Bay of Seine (France). *Harmful algae*, 68, 192–205. Publisher : Elsevier.

Thrush, S. F., Halliday, J., Hewitt, J. E., & Lohrer, A. M. (2008). The Effects of Habitat Loss, Fragmentation, and Community Homogenization on Resilience in Estuaries. *Ecological Applications*, 18(1), 12–21. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1890/07-0436.1.

Thyssen, M., Grégori, G. J., Grisoni, J.-M., Pedrotti, M. L., Mousseau, L., Artigas, L. F., Marro, S., Garcia, N., Passafiume, O., & Denis, M. J. (2014). Onset of the spring bloom in the northwestern Mediterranean Sea : influence of environmental pulse events on the in situ hourly-scale dynamics of the phytoplankton community structure. *Frontiers in microbiology*, 5, 387. Publisher : Frontiers.

Tilman, D. (2001). Functional diversity. *Encyclopedia of biodiversity*, 3(1), 109–120.

Timsit, O., Sylvand, B., & Lefeuvre, J.-C. (2004). Évolution du macrozoobenthos intertidal de la baie des Veys de 1985 à 2000. *Comptes Rendus Biologies*, 327(1), 51–64.

Tomas, C. R. (1997). *Identifying Marine Phytoplankton*. Tomas carmelo r. edition.

Trainer, V. L., Bates, S. S., Lundholm, N., Thessen, A. E., Cochlan, W. P., Adams, N. G., & Trick, C. G. (2012). Pseudo-nitzschia physiological ecology, phylogeny, toxicity, monitoring and impacts on ecosystem health. *Harmful algae*, 14, 271–300. Publisher : Elsevier.

Tynkkynen, N., Schönach, P., Pihlajamäki, M., & Nechiporuk, D. (2014). The Governance of the Mitigation of the Baltic Sea Eutrophication : Exploring the Challenges of the Formal Governing System. *AMBIO*, 43(1), 105–114.

Tyrrell, T. & Merico, A. (2004). Emiliania huxleyi : bloom observations and the conditions that induce them. In H. R. Thierstein & J. R. Young (Eds.), *Coccolithophores : From Molecular Processes to Global Impact* (pp. 75–97). Berlin, Heidelberg : Springer Berlin Heidelberg.

Ubertini, M., Lefebvre, S., Gangnery, A., Grangeré, K., Gendre, R. L., & Orvain, F. (2012). Spatial Variability of Benthic-Pelagic Coupling in an Estuary Ecosystem : Consequences for Microphytobenthos Resuspension Phenomenon. *PLOS ONE*, 7(8), e44155. Publisher : Public Library of Science.

Ulén, B., Bechmann, M., Fölster, J., Jarvie, H. P., & Tunney, H. (2007). Agriculture as a phosphorus source for eutrophication in the north-west European countries, Norway, Sweden, United Kingdom and Ireland : a review. *Soil Use and Management*, 23(s1), 5–15. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1475-2743.2007.00115.x.

Umhau, B. P., Benitez-Nelson, C. R., Anderson, C. R., McCabe, K., & Burrell, C. (2018). A Time Series of Water Column Distributions and Sinking Particle Flux of Pseudo-Nitzschia and Domoic Acid in the Santa Barbara Basin, California. *Toxins*, 10(11), 480. Number : 11 Publisher : Multidisciplinary Digital Publishing Institute.

Vallina, S. M., Follows, M. J., Dutkiewicz, S., Montoya, J. M., Cermeno, P., & Loreau, M. (2014). Global relationship between phytoplankton diversity and productivity in the ocean. *Nature Communications*, 5(1), 4299. Number : 1 Publisher : Nature Publishing Group.

Van Ael, E., Covaci, A., Blust, R., & Bervoets, L. (2012). Persistent organic pollutants in the Scheldt estuary : Environmental distribution and bioaccumulation. *Environment International*, 48, 17–27.

Van de Waal, D. B. & Litchman, E. (2020). Multiple global change stressor effects on phytoplankton nutrient acquisition in a future ocean. *Philosophical Transactions of the Royal Society B : Biological Sciences*, 375(1798), 20190706. Publisher : Royal Society.

van der Velde, I. R., van der Werf, G. R., Houweling, S., Maasakkers, J. D., Borsdorff, T., Landgraf, J., Tol, P., van Kempen, T. A., van Hees, R., Hoogeveen, R., Veefkind, J. P., & Aben, I. (2021). Vast CO2 release from Australian fires in 2019–2020 constrained by satellite. *Nature*, 597(7876), 366–369. Number : 7876 Publisher : Nature Publishing Group.

Van Dolah, F. M. (2000). Marine algal toxins : origins, health effects, and their increased occurrence. *Environmental health perspectives*, 108(suppl 1), 133–141.

Van Hemert, C., Schoen, S. K., Litaker, R. W., Smith, M. M., Arimitsu, M. L., Piatt, J. F., Holland, W. C., Ransom Hardison, D., & Pearce, J. M. (2020).

Algal toxins in Alaskan seabirds : Evaluating the role of saxitoxin and domoic acid in a large-scale die-off of Common Murres. *Harmful Algae*, 92, 101730.

Van Heukelem, L. & Thomas, C. S. (2001). Computer-assisted high-performance liquid chromatography method development with applications to the isolation and analysis of phytoplankton pigments. *Journal of Chromatography A*, 910(1), 31–49. Publisher : Elsevier.

Van Meerssche, E., Greenfield, D. I., & Pinckney, J. L. (2018). Coastal eutrophication and freshening : Impacts on Pseudo-nitzschia abundance and domoic acid allelopathy. *Estuarine, Coastal and Shelf Science*, 209, 70–79.

Van Meerssche, E. & Pinckney, J. L. (2017). The influence of salinity in the domoic acid effect on estuarine phytoplankton communities. *Harmful Algae*, 69, 65–74.

Velo-Suárez, L., González-Gil, S., Gentien, P., Lunven, M., Bechemin, C., Fernand, L., Raine, R., & Reguera, B. (2008). Thin layers of Pseudo-nitzschia spp. and the fate of Dinophysis acuminata during an upwelling–Downwelling cycle in a Galician Ria. *Limnology and Oceanography*, 53(5), 1816. Publisher : Citeseer.

Villa, M., Camp, J., & Berdalet, E. (2020). Toxic microalgae and global change : why have proliferations increased along the Mediterranean coast ? *Revista Mètode*. Section : Monographs.

Villarino, M. L., Figueiras, F. G., Jones, K. J., Alvarez-Salgado, X. A., Richard, J., & Edwards, A. (1995). Evidence of in situ diel vertical migration of a red-tide microplankton species in Ría de Vigo (NW Spain). *Marine Biology*, 123(3), 607–617.

Vivier, B., Claquin, P., Lelong, C., Lesage, Q., Peccate, M., Hamel, B., Georges, M., Bourguiba, A., Sebaibi, N., Boutouil, M., Goux, D., Dauvin, J.-C., & Orvain, F. (2021). Influence of infrastructure material composition and microtopography on marine biofilm growth and photobiology. *Biofouling*, 37(7), 740–756. Publisher : Taylor & Francis _eprint : https ://doi.org/10.1080/08927014.2021.1959918.

Vollenweider, R. A. & Kerekes, J. (1980). The loading concept as basis for controllin... - Google Scholar.

Wagner, H., Fanesi, A., & Wilhelm, C. (2016). Title : Freshwater phytoplankton responses to global warming. *Journal of Plant Physiology*, 203, 127–134.

Wainman, B. & Smith, R. (1997). Can physicochemical factors predict lipid content in phytoplankton? *Freshwater Biology*, 38(3), 571–579. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1046/j.1365-2427.1997.00228.x.

Ward, B. A. & Follows, M. J. (2016). Marine mixotrophy increases trophic transfer efficiency, mean organism size, and vertical carbon flux. *Proceedings of the National Academy of Sciences*, 113(11), 2958–2963. Publisher : National Academy of Sciences Section : Biological Sciences.

Washburn, T. W., Turner, P. J., Durden, J. M., Jones, D. O. B., Weaver, P., & Van Dover, C. L. (2019). Ecological risk assessment for deep-sea mining. *Ocean & Coastal Management*, 176, 24–39.

Wasmund, N., Tuimala, J., Suikkanen, S., Vandepitte, L., & Kraberg, A. (2011). Long-term trends in phytoplankton composition in the western and central Baltic Sea. *Journal of Marine Systems*, 87(2), 145–159.

Watson, A. J., Schuster, U., Shutler, J. D., Holding, T., Ashton, I. G. C., Landschützer, P., Woolf, D. K., & Goddijn-Murphy, L. (2020). Revised estimates of ocean-atmosphere CO2 flux are consistent with ocean carbon inventory. *Nature Communications*, 11(1), 4422. Number : 1 Publisher : Nature Publishing Group.

Weithoff, G. & Beisner, B. E. (2019). Measures and approaches in trait-based phytoplankton community ecology–from freshwater to marine ecosystems. *Frontiers in Marine Science*, 6, 40. Publisher : Frontiers.

Wells, M. L., Trainer, V. L., Smayda, T. J., Karlson, B. S. O., Trick, C. G., Kudela, R. M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D. M., & Cochlan, W. P. (2015). Harmful algal blooms and climate change : Learning from the past and present to forecast the future. *Harmful Algae*, 49, 68–93.

Wentzky, V. C., Tittel, J., Jäger, C. G., Bruggeman, J., & Rinke, K. (2020). Seasonal succession of functional traits in phytoplankton communities and their interaction with trophic state. *Journal of Ecology*, 108(4), 1649–1663. Publisher : Wiley Online Library.

West, W. E., McCarthy, S. M., & Jones, S. E. (2015). Phytoplankton lipid content influences freshwater lake methanogenesis. *Freshwater Biology*, 60(11), 2261–2269. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/fwb.12652.

White, D. A., Widdicombe, C. E., Somerfield, P. J., Airs, R. L., Tarran, G. A., Maud, J. L., & Atkinson, A. (2015). The combined effects of seasonal community succession and adaptive algal physiology on lipid profiles of coastal phytoplankton in the Western English Channel. *Marine Chemistry*, 177, 638–652.

Whyte, C., Swan, S., & Davidson, K. (2014). Changing wind patterns linked to unusually high Dinophysis blooms around the Shetland Islands, Scotland. *Harmful Algae*, 39, 365–373.

Wickham, H. (2016). H. Wickham. ggplot2 : Elegant Graphics for Data Analysis. Springer-Verlag New York, 2016.

Widdicombe, C. E., Archer, S. D., Burkill, P. H., & Widdicombe, S. (2002). Diversity and structure of the microplankton community during a coccolithophore bloom in the stratified northern North Sea. *Deep Sea Research Part II : Topical Studies in Oceanography*, 49(15), 2887–2903.

Widdicombe, C. E., Eloire, D., Harbour, D., Harris, R. P., & Somerfield, P. J. (2010). Long-term phytoplankton community dynamics in the Western English Channel. *Journal of Plankton Research*, 32(5), 643–655.

Widdicombe, C. E. & Harbour, D. (2021). Phytoplankton taxonomic abundance and biomass time-series at Plymouth Station L4 in the Western English Channel, 1992-2020.

Wiltshire, K. H., Boersma, M., Carstens, K., Kraberg, A. C., Peters, S., & Scharfe, M. (2015). Control of phytoplankton in a shelf sea : Determination of the main drivers based on the Helgoland Roads Time Series. *Journal of Sea Research*, 105, 42–52.

Wiltshire, K. H., Malzahn, A. M., Wirtz, K., Greve, W., Janisch, S., Mangelsdorf, P., Manly, B. F. J., & Boersma, M. (2008). Resilience of North Sea phytoplankton spring bloom dynamics : An analysis of long-term data at Helgoland Roads. *Limnology and Oceanography*, 53(4), 1294–1302. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.4319/lo.2008.53.4.1294.

Winder, M., Carstensen, J., Galloway, A. W. E., Jakobsen, H. H., & Cloern, J. E. (2017). The land–sea interface : A source of high-quality phytoplankton to support secondary production. *Limnology and Oceanography*, 62(S1), S258–S271. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1002/lno.10650.

Winder, M. & Cloern, J. E. (2010). The annual cycles of phytoplankton biomass. *Philosophical Transactions of the Royal Society B : Biological Sciences*, 365(1555), 3215–3226. Publisher : The Royal Society.

Winder, M. & Schindler, D. E. (2004). Climatic effects on the phenology of lake processes. *Global Change Biology*, 10(11), 1844–1856. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-2486.2004.00849.x.

Winder, M. & Sommer, U. (2012). Phytoplankton response to a changing climate. *Hydrobiologia*, 698(1), 5–16.

Wollschläger, J., Wiltshire, K. H., Petersen, W., & Metfies, K. (2015). Analysis of phytoplankton distribution and community structure in the German Bight with respect to the different size classes. *Journal of sea research*, 99, 83–96. Publisher : Elsevier.

Xiao, W., Liu, X., Irwin, A. J., Laws, E. A., Wang, L., Chen, B., Zeng, Y., & Huang, B. (2018). Warming and eutrophication combine to restructure diatoms and dinoflagellates. *Water Research*, 128, 206–216.

Yamaguchi, R. & Suga, T. (2019). Trend and Variability in Global Upper-Ocean Stratification Since the 1960s. *Journal of Geophysical Research : Oceans*, 124(12), 8933–8948. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1029/2019JC015439.

Yan, H. F., Kyne, P. M., Jabado, R. W., Leeney, R. H., Davidson, L. N., Derrick, D. H., Finucci, B., Freckleton, R. P., Fordham, S. V., & Dulvy, N. K. (2021).

Overfishing and habitat loss drive range contraction of iconic marine fishes to near extinction. *Science Advances*, 7(7), eabb6026. Publisher : American Association for the Advancement of Science.

Yasakova, O. N. (2013). The seasonal dynamics of potentially toxic and harmful phytoplankton species in Novorossiysk Bay (Black Sea). *Russian Journal of Marine Biology*, 39(2), 107–115.

Young, N., Sharpe, R. A., Barciela, R., Nichols, G., Davidson, K., Berdalet, E., & Fleming, L. E. (2020). Marine harmful algal blooms and human health : A systematic scoping review. *Harmful Algae*, 98, 101901.

Zapata, M., Fraga, S., Rodríguez, F., & Garrido, J. L. (2012). Pigment-based chloroplast types in dinoflagellates. *Marine Ecology Progress Series*, 465, 33–52.

Zingone, A., Phlips, E. J., & Harrison, P. J. (2010). Multiscale Variability of Twenty-Two Coastal Phytoplankton Time Series : a Global Scale Comparison. *Estuaries and Coasts*, 33(2), 224–229.

Zohary, T., Padisák, J., & Naselli-Flores, L. (2010). Phytoplankton in the physical environment : beyond nutrients, at the end, there is some light. *Hydrobiologia*, 639(1), 261–269.

Zwart, J. A., Solomon, C. T., & Jones, S. E. (2015). Phytoplankton traits predict ecosystem function in a global set of lakes. *Ecology*, 96(8), 2257–2264. _eprint : https ://onlinelibrary.wiley.com/doi/pdf/10.1890/14-2102.1.

Álvarez, E., Nogueira, E., & López-Urrutia, (2017). In vivo single-cell fluorescence and size scaling of phytoplankton chlorophyll content. *Applied and Environmental Microbiology*. Publisher : American Society for Microbiology 1752 N St., N.W., Washington, DC.

Impact of changing environment on phytoplankton : integrating ecological niches and functional traits approaches to community studies in the Bay of Seine

Résumé

Les écosystèmes côtiers font face à un environnement changeant qu'il soit d'origine naturelle ou anthropique. Le phytoplancton, à la base des réseaux trophiques marins, se situe au coeur du fonctionnement des écosystèmes. Les objectifs de cette thèse s'intègrent dans le cadre du projet S3-EUROHAB, et visent à évaluer la variabilité spatio-temporelle des communautés phytoplanctoniques au sein de divers systèmes de Manche Est, notamment en Baie de Seine. Pour répondre à ces objectifs, des approches allant de la physiologie à la communauté, et des unités taxonomiques aux caractéristiques fonctionnelles ont été explorées. Si l'approche communautaire permet de rendre compte du faible niveau de déviation inter-annuel au sein des assemblages phytoplanctoniques, elle révèle également des différenciations spatiales où chaque communauté est sous forte influence des facteurs environnementaux locaux. Ces patrons de variabilité spatiale sont également retrouvés au travers de l'approche fonctionnelle. Par ailleurs, la relation traits-environnement permet d'étudier l'adéquation entre stratégies fonctionnelles et distribution environnementale (niche écologique). Les résultats montrent que, malgré la forte diversité des organismes étudiés et le choix de traits, des taxons partageant des similarités fonctionnelles partagent également des niches écologiques similaires. En complément d'une approche fonctionnelle communautaire, une approche expérimentale a été développée afin d'évaluer la plasticité du phytoplancton, notamment de contenus intracellulaires. Cette dernière révèle ainsi des adaptations spatiales et temporelles des teneurs en lipides et en chlorophylle-*a* des organismes phytoplanctoniques, en réponse aux besoins en lumière et pour le maintien du bon fonctionnement de la cellule selon les gradients environnementaux. Enfin, la relation entre les facteurs environnementaux et la dynamique de deux taxons toxiques *Dinophysis* spp. et *Pseudo-nitzschia* spp. a été étudiée. Dans un premier temps, cela met en évidence entre autre l'affinité de *Dinophysis* spp. avec l'augmentation de température et la stratification qu'elle induit au sein de deux environnements contrastés ; britannique et français. Dans un second temps, les circonstances des efflorescences de *Pseudo-nitzschia* spp. suggèrent l'existence de pressions biotiques contraignantes et possiblement causes des épisodes de toxicités observées de 2011 à 2014.

Mots clés : Phytoplancton marin, communauté, environnement, algues toxiques, traits fonctionnels, niche écologique, variabilité spatio-temporelle

Summary

Coastal ecosystems are facing changing environments whether of natural or anthropogenic origin. Phytoplankton, at the base of marine food webs, is central to ecosystems functioning. The objectives of this thesis, as part of the S3-EUROHAB project, aim at assessing the spatio-temporal variability of phytoplankton communities within various systems of the Eastern Channel, particularly the Bay of Seine. To meet these objectives, approaches ranging from physiology to community, and from taxonomic units to functional characteristics have been explored. If the community approach indicates a low level of inter-annual deviation within phytoplankton assemblages, it also reveals spatial differentiation where each community is under strong influence of local environmental factors. These patterns of spatial variability are being found through the functional approach as well. In addition, the trait-environment relationship makes it possible to study the adequacy between functional strategies and environmental distribution (ecological niche). The results show that, despite the high diversity of organisms studied and the choice of traits, taxa sharing functional similarities also share similar ecological niches. In addition to a community functional approach, an experimental approach has been developed to assess the plasticity of phytoplankton, particularly of intracellular content. The latter thus reveals spatial and temporal adaptations of phytoplankton lipid and chlorophyll-*a* cell contents, in order to meet light requirements and maintain proper cell functioning regarding environmental conditions. Finally, the relationship between environmental factors and the dynamics of two toxic taxa *Dinophysis* spp. and *Pseudo-nitzschia* spp. has been studied. Firstly, it highlights the common affinity of *Dinophysis* spp. with the increase in temperature and the stratification it induces within two different environments ; British and French. Secondly, the circumstances of the blooms of *Pseudo-nitzschia* spp. suggest the existence of constraining biotic pressures, which could have caused toxicity outbreaks between 2011 and 2014.

Keywords : Marine phytoplankton, community, environment, harmful algal bloom, functional traits, ecological niche, spatio-temporal variability