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Structure et fonctionnement planctonique des marais des Pertuis-Charentais : effet de l'aléa submersion sur leurs fonctions écologiques

Lauriane Bergeon

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Laboratoire écologie
fonctionnelle
et environnement

Thèse de Doctorat

ÉCOLE DOCTORALE
N°618 Euclide

Structure et fonctionnement planctonique des marais des Pertuis-Charentais : effet de l'aléa submersion sur leurs fonctions écologiques

Thèse présentée par :

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1. Zones humides côtières

1.1 Etat des lieux à l'échelle du globe

D'après la définition donnée par le Muséum National d'Histoire Naturelle (MNHN) se basant sur la loi de l'eau (1992), les zones humides représentent « des terrains, exploités ou non, habituellement inondés ou gorgés d'eau douce, salée ou saumâtre de façon permanente ou temporaire, ou dont la végétation, quand elle existe, y est dominée par des plantes hygrophiles pendant au moins une partie de l'année ». Il existe une vaste diversité de zones humides à travers le monde (*e.g.*, marais, mangroves, estuaires) bien que ces environnements ne représentent qu'environ 6 % des écosystèmes présents sur la surface terrestre. Les zones humides contiennent une grande biodiversité et sont des habitats refuge propices à de nombreuses espèces migratrices (Jude et Pappas, 1992 ; Junk et al., 2006 ; Yang et al., 2017). Malgré l'importance de ces écosystèmes, leur étendue a largement diminué au cours des siècles (Figure 0.1). D'après le rapport de la convention de Ramsar en 2015, la diminution de la surface des zones humides au XX^e siècle à l'échelle de la planète est de l'ordre de 64 à 71 %.

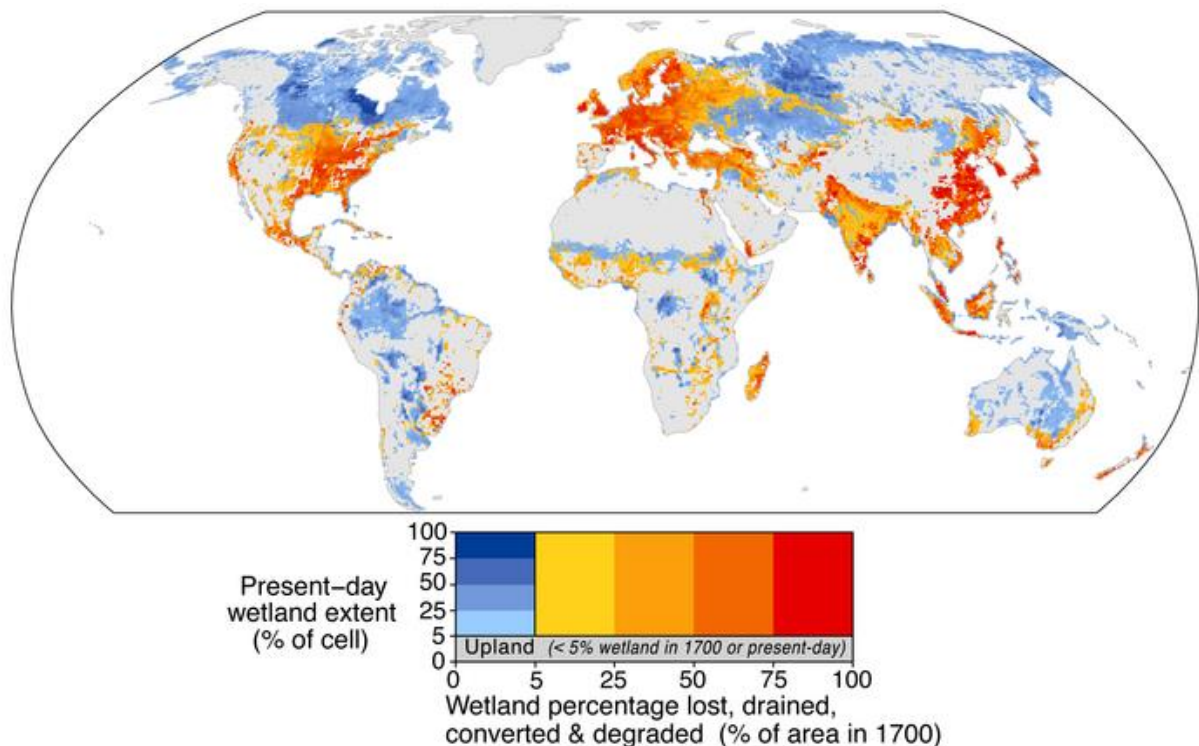


Figure 0. 1 : Carte présentant le pourcentage de perte de surface des zones humides entre les années 1700 et 2020 à l'échelle mondiale (auteur : Etienne Fluet-Chouinard, McGill University).

En plus de la perte conséquente de biodiversité que cela implique, les services écosystémiques et fonctions écologiques fournies par ces écosystèmes sont tout autant menacées. Afin de mieux appréhender la nécessité de préserver ces écosystèmes clés, il est important de comprendre leur importance autant au niveau naturel qu'économique et social. Dans cette thèse, l'évaluation se focalisera sur un seul type de zone humide : les marais côtiers.

1.2 Typologie des marais côtiers

Les marais côtiers peuvent être d'origine naturelle, situés à différents niveaux du bassin versant et recevoir de l'eau par les marées ou par ruissellement des cours d'eau en amont et précipitations (Figure 0.2), ou bien d'origine anthropique, c'est-à-dire que les apports d'eau sont régulés par des ouvrages (*e.g.*, digues, écluses). Dans le cas des marais naturels, ils se forment généralement dans des zones planes où le drainage des eaux dans les nappes phréatiques est faible à cause de l'imperméabilité du sédiment. Dans le cas des marais créés par l'Homme, ces écosystèmes ont souvent été mis en place comme source d'eau, autant pour approvisionner les infrastructures, l'arrosage des champs et que pour abreuver le bétail.

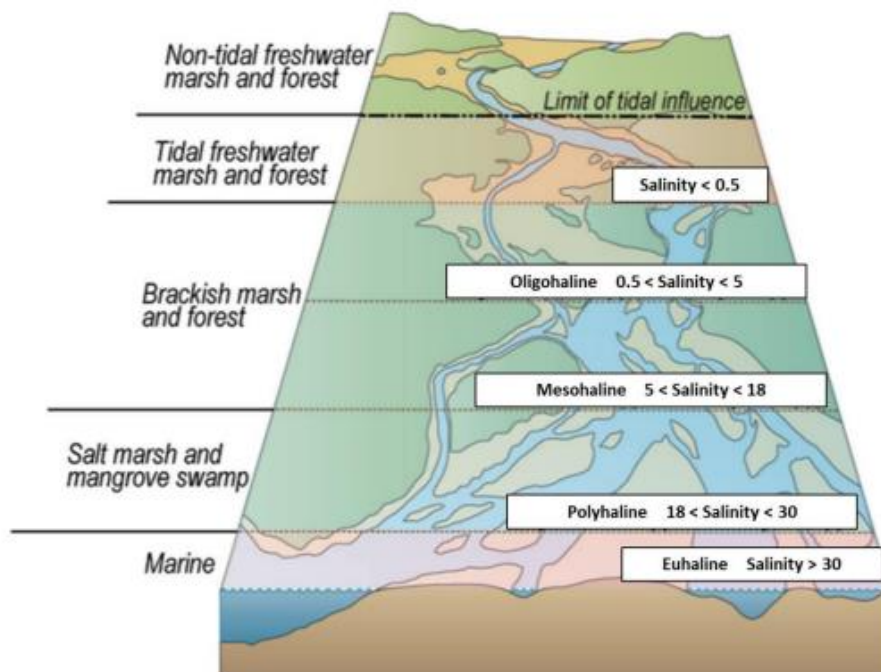


Figure 0. 2 : Segmentation du bassin versant selon les différents types de marais retrouvés (source : Luo et al., 2017).

Les marais salés sont les marais ayant une salinité supérieure à 18. Entre 0,5 et 18, ils sont qualifiés de marais saumâtres. En dessous de 0,5, ils sont qualifiés de marais doux. Les marais côtiers abritent généralement de nombreux macrophytes, dont la diversité varie selon le type de marais. Les marais salés et saumâtres sont par exemple peuplés d'espèces végétales halophiles (*i.e.*, tolérante à la salinité). Ces écosystèmes ont tendance à se former dans des zones lenticques du réseau hydrographique du bassin versant, où l'eau s'évacue peu dû à l'imperméabilité des sédiments (tourbe, vase). Une grande partie de ces marais ont été réaménagés par l'Homme au cours du temps pour la saliculture (Buron, 1999), la pisciculture (Hussenot, 2003 ; Guerra-Garcia et al., 2023), ou encore la conchyliculture (Holdich, 1993), et également asséchés voir comblés pour l'urbanisation (Wang et al., 2011).

1.3 Identité patrimoniale des marais côtiers

L'identité patrimoniale est définie comme l'ensemble des composantes du patrimoine propre à un territoire (Requier-Desjardins, 2009). Elle regroupe trois types de composantes patrimoniales : d'une part, le patrimoine culturel qui est défini par Faro (2005) comme « un ensemble de ressources héritées du passé que des personnes considèrent, par-delà le régime de propriété des biens, comme un reflet et une expression de leurs valeurs, croyances, savoirs et traditions en continuelle évolution. Cela inclut tous les aspects de l'environnement résultant de l'interaction dans le temps entre les personnes et les lieux ». Dans le cas d'un marais côtier, il peut s'agir d'un ouvrage créé par l'Homme (pont, digue). D'autre part, le patrimoine paysager comprend tout élément naturel ou construit qui compose le paysage. Enfin, le patrimoine naturel qui regroupe l'ensemble de la biodiversité présente dans cet écosystème. La conservation de l'identité patrimoniale des marais représente un enjeu majeur à la fois pour préserver l'attractivité de l'environnement, mais également l'ensemble des services écosystémiques qu'il fournit.

1.4 Services écosystémiques et fonctions écologiques des marais

Les marais côtiers offrent de nombreux services écosystémiques. Comme présenté précédemment, ils peuvent être aménagés pour fournir des ressources et de la nourriture (*e.g.*, poisson, sel). Ils peuvent dans certains cas servir de bassins pluviaux afin de recycler l'eau de pluie pour différents usages comme l'approvisionnement en eau potable, l'abreuvement des

élevages ou encore l'irrigation des cultures (Moody, 2016). De plus, l'attractivité des environnements côtiers fait de ces milieux des espaces de loisirs à la fois pour les résidents des villes alentours mais également dans le cadre du tourisme, représentant un atout économique important. Selon un rapport de l'INSEE et de l'observatoire du littoral, à l'échelle mondiale, plus de 60 % de la population habite en zone côtière.

En plus des services exploitables par l'Homme, les marais côtiers fournissent de nombreux services pour sa biodiversité. La végétation qui s'y développe offre des habitats refuges à de nombreuses espèces d'amphibiens et d'oiseaux (Hammer, 2020), mais également aux alevins qui augmentent leur chance d'échapper à la prédation et de continuer leur développement. Ces alevins sont dans les marais côtiers car ces écosystèmes fournissent suffisamment de ressources pour qu'ils se nourrissent jusqu'à l'âge adulte (Okyere et al., 2011 ; Davis et al., 2012). Les marais côtiers jouent également un rôle dans le maintien d'une bonne qualité des eaux (Lefevre et al., 2004) par sédimentation des matières en suspension dans la colonne d'eau et par l'action bactérienne de dégradation de la matière (Wang et al., 2014 ; Peng et al., 2023).

L'ensemble de ces services se trouve néanmoins menacé par la disparition des zones humides côtières du fait de leur vulnérabilité aux pressions qu'elles subissent (Ayyam et al., 2019).

1.5 Vulnérabilité des marais côtiers

1.5.1 Perturbations anthropiques

Une des pressions majeures de la disparition des marais côtiers vient de l'urbanisation du littoral. A l'échelle de la France métropolitaine, ces écosystèmes représentent 4% de la superficie totale du pays et abrite près de 10 % de la population française (Zanietti, 2006). Cette urbanisation a causé le drainage et le remblaiement de nombreux marais côtiers au profit d'expansion des villes côtières et de l'aménagement d'infrastructures liées aux activités balnéaires (Lee et al., 2006 ; Yi et al., 2018). Certains marais ont également été abandonnés et l'absence de gestion a engendré un comblement de ces marais par la végétation et les sédiments (Turner, 1990). La construction de nombreuses digues afin de limiter l'impact des inondations et augmenter la surface des terres pour l'agriculture a dans certains cas induit l'assèchement de zones humides côtières (Gueben-Venièrre, 2015). Ces environnements aquatiques sont également soumis à la pollution, que ce soit par rejets industriels non traités ou par lessivage

des pesticides en zone agricole (Clark et al., 1993 ; Mallin et al., 2001 ; Zhao et al., 2021), qui impacte directement la biodiversité des marais.

1.5.2 Perturbations naturelles

Les marais côtiers sont également soumis à diverses perturbations d'origine naturelle. En cas d'eutrophisation (*i.e.*, trop grande concentration de nutriments dans la colonne d'eau), certaines algues peuvent proliférer et occuper la totalité de la zone euphotique créant une compétition pour la lumière avec d'autres organismes photoautotrophes (Kosten et al., 2011 ; Vanderstukken et al., 2014). Les espèces proliférant dans les marais ne sont pas forcément des espèces indigènes : des espèces invasives exotiques plus compétitrices sont de plus en plus observées dans ces marais et entraînent une diminution de la biodiversité autant animale que végétale. Par exemple, en France métropolitaine, de nombreux marais sont peuplés par des ragondins (*Myocastor coypus*), initialement originaire d'Amérique du Nord, qui se développent massivement car leurs prédateurs d'origine ne sont pas présents en France. Concernant la végétation, la jussie rampante (*Ludwigia peploides*) se développe très rapidement dans des cas d'abandon de gestion des marais. Certains phénomènes naturels extrêmes (*e.g.*, tempête), dont la fréquence tend à augmenter avec le changement climatique, peuvent modifier sur court ou long terme l'hydrologie de ces milieux (Grieger et al., 2019 ; David et al., 2020) ainsi que modifier la biodiversité, et donc affecter les fonctions écologiques et services écosystémiques fournies par les marais côtiers. C'est le cas par exemple des phénomènes de submersion marine (cf paragraphe 2.5.1).

1.6 Gestion et restauration des marais côtiers

Au cours du dernier siècle, la prise de conscience de l'importance des services fournis par les marais côtiers a augmenté, et différentes opérations de gestion ont été mises en œuvre afin de préserver au mieux ces écosystèmes. Une des actions les plus réalisées a été la dépoldérisation qui consiste à retirer les digues et aménagements préalablement construits pour rétablir l'hydrologie naturelle du milieu (Goeldner-Gianella et Verger, 2009). Cette action est qualifiée de « stratégie de laisser faire » car elle implique un arrêt de la gestion hydraulique de ces marais par l'Homme, une fois le nouveau plan de gestion appliqué. En outre, différents projets de restauration des marais côtiers dans le but de protéger la biodiversité ont vu le jour. Par exemple, le programme « Life Natur'Adapt » (<https://naturadapt.com/>) cherche à faire intégrer la problématique du changement climatique sur différents écosystèmes par un maximum de

réserve naturelle : la réserve de Lilleau des Niges sur l'Île de Ré fait partie des réserves en phase d'expérimentation de cette intégration sur les marais salés. Également, le but du projet PAMPAS (<https://pampas.recherche.univ-lr.fr/>) incluant ces travaux de thèse est, à terme, de pouvoir fournir un outil numérique aux gestionnaires de zones humides côtières pour les aider à adapter au mieux leur mode de gestion des marais des Pertuis Charentais face à la submersion marine, dans le but de préserver leur identité patrimoniale dans le contexte du changement climatique. Néanmoins, la majorité des projets de gestion focalisent leurs actions pour protéger la biodiversité « visible », en omettant l'impact que ces nouveaux aménagements pourraient avoir sur la biodiversité « non visible » pourtant tout aussi essentielle dans ces écosystèmes, comme les communautés planctoniques.

2. Communautés planctoniques

2.1 Définition générale

Un organisme est défini comme planctonique quand il n'a pas ou peu de capacité de mouvement et se laisse principalement porter par les courants. Bien que la majorité du plancton soit composé d'organismes non visibles à l'œil nu, il existe une grande diversité de forme et de taille allant du femtoplancton (*e.g.*, virioplancton) jusqu'au mégaplancton (*e.g.*, méduses, poisson-lune). Les communautés planctoniques représentent plusieurs dizaines de milliers d'espèces différentes peuplant les eaux salées, douces ou saumâtres (océans, mer, lac, rivière, marais, estuaire, etc.). Le plancton est présent depuis les niveaux superficiels de la colonne d'eau jusqu'au niveau benthique (Marrari et al., 2011 ; Weiner et al., 2012), et effectuent des migrations verticales en suivant le rythme nyctéméral (Fortier et Leggett, 1983 ; Gibson et al., 2016). Les organismes planctoniques peuvent être regroupés en différents compartiments selon leur ordre de taille, leur régime trophique et/ou les fonctions écologiques auxquelles ils contribuent.

2.1.1 Bactérioplancton

Le bactérioplancton comprend plusieurs groupes bactériens et archées présents dans la colonne d'eau et acteurs principaux de l'écologie microbienne. Certaines de ces bactéries sont autotrophes et réalisent la photosynthèse, comme les cyanobactéries, tandis que d'autres sont chimiotrophes et produisent leur énergie en dégradant de la matière organique présente en suspension dans l'eau (Ferrara et al., 2011 ; Urakawa et Bernhard, 2017). Le bactérioplancton représente un acteur clé au sein des cycles biogéochimiques aquatiques comme le cycle de

l'azote et du carbone (Portillo et al., 2012), et joue également un rôle dans le maintien d'une bonne qualité de l'eau en éliminant des polluants (Chi et al., 2021). Ce compartiment planctonique est principalement utilisé comme ressource nutritive par des compartiments planctoniques supérieurs dans le réseau trophique aquatique.

2.1.2 *Phytoplancton*

Le phytoplancton comprend l'ensemble des organismes planctoniques autotrophes appartenant au règne végétal. Il est composé à la fois d'organismes unicellulaires comme pluricellulaires (*i.e.*, colonies d'organismes pluricellulaires comme les diatomées en chaîne). De la même manière que les macroalgues, ces organismes contiennent des pigments photosynthétiques leur permettant de produire les composés nécessaires à leur développement en captant la lumière et les nutriments (*e.g.*, azotés) présents dans la colonne d'eau (Rojo et al., 2010). Le phytoplancton comprend des organismes de différentes tailles tels que le picophytoplancton (organismes inférieurs à 3 μm ; *e.g.*, *Picochlorum* sp.), le nanophytoplancton (organismes entre 3 et 20 μm ; *e.g.*, certains dinoflagellés) et le microphytoplancton (organismes supérieurs à 20 μm ; *e.g.*, diatomées). Dans le réseau trophique aquatique, le phytoplancton représente les producteurs primaires et la base de ce réseau. De plus, le phytoplancton océanique représente le « premier poumon de la planète » devant la forêt Amazonienne par sa production abondante de dioxygène via photosynthèse (Falkowski et al., 2003) : ces organismes sont des acteurs essentiels à diverses fonctions écologiques et services écosystémiques clés qu'il est important de préserver.

2.1.3 *Protistes hétéro-mixotrophes*

Les protistes hétéro-mixotrophes regroupent des organismes unicellulaires microscopiques (*i.e.*, ciliés, certains dinoflagellés, nanoflagellés) qui ont pour particularité d'adopter un régime trophique autotrophe, hétérotrophe ou « hybride » selon l'environnement où ils se développent et les ressources dont ils disposent (Dupuy, 1999). Cette polyvalence dans l'adaptation de leur régime trophique permet une acclimatation de ces organismes face aux perturbations subies par leur milieu (Jones, 2000). Ils peuvent ainsi dans certaines conditions devenir acteurs principaux de la production primaire (comme le cilié *Myrionecta rubra*) si le phytoplancton se retrouve en faible abondance dans la colonne d'eau. De plus, depuis la mise en lumière de l'abondance des organismes planctoniques mixotrophes (Sanders, 1991), davantage d'études montrent l'importance de la mixotrophie dans les flux de matière au sein des réseaux trophiques planctoniques (Stoecker, 1998 ; Hansen et al., 2019). Il est donc essentiel de prendre en compte

la variabilité pouvant être apportée par les protistes hétéro-mixotrophes lors de l'étude des fonctions écologiques planctoniques (Mittra et al., 2014 ; Selosse et al., 2016).

2.1.4 Métazooplancton

Le zooplancton métazoaire (*i.e.*, métazooplancton) comprend l'ensemble des organismes planctoniques hétérotrophes appartenant au règne animal. Au sein du métazooplancton, on distingue deux groupes majeurs. D'une part l'holoplancton, aussi appelé « vrai plancton », correspondant à des organismes qui sont planctoniques sur l'ensemble de leur cycle de vie (Définition de Holoplancton - Dictionnaire - Encyclopædia Universalis). On y retrouve de nombreux microcrustacés comme les copépodes et les cladocères, des protostomiens microscopiques comme les rotifères, mais également des organismes gélatineux de plus grande taille (*e.g.*, méduses, siphonophores). D'autre part le méroplancton, aussi appelé « plancton temporaire », correspondant à des organismes qui sont planctoniques seulement dans les premiers stades de leur cycle vie (Définition de Méroplancton - Dictionnaire - Encyclopædia Universalis). C'est par exemple le cas de différents Bivalves, Brachyourses et différentes crevettes (groupe paraphylétique), mais aussi l'ichtyofaune, qui passe les premiers stades de leur cycle de vie sous forme de larves planctoniques, mais ne font plus partie du métazooplancton à leurs stades juvéniles et adultes. A l'échelle du réseau trophique aquatique, le métazooplancton représente les consommateurs primaires : selon les espèces, leur régime trophique varie de l'ingestion non sélective d'organismes et particules de matière organique ou inorganique à une prédation plus ciblée, visant parfois d'autres organismes zooplanctoniques plus petits (Bern, 1990 ; Irigoien et al., 2003 ; Beninger et Decottignies, 2005 ; Zhang et al., 2021).

2.2 Fonctions écologiques planctoniques

2.2.1 Production primaire

La production primaire représente la quantité de matière organique produite par les organismes autotrophes par photosynthèse (Robarts et al., 1995 ; Reeder et al., 2001). Dans le cas des communautés planctoniques, cette fonction est assurée principalement par le phytoplancton, mais aussi par certains protistes hétéro-mixotrophes. Cette production correspond à la transformation d'une quantité de matière organique en masse de carbone assimilé sur une période (Robarts et al., 1995). Deux types de productions primaires sont à différencier : la

production primaire brute (PPB) correspond à la quantité de matière organique qui est assimilée par les organismes autotrophes via la photosynthèse, alors que la production primaire nette (PPN) correspond à la PPB moins la quantité de matière organique consommée par la respiration. En écologie, la production primaire à l'échelle d'un écosystème est calculée pour à la fois évaluer sa productivité ainsi que d'évaluer comment se porte la biodiversité fournissant cette fonction écologique (Adame et al., 2017).

2.2.2 Fonction séquestration carbone atmosphérique

La séquestration du carbone atmosphérique correspond au transfert du carbone atmosphérique capté par photosynthèse, dont une partie est excrétée sous forme de carbone organique qui décante au niveau des sédiments, où elle approvisionne le stock de carbone organique préalablement contenu et séquestré dans les sédiments (Nag et al., 2019). L'autre partie est conservée dans la biomasse vivante. Ce carbone stocké dans des écosystèmes aquatiques tels que les marais côtiers est qualifié de « carbone bleu ». Lorsque la différence entre la quantité de carbone séquestrée et la quantité de carbone émise par l'écosystème est positive, cet écosystème est considéré comme un « puit de carbone ». A l'inverse, si cette différence est négative, l'écosystème est considéré comme une « source de carbone ». L'hydrodynamisme du milieu (marées, courant) favorise le stockage du carbone bleu car davantage de matière organique peut être importée dans les marais côtiers (Yu et al., 2023).

2.2.3 Fonction épuratrice

La fonction épuratrice, souvent présente dans les marais, correspond à la captation et la réduction des nutriments et de la matière en suspension (organique et inorganique) dans la colonne d'eau par les organismes. Dans le cas des communautés planctoniques, cette fonction est principalement assurée par le phytoplancton qui, à l'instar des végétaux, capte les nutriments présents dans la colonne d'eau et les utilise pour leur développement (Mallin et al., 2004). De plus, le mézozooplancton suspensivore (*i.e.*, qui se nourrit de particules en suspension dans la colonne d'eau) peut également contribuer à cette fonction en filtrant, de façon sélective ou non, des particules de matières organiques et inorganiques. La fonction épuratrice concerne également l'absorption de particules chimiques et polluants (*e.g.*, métaux lourds, microplastiques) par ces organismes, qui sont de fait des bioindicateurs clés pour évaluer le niveau d'eutrophisation et la qualité de l'eau dans les écosystèmes aquatiques (Marcus, 2004). Par exemple, Cole et al. (2016) ont montré l'ingestion de microplastiques par des Copépodes (*Calanus helgolandicus*) en analysant leur fèces et contenus stomachaux par fluorimétrie.

2.2.4 Fonction nourricerie

La fonction nourricerie correspond à la quantité de nourriture disponible dans un habitat défini où les juvéniles d'espèces mobiles (*e.g.*, alevins) vont se nourrir pendant les premiers stades de leur développement. Les communautés planctoniques représentent à elles seules la majeure partie de la biomasse des premiers niveaux des réseaux trophiques aquatiques (Sierszen et al., 2006). Les marais côtiers représentent des zones refuges pour de nombreuses espèces migratrices, comme l'anguille d'Europe (*Anguilla anguilla*) ou encore le canard souchet (*Spatula clypeata*), mais sont également des habitats propices à l'ichtyofaune indigène planctonophage comme l'épinoche (*Gasterosteus aculeatus*). Une forte abondance des communautés planctoniques pendant la période de développement des juvéniles dans ces milieux traduit une bonne fonction nourricerie.

2.3 Dynamique saisonnière des communautés planctoniques

L'abondance et la diversité des communautés planctoniques varient périodiquement au cours du temps, ce qui influence la présence et l'efficacité de leurs fonctions écologiques associées. La dynamique saisonnière des communautés planctoniques la plus souvent observée au cours d'une année dans les marais côtiers sur la côte Atlantique est la suivante (Figure 0.3) : en hiver, les abondances planctoniques sont généralement les plus basses. A la fin de l'hiver, l'apport de matière minérale et organique par le lessivage des sols dû aux précipitations et l'augmentation progressive de la température et l'allongement de la phase diurne permettent le développement du bactérioplancton, des protistes hétéro-mixotrophes et du phytoplancton. Ce climat favorable tout au long du printemps induit souvent des « blooms » (*i.e.*, forte croissance rapide) des communautés phytoplanctoniques au niveau de la zone euphotique (*i.e.*, couche superficielle de la colonne d'eau où suffisamment de lumière pénètre pour permettre la photosynthèse), ce qui renforce la production primaire, la séquestration du carbone atmosphérique et la fonction épuratrice du marais. Le maintien des hautes températures et de l'apport en nutriment pendant l'été permet une forte croissance du métazooplancton qui, en plus de renforcer la fonction de nourricerie, régule les populations de phytoplancton par broutage. L'abondance des communautés planctoniques se fait progressivement plus réduite dans le courant de l'automne, lorsque la température baisse et que les nutriments azotés deviennent limitants après leur forte consommation pendant les deux précédentes saisons. Les abondances planctoniques redeviennent faibles au moment de l'hiver suivant et le cycle se répète. D'autres types de

dynamiques saisonnières peuvent être observés dans d'autres milieux côtiers (Dugenne, 2017 ; Couteyen Carpaye, 2022) : en Méditerranée par exemple, le « système productif » est généralement observé en automne.

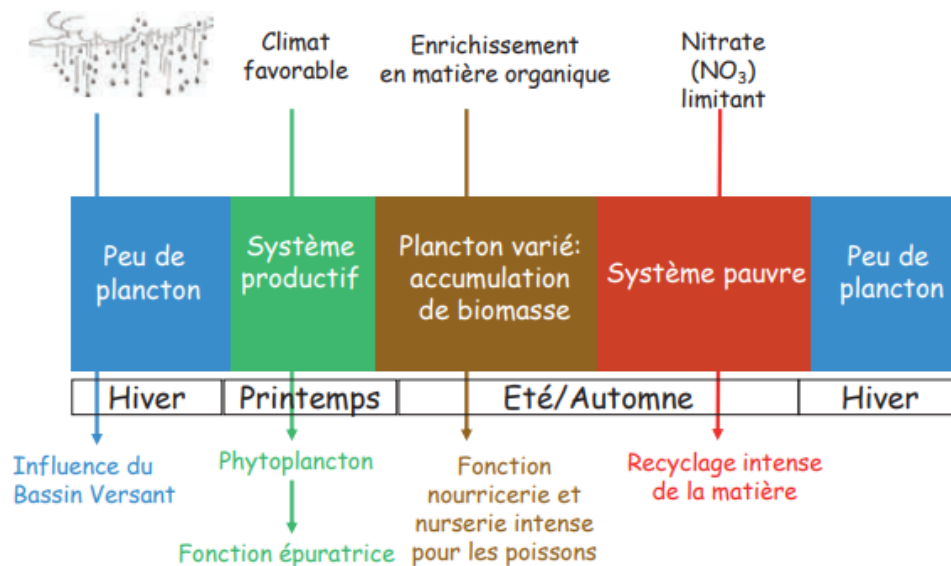


Figure 0. 3 : Dynamique saisonnière des communautés planctoniques dans les milieux côtiers (d'après la présentation de Christine Dupuy et Alain Dupuy au colloque « Adaptation des marais littoraux au changement climatique » en 2018 à La Rochelle, sur la base des données de Tortajada et al. (2011) et Masclaux et al. (2014)).

2.4 Différents types de réseaux trophiques planctoniques

L'étude de l'abondance et de la diversité des différentes communautés planctoniques couplées aux mesures de nutriments et paramètres abiotiques permettent de déterminer le type de réseau trophique planctonique présent dans le milieu à un instant donné (Legendre et Rassoulzadegan, 1995 ; Tortajada et al., 2011 ; Masclaux et al., 2014), et d'évaluer, dans son ensemble, les fonctions écologiques fournies par le plancton. La détermination de ces réseaux peut être affinée par l'étude des flux de matières entre les différents compartiments planctoniques. Cette détermination peut s'avérer complexe dans le cas où les données reflètent un état intermédiaire entre deux types de réseaux (Figure 0.4). Néanmoins, différents types de réseaux trophiques planctoniques ont été déterminés et retrouvés dans plusieurs études en milieux marins et côtiers :

- Un « hiver biologique » est caractérisé par de faibles abondances planctoniques associées à des concentrations variables en nutriments azotés et phosphorés dans la colonne d'eau. Peu d'activité photosynthétique et chimiosynthétique sont également relevées.

- Dans le cas d'un réseau herbivore, l'abondance et la production des communautés phytoplanctoniques pour l'ensemble des classes de taille est élevée, et le microphytoplancton est très abondant. Les nutriments ne sont pas limitants, et la zone euphotique est importante. Le métazooplancton est peu abondant, la pression de broutage sur le phytoplancton est moins importante que leur développement : le phytoplancton est donc dominant dans la colonne d'eau.
- Dans le cas d'une boucle microbienne, l'activité du recyclage de matière organique particulaire en matière organique et inorganique dissoute du bactérioplancton est prédominante. Une forte concentration de nutriments tels que l'ammonium (NH_4) est un indicateur de cette activité. Les communautés picophytoplanctoniques et nanophytoplanctoniques sont également abondantes, et peuvent être en compétition pour la ressource avec le bactérioplancton hétérotrophe (Fouilland et al., 2007).
- Dans le cas d'un réseau microbien, le pico- et nanophytoplancton est abondant et régulé par les protistes hétéro-mixotrophes, qui sont eux-mêmes régulés par les populations métazooplanctoniques. La production primaire des organismes autotrophes est principalement basée sur un seul composé azoté, l'ammonium (NH_4), relargué par les sédiments (Mostajir et al., 2012).
- Dans le cas d'un réseau multivore, l'ensemble des communautés planctoniques sont abondantes dans la colonne d'eau. Les pressions de broutage du métazooplancton et des protistes hétéro-mixotrophes sont équivalentes (Mostajir et al., 2012). Selon si le réseau multivore est considéré « faible » ou « fort », l'activité photosynthétique et chimiosynthétique sont variables.

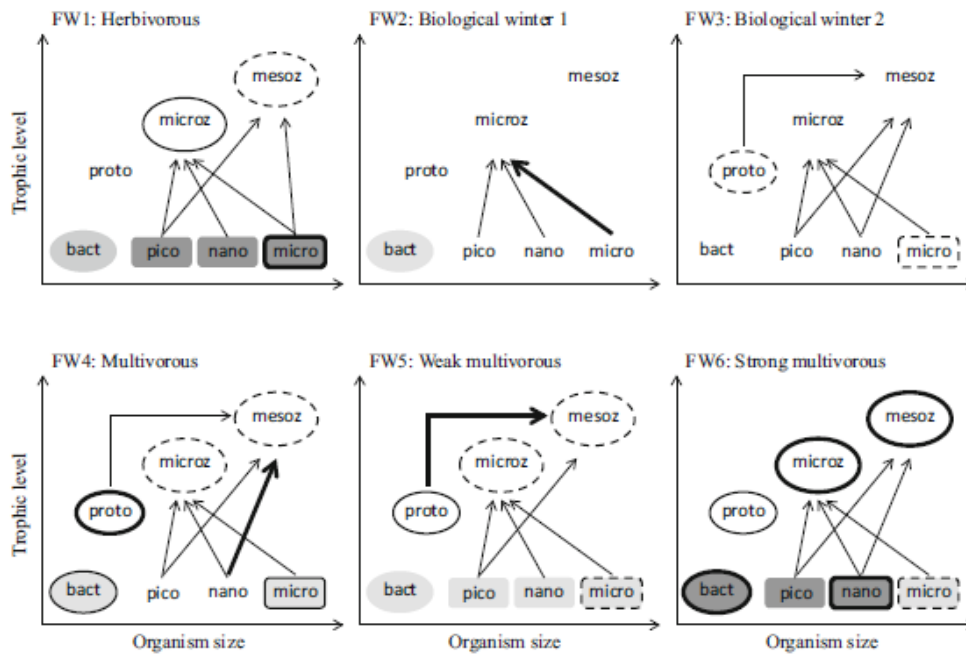


Figure 0. 4 : Exemples de réseaux trophiques planctoniques déterminés en marais côtiers de Charente-Maritime (d'après Masclaux et al., 2014).

2.5 Indicateurs de changements environnementaux

Du fait de leur sensibilité aux perturbations subies par leur environnement, les communautés planctoniques sont considérées comme de bons bioindicateurs pour évaluer la qualité de l'eau (Fonge et al., 2012 ; Singh et Sharma, 2020). Par exemple, une augmentation soudaine de la température de l'eau peu rapidement induire un bloom de phytoplancton si les nutriments ne sont pas limitants (Trombetta et al., 2019). Une augmentation de la turbidité dans la colonne d'eau peut à la fois booster l'activité chimiosynthétique du bactérioplancton, mais aussi diminuer l'abondance phytoplanctonique à cause de la réduction de la zone euphotique empêchant la photosynthèse et le développement des organismes. De plus, l'abondance métazooplanctonique peut diminuer car la turbidité diminue la visibilité dans la colonne d'eau ce qui impacte la prédation (Lougheed et Chow-Fraser, 1998). Dans le cas où les changements environnementaux sont de courte durée, le temps de génération rapide du plancton leur permet de s'acclimater rapidement (Angeler et Moreno, 2007 ; Nche-Fambo et al., 2015). En revanche, dans le cas de perturbations répétées, il est possible que l'assemblage de communautés soit modifié sur le long terme, induisant potentiellement une modification des réseaux trophiques planctoniques, ainsi que de leur fonctions écologiques associées. Un des phénomènes majeur

affectant les marais côtiers et leur biodiversité, et dont la fréquence risque d'augmenter dans les prochaines années, est la submersion marine

2.5.1 Submersion marine

Une submersion marine est causée par des conditions météorologiques extrêmes et correspond à une inondation temporaire de la zone littorale sur une durée allant de quelques heures à plusieurs jours. Dans le contexte du changement climatique, les phénomènes de submersion marine sont voués à se produire de plus en plus fréquemment en milieux côtiers (David et al., 2020). En plus d'affecter la topographie des marais côtiers, ces phénomènes impactent directement la biodiversité, notamment les communautés planctoniques. Un apport soudain d'un volume important d'eau de mer, couplé au lessivage des sols, a la capacité de modifier simultanément beaucoup de paramètres environnementaux. Il peut induire une augmentation ou diminution de la température et/ou de la salinité, accompagné d'une augmentation de la turbidité par l'apport de matière venant du lessivage ainsi que la remise en suspension des sédiments dans la colonne d'eau. L'ensemble de ces perturbations affectent directement les communautés planctoniques et leurs fonctions, et par effet en cascade l'ensemble du réseau trophique aquatique (Figure 0.5).

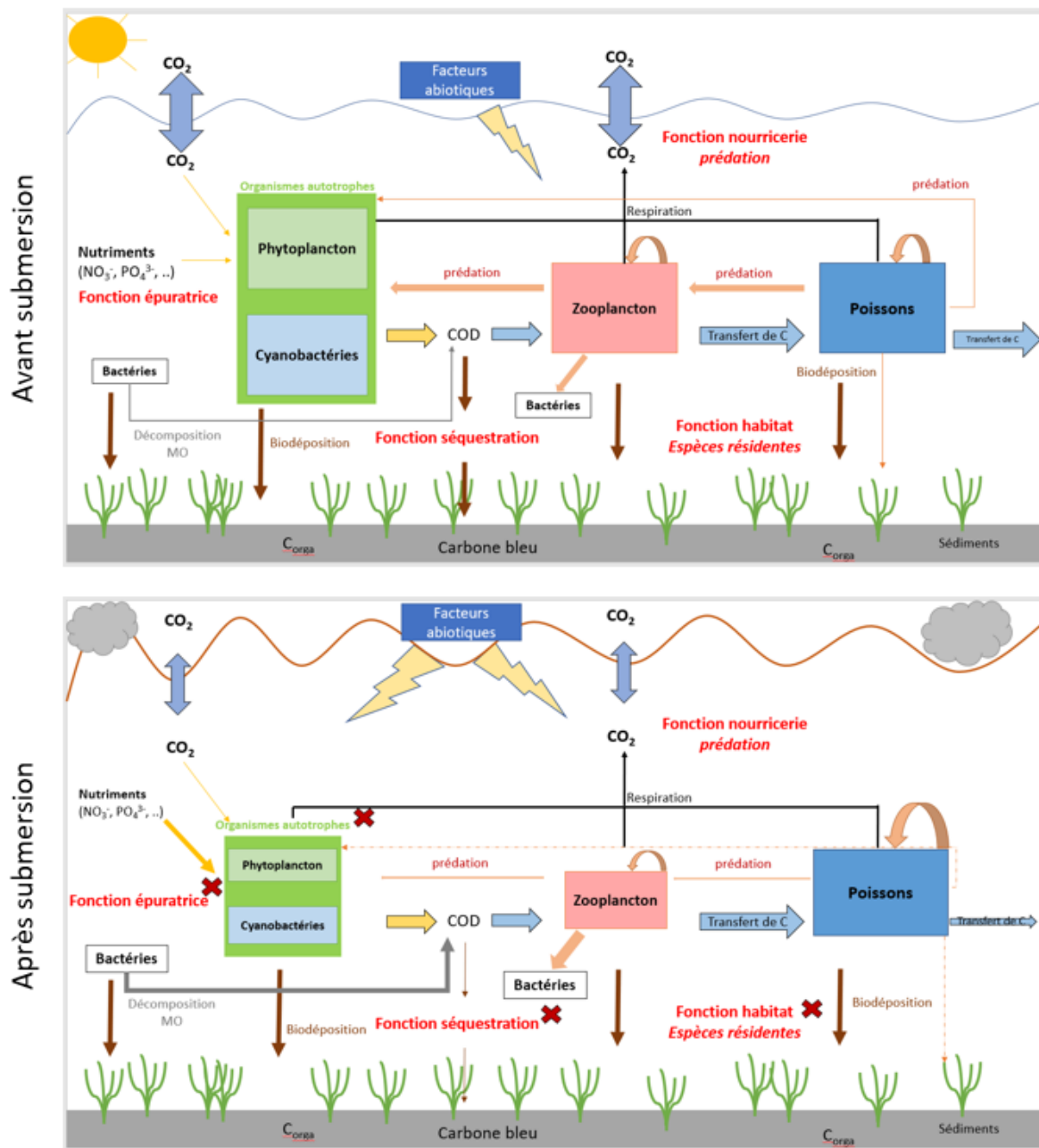


Figure 0. 5 : Schéma des potentiels effets de la submersion marine en marais côtier sur le réseau trophique aquatique (Auteurs : Lauriane Bergeon, Mireia Kohler, Jérémy Mayen).

3) Projet PAMPAS

Le projet ANR PAMPAS (« Evolution de l'identité PATrimoniale des Marais des Pertuis charentais en réponse à l'Aléa de Submersion marine ») est un projet interdisciplinaire visant à caractériser le fonctionnement des marais côtiers des Pertuis-Charentais, en prenant en compte leur mode de gestion, face à la submersion marine (<https://pampas.recherche.univ-lr.fr/presentation-du-projet/>). Ce projet sur 5 ans (2019 - 2023) possède 3 objectifs : 1) caractériser l'identité patrimoniale de ces marais dans leur ensemble (composantes culturelle, paysagère et naturelle), 2) évaluer l'impact de l'aléa de submersion marine sous un angle socio-écosystémique, 3) utiliser ces résultats pour déterminer différents scénarios possibles de l'évolution de l'identité patrimoniale des marais côtiers selon leur potentiel adaptatif. La finalité de ce projet est de pouvoir fournir un outil permettant aux gestionnaires d'adopter des plans de gestions durables préservant l'ensemble du patrimoine de ces marais.

Ces travaux de thèses sont inscrits dans le projet PAMPAS, plus précisément dans la caractérisation du patrimoine naturel des marais côtiers des Pertuis-Charentais, et se focalisent sur l'étude des communautés planctoniques et leurs fonctions écologiques associées, qui sont peu étudiées actuellement dans le contexte d'établissement de plan de gestion et de préservation de la biodiversité des marais côtiers.

4) Objectifs de la thèse

Le but de ces travaux de thèse est, dans un premier temps, d'évaluer la structure et le fonctionnement des communautés planctoniques de différents marais côtiers, en évaluant également les fonctions écologiques associées qu'elles fournissent à ces écosystèmes à travers le prisme de l'étude des communautés planctoniques. Dans un second temps, ces travaux visent à déterminer l'impact potentiel du phénomène de submersion marine sur les communautés planctoniques et leur fonctions écologiques. Ces deux objectifs de thèse sont liés par la volonté d'adapter au mieux le mode de gestion des marais côtiers afin de préserver leur identité patrimoniale sur le long terme. Ces études sont réalisées, pour la première partie, par des séries d'échantillonnages saisonniers sur trois marais côtiers situés en Charente-Maritime (Figure 0.6) : le marais du Fier d'Ars, le marais de Tasdon et le marais de Brouage.

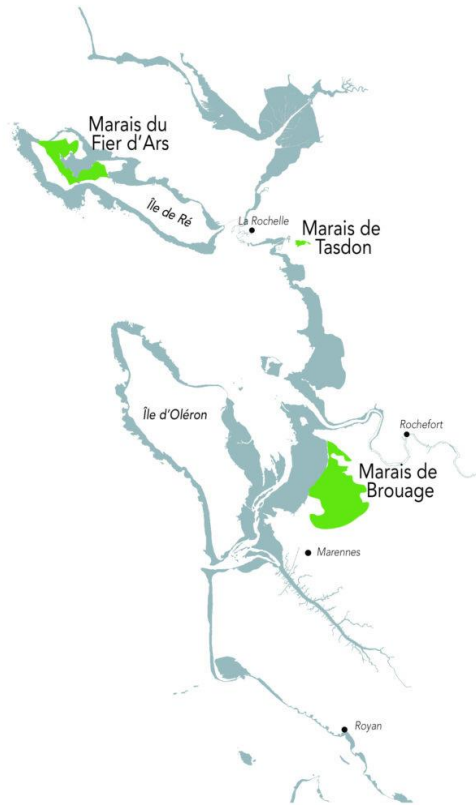


Figure 0. 6 : Localisation des trois sites d'études en Charente-Maritime sur la côte Ouest Atlantique française (source : site du projet PAMPAS).

En raison de l'impossibilité de faire des prélèvements en été et en automne à cause de niveaux d'eau trop faibles au marais de Brouage, l'étude s'est finalement focalisée uniquement sur les marais du Fier d'Ars et de Tasdon.

Pour l'étude de l'impact potentiel de la submersion marine, une expérience *in situ* simulant une submersion marine a été réalisée au site expérimental de l'Houmeau (CNRS) car au cours de la thèse, aucune submersion naturelle s'est produite.

Ce manuscrit est composé de trois chapitres : chacun d'entre eux contient en détails les méthodes et matériel utilisés pour chaque suivi et analyse.

Le premier chapitre « Distribution and trophic functioning of planktonic communities in coastal marshes in Atlantic Coast of France » présente une comparaison de la structure des communautés planctoniques dans deux marais côtiers (un marais salé et un marais doux) en prenant en compte les modalités de gestion similaires entre ces deux marais.

Le second chapitre « Impact of changing the management of an urban wetland on its ecological functions through the study of planktonic communities: the case of the Tasdon marsh (Charente-Maritime, France) » est focalisée sur le marais côtier périurbain de Tasdon, où sont comparées

les communautés zooplanctoniques et leurs fonctions écologiques avant et après sa restauration (2020).

Le troisième chapitre « Impact of short-term marine submersion on planktonic communities: an *in situ* simulated experiment » présente une expérience innovante *in situ* destinée à évaluer l'impact potentiel d'un phénomène de submersion marine modéré sur un temps court (3 jours) sur les communautés planctoniques.

À la suite de ces chapitres, une dernière partie discutera des points clés tirés de ces différentes études réalisées pendant cette thèse, et en complément, apportera différentes perspectives et idées pour compléter les résultats clés amenés par ces études, ainsi que l'avantage de la transmission de ces résultats produits aux gestionnaires des marais côtiers. L'objectif final de cette discussion est d'apporter les pistes d'une réflexion concrète sur la préservation des communautés planctoniques et de leurs fonctions écologiques associées dans les marais côtiers.

Chaque partie et chapitre sera suivie de sa bibliographie associée.

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Chapitre 1 : Distribution and trophic functioning of planktonic communities in coastal marshes in Atlantic Coast of France

Cette étude sur un an vise à comparer les réseaux trophiques planctoniques et les fonctions écologiques fournies entre ces deux marais dans le but d'évaluer si les modalités de gestion mises en place permettent le maintien des fonctions nourricière et épuratrice. Ce chapitre a été publié en tant qu'article en premier auteur dans le journal scientifique « Estuarine Coastal and Shelf Science » (<https://doi.org/10.1016/j.ecss.2023.108430>).

Distribution and trophic functioning of planktonic communities in coastal marshes in Atlantic Coast of France

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Abstract:

Coastal marshes are submitted to huge management due to anthropogenic pressure and thus, it is essential to preserve their biodiversity, their ecological functions and the ecosystem services they can provide. This study investigates the diversity and abundance of planktonic communities (heterotrophic prokaryotes, heterotrophic protists, microphytoplankton and metazooplankton). The aim of this study is to provide a first quantitative inventory on the plankton communities present in two marshes and to construct the different typologies of planktonic food webs in these marshes. Seasonal samplings (4) for environmental variables, nutrient concentrations and planktonic communities were conducted at 2-3 stations on each marsh during a year. A total of five different types of planktonic food web were determined, three of them were found in both marshes. The saltmarsh phytoplanktonic communities were dominated by Cryptophyta, nanoflagellates and Cyanobacteria. The freshwater marsh was dominated by Cryptophyta in autumn and winter and by a diverse phytoplankton community in spring. Marine copepods (Calanoida and Harpacticoida) characterized the saltwater metazooplanktonic communities, Cladocerans and Rotifera the freshwater ones. Overall, the

planktonic diversity was higher in the freshwater marsh (102 taxa) than in the saltwater marsh (54 taxa). Phytoplankton blooms represented nutrient and CO₂ uptake in both marshes and this reification function seemed most efficient in autumn in the saltmarsh. Considerable zooplankton communities represented a potential for nursery. Of the three management actions performed, only periodic water renewals might affect the seasonal dynamics of planktonic communities.

Keywords: plankton, purification function, nursery function, salt- and freshwater marshes, food web

Highlights

- Planktonic diversity differs highly between the salt- and freshwater marsh.
- Similar planktonic ecological functions can be found in both marshes.
- Seasonal variations might be affected by management operation.
- Monitoring planktonic communities is essential to adapt coastal marsh management.

1.1 Introduction

Coastal marshes are habitats with high biological productivity, sustaining many ecological functions (Vernberg, 1993; Więski et al., 2010). According to their uses and management, these environments can provide several ecosystem services. Some of the most common services are directly linked to the supply of human food resources, such as salt production, shellfish farming (Guillou, 1997; Leloup et al., 2008), and fisheries (Maltby, 1991). Moreover, coastal marshes can provide regulation services by forming a buffer zone against flooding of nearby inhabited areas (Sheng et al., 2022). They can also provide cultural services as recreational spaces for the human population (Ghermandi and Nunes, 2013) or provide refuge areas for migratory birds (Bradshaw et al., 2020). Overall, these different services are often valued by their economic value (Woodward and Wui, 2001), which drives the type of management applied to these environments. For example, in North America, dikes were constructed on some marshes to directly control flooding to favor the development of specific marsh grass for salt hay farming (Hinkle and Mitsch, 2005).

The various ecological functions and ecosystem services provided depend to a high extent on the biodiversity present in coastal marshes. Halophyte vegetations and macrophytes provide shelter for breeding and nesting for a wide diversity of animals from invertebrates to migratory birds (Pétillon et al., 2014; Jerabek et al., 2017; Joyeux et al., 2017). In addition, coastal marshes constitute crucial nurseries for juveniles of mobile species (*i.e.*, fish) that find requested trophic resources before migrating to a new habitat (Cattrijsse and Hampel, 2006). One of the main resources of fish juveniles using these habitats is metazooplankton (Stephenson, 1990; Kaneko et al., 2018; Talanda et al., 2022).

Planktonic communities are one of the actors of many ecological functions (Harris, 2012; D'Alelio et al., 2016; Hébert et al., 2016). For instance, in coastal marshes, they are known to take part in the water purification function by retaining suspended matter and nutrients and pollutants in the water column, thus preventing eutrophication (Azim et al., 2005; Verhoeven et al., 2006; Nyman, 2011). Bradley et al. (2010), showed that phytoplanktonic communities, especially picophytoplankton, were able to consume both organic and inorganic nitrogen sources. While many papers consider the importance of benthic communities on marsh ecology (Craft, 2000; Sullivan and Currin, 2002; Nordström et al., 2014), few studies focus on the planktonic communities and their ecological associated functions in coastal fresh and saltwater marshes (Quintana et al., 1998; Kobayashi et al., 2009). Even less consider the effect of management measures on plankton communities and associated functions and ecosystem services. David et al. (2020) studied the effect of human activities on phyto- and zooplankton diversity in specifically drained marshes; they demonstrated that water replenishment and urbanization have a strong effect on planktonic diversity and eutrophication. Koch and Gobler (2009) showed that draining in salt marshes directly affects water quality and can increase development of diatoms and dinoflagellates (*i.e.*, bloom). The introduction of species such as fish stocking for recreational fisheries can reshape planktonic diversity (Reissig et al., 2006) and might also bring non-native planktonic species. These invasive species might take over on native species if they are suited to the environmental conditions in the marshes (Dexter et al., 2020). The aim of this study is to provide a first quantitative inventory on the plankton communities present in the Fiers d'Ars and Tadon marsh, located on the west coast of France, and to construct the different typologies of planktonic food webs in these marches. Both marches being submitted to management practices, some considerations are formulated concerning the potential impact of these on the plankton community composition, abundance

and associated ecological functions, especially the water purification function and nursery function.

In this study, the term metazooplankton is used to cover meso- and microzooplankton. Management actions applied on the marshes were: (1) an annual drought, (2) the management of water inlet and renewal in the marshes and (3) the introduction of non-native species. The potential effect of these actions was compared to seasonal changes as observed in the planktonic communities during the study period.

Based on the collected data and the study of Masclaux et al., (2014), who quantified both abundances and flux between different planktonic compartments in a similar marsh also situated in Charente -Maritime (France) and supported by literature references, we deduce the most likely trophic pathways present in the studied marshes.

In short, microbial loops are found when both picophytoplankton and heterotrophic prokaryote abundances are high, (Legendre and Rassoulzadegan, 1995). Herbivorous food webs can be found when the temperature rises enough and nutrient concentration in the water column is sufficient to sustain phytoplankton blooms (Huppert et al., 2002; Masclaux et al., 2014; Trombetta et al., 2019). Multivorous food webs are likely when all planktonic communities are present and active in the water column (Masclaux et al., 2014). Biological winters reflect situations where abundance and activity of planktonic communities are low despite considerable concentrations of nutrients in the water column (Masclaux et al., 2014). More details on these characterizations are given in the discussion of the specific situations found in this study.

1.2 Methods

1.2.1 Study areas

The two marshes are located in Charente-Maritime, on the west coast of France (Figure 1.1). This area contains several coastal marshes (salt and freshwater type) with variable uses and management types and is considered as one of the biggest wetland zones in France (almost 100 000 ha) (David et al., 2020).

The saltwater marsh (salinity between 22.9 and 37.6 throughout the year) studied is the Fier d'Ars marsh, located at the North of the Ré-Island. This area is protected by a dike and is a highly touristic site where traditional shellfish and salt farming activities are carried out (Figure

1.1a). The vegetation around the marsh is mainly composed of *Halimione* sp., *Salsola soda* and *Tamarix* sp.. A part of this marsh is included in a natural reserve managed by the “Ligue pour la Protection des Oiseaux” (LPO). Sampling stations were selected in two areas. The first station FA (N 46° 14' 5.964"; W 1° 30' 20.707") is a 40 097 m² polyhaline basin with an average depth of 0.6 m located in the natural reserve. It is located about 0.1 km from the sea and connected to it by a channel. The management of this basin does not include dredging or cleaning and no species have been introduced in addition to the resident species in the marsh. The second station FB (N 46° 13' 26.4"; W 1° 27' 21.599") is an 8 483 m² polyhaline basin with an average depth of 0.75 m. It is located about 2 km from the sea and connected to it by a channel; when the tidal range reaches about 5.5 m, the water crossing the channels can enter the marshes. Thus, juvenile fish can enter the marsh. The management of this basin includes dredging once a year in March. As for FA, no species have been introduced in FB. The water inlets are regulated by a weir followed by a floodgate to control water renewals depending on the season and the tidal range.

The freshwater marsh (salinity between 0.1 and 0.5 through the year) studied is the urban Tasdon marsh located between La Rochelle and Aytré (Figure 1.1b). The vegetation around the marsh is mainly composed of *Arrhenatheretea elatioris*. Sampling stations were selected in three distinct areas located between 1.5 and 2.5 km from the sea. The first station TA (N 46° 8' 56.4"; W 1° 7' 26.4") is a 72 000 m² freshwater lake with a maximum depth of 1.35 m. The second station TB (N 46° 9' 3.6"; W 1° 8' 9.599") is a 21 400 m² freshwater basin with a maximum depth of 0.8 m. The third station labelled as TC (N 46° 8' 49.2"; W 1° 8' 13.2") is a 23 700 m² elongated freshwater basin with a maximum depth of 1 m. The management of these three stations does not include dredging nor cleaning. However, freshwater fish such as black-bass and sunfish have been introduced in these areas (early 2019) and tend to develop faster than the native fishes present in the marsh, such as *Carassius* spp. and *Gambusia* spp.. Water inlets are coming from an adjacent river connected to the stations: TB and TC located further downstream than at TA.

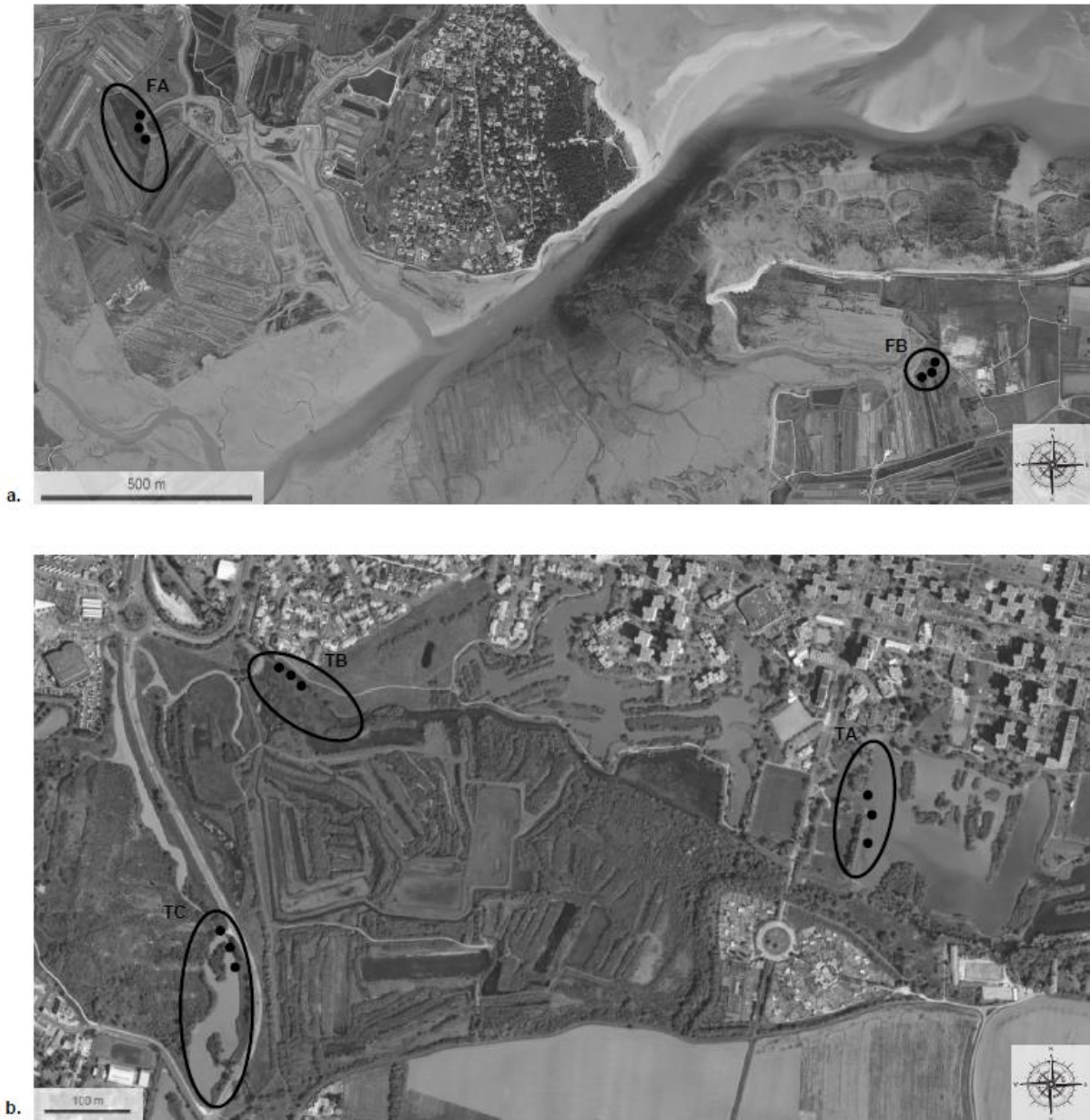


Figure 1. 1: Satellite view map of the two marshes studied showing the sampling stations: a. the Fier d'Ars saltwater marsh (FA: N 46° 14' 5.964"; W 1° 30' 20.707"; FB: N 46° 13' 26.4"; W 1° 27' 21.599") , b. the Tasdon freshwater marsh (TA: N 46° 8' 56.4"; W 1° 7' 26.4"; TB: N 46° 9' 3.6"; W 1° 8' 9.599"; TC: N 46° 8' 49.2"; W 1° 8' 13.2"). The series of dots for each station indicates the sampling points (triplicates). Map background issued and modified from the geoportal website. Pictures of each marsh are in Appendix 1.1.

1.2.2 Sampling methods

Four seasonal samplings, corresponding to a season cycle (winter, spring, summer, autumn) were conducted in 2019. All samplings were made in triplicate at each station at 0.5 m depth (sub-surface; measured with a measuring rod). Temperature, salinity, pH, and dissolved oxygen concentration were measured using a multiparametric probe (VWR™). A total of 5 L of water was sampled in polythene bottles (mid water column) for quantification of Suspended Particulate Matter (SPM: Suspended Particulate Inorganic Matter (PIM) and Suspended Particulate Organic Matter (POM)), dissolved nutrient analysis (NO₂, NO₃, NH₄, PO₄, Si), chlorophyll *a* concentration and abundances of different planktonic compartments (see after). These samples were preserved from light in opaque black plastic bags. To estimate the abundance of heterotrophic prokaryotes and pico-nanophytoplankton, 1.5 mL of water was directly transferred in cryotubes containing a mixture of glutaraldehyde (final concentration 0.2%) and poloxamer (final concentration 0.001%). These fixed samples were frozen in liquid nitrogen and then stored at -80°C in the lab. To study the diversity and abundance of microphytoplankton, 50 mL of water sample were directly fixed with alkaline lugol iodine (final concentration of 4%). For heterotrophic nanoflagellates (HNF), a 60 mL water sample was fixed with paraformaldehyde filtered at 0.22 µm (final concentration of 1%). Metazoan microzooplankton was sampled by filtering 6 L of water through a 63 µm mesh stainless-steel sieve and then fixed with buffered formaldehyde (final concentration 4%). Horizontal hauls were done at each station with a standard WP2 (200 µm mesh net) with an attached flow meter (Mechanical Flow Meter with back-run stop, Model 438 115) to sample mesozooplanktonic communities. The content of the net collector was fixed with buffered formaldehyde (final concentration 4%). Since the maximum depth was 1.35 m (TA), the effect of planktonic vertical migration was considered as low (Gliwicz, 1986; Semyalo et al., 2009; Das et al., 2020). Horizontal hauls were then sufficient to sample planktonic communities in the water column; thus, no additional vertical hauls were done. Except for samples contained in cryotubes, all the samples were kept at 4°C in a cold-storage room until analysis.

1.2.3 Sample analyses

The concentration of nitrate (NO₃), nitrite (NO₂), ammonium (NH₄), phosphate (PO₄) and silicate (Si) was determined on filtered water (0.7 µm GF/F glass fiber membrane, Whatman) using a SEALAA3 autoanalyzer with the detection limit of: 0.02 µmol.L⁻¹ (NO₃), 0.003 µmol.L⁻¹ (NO₂), 0.06 µmol.L⁻¹ (NH₄), 0.01 µmol.L⁻¹ (PO₄), 0.04 µmol.L⁻¹ (Si) according to the protocol of Aminot and K erouel (2004). SPM were measured by weighing filters according to the

protocol of Aminot and K erouel (2004). PIM was also measured by weighing filters after acidification. POM was calculated as the difference between SPM and PIM weight.

The concentration of chlorophyll *a* and phaeopigments was measured for each replicate for three size classes: microphytoplankton (> 20 μm), nanophytoplankton (between 3 and 20 μm) and picophytoplankton (< 3 μm). To do this, a triplicate filtration for each sampling was first performed on a 20 μm nylon fiber membrane (Millipore). Then, a fraction of the resulting filtrate was filtered onto a 3 μm nucleopore membrane (Whatman) and the rest of the filtrate onto a 0.7 μm GF/F glass fiber membrane (Whatman). Chlorophyll *a* and phaeopigments (*i.e.*, concentration of degraded chlorophyll pigment) concentrations were quantified by fluorimetry according to the protocol of Lorenzen (1966). The proportion of active chlorophyll *a* was measured by calculating the ratio of concentration of phaeopigments to phaeopigment plus chlorophyll *a* initially measured.

FlowCam analyses were conducted rapidly after field work at the laboratory on living microplanktonic organisms for each replicate using water from the polythene bottles. The abundance of microplanktonic groups (phytoplankton and heterotrophic protists) were determined by FlowCam analyses following the protocol of Buskey and Hyatt (2006). Microphytoplanktonic organisms (samples fixed with lugol) were identified at the highest taxonomic level possible and counted under an inverted microscope (IX70 Olympus) coupled with a camera (DFC 450C Leica) (mainly at x400) according the Uterm ohl protocol (1958). One sample for each station-season were processed.

The abundance of heterotrophic prokaryotes, pico- and nanophytoplankton were determined by flow cytometry analyses performed with a FACS CantoII flow cytometer according to the method described in Marie et al. (1999). The abundance of HNF from 2 to 20 μm was assessed by counting cells by epifluorescence microscopy using the method of Bloem et al. (1986). Micro- and mesozooplanktonic organisms were identified and counted with binocular microscope observations using the protocol of Postel et al. (2000). Identification of micro- and mesozooplankton was performed to the species level whenever possible (genus or order if damaged). To achieve species level identification, crustaceans were dissected and observed with an optical microscope (x400) when necessary. All five copepodite stages were regrouped for each copepod order. Planktonic larvae were identified to order directly under a stereomicroscope (x120) without prior dissection.

1.2.4 Statistical analyses

All statistical analyses were conducted with R software (version 4.0.3.). First, heatmaps including dendrograms based on euclidean distances were done to evaluate phytoplanktonic and metazooplanktonic diversities on both marshes for each sampling station on the four seasons. In addition, the data set obtained in this study was analyzed using a Multiple Factor Analysis (MFA) (Pagès, 2002), with FactoMineR and factoextra packages, to determine key variables guiding the seasonal dynamics of planktonic communities on both marshes. Quantitative variables were divided in three groups: a group including all abiotic parameters, a group including metazooplanktonic taxa and a group including phytoplanktonic taxa. The management actions, including annual drought, water inlet and renewal and introduction of non-native species, were used as descriptive qualitative variables (see Appendix 1.2). Then, boxplots (package ggplot2) with associated Permanova and Fisher test (package vegan) were done to determine the different types of planktonic food web (FW) per group, as described by Masclaux et al. (2014). These analyses allow to compare, for each station-season couple, the concentration of nutrients (NO₂, NO₃, NH₄), PIM, the proportion of active chlorophyll *a* and the concentration of chlorophyll *a* for the three size classes (larger than 20 µm, between 20 and 3 µm, less than 3 µm), and the abundance of micro- and mesozooplankton, ciliates, diatoms and heterotrophic prokaryotes.

1.3 Results

1.3.1 Diversity of microphytoplankton and metazooplankton

A total of 54 taxa for the Fier d'Ars marsh and 102 taxa for the Tasdon marsh were determined for the microphytoplanktonic compartment. Taxa which were only present at one season for a single sampling station were removed to retain the most representative taxa of the total abundance corresponding to 98% of the total abundance. Therefore, respectively 33 and 64 taxa for the Fier d'Ars marsh and the Tasdon marsh were kept to study relative abundances of microphytoplanktonic communities per season-station with a heatmap. For the Fier d'Ars marsh (Figure 1.2a), the dominant phytoplanktonic species was *Teleaulax amphioxeia* (Cryptophyta), which was most abundant in autumn at both FA and FB and in winter in FA. In summer, flagellates sp2 (not determined) were most abundant at FB whereas *Planktolyngbya limnetica* (Cyanobacteria) was the most abundant at FA for the same season. Considering the distribution of microphytoplankton communities between stations and by season (results of

clustering on heatmap), three groups could be distinguished: a first group including FB station in spring and summer, a second group including both FA and FB in autumn and FA in winter, and finally a third group including FA in summer and spring and also FB in winter.

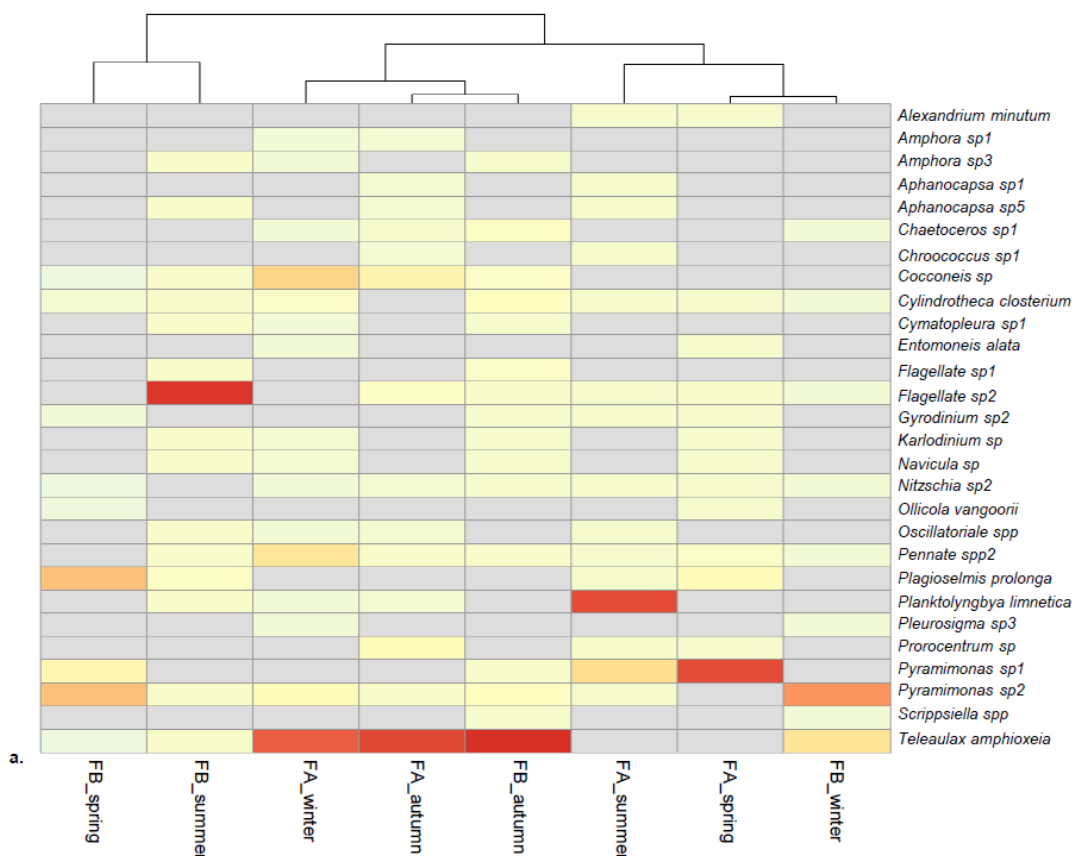
For the Tasdon marsh (Figure 1.2b), the dominant phytoplanktonic species was *Plagioselmis nannoplanctica* (Cryptophyta) which was most abundant in autumn and winter at TA and in autumn at TB. In summer, microalgae of the genus *Scenedesmus* and *Willea rectangularis* (Chlorophyta) were most abundant at TA and TB while *Lepocinclis acus* (Euglenozoa), *Haslea* sp., *Aulacoseira granulata* (diatoms), and cyanobacteria of the genus *Aphanocapsa* were most abundant at TC. In spring, *Dinobryon* sp. (Chrysophyceae) and flagellates were the most present at TA while green algae of the genus *Monoraphidium* were dominant at TB. In the same season, *Monoraphidium* algae were also found with a high abundance at TC with also *Haslea* sp., *Cryptomonas curvata* and flagellates sp6. Again considering, only the distribution of phytoplankton communities (results of clustering on heatmap), four groups could be distinguished: a first group including TA and TB in summer, a second group including TA and TC in spring and TC in summer, a third group including all stations in autumn, and TA and TB in winter, and a fourth group including TB in spring and TC in winter.

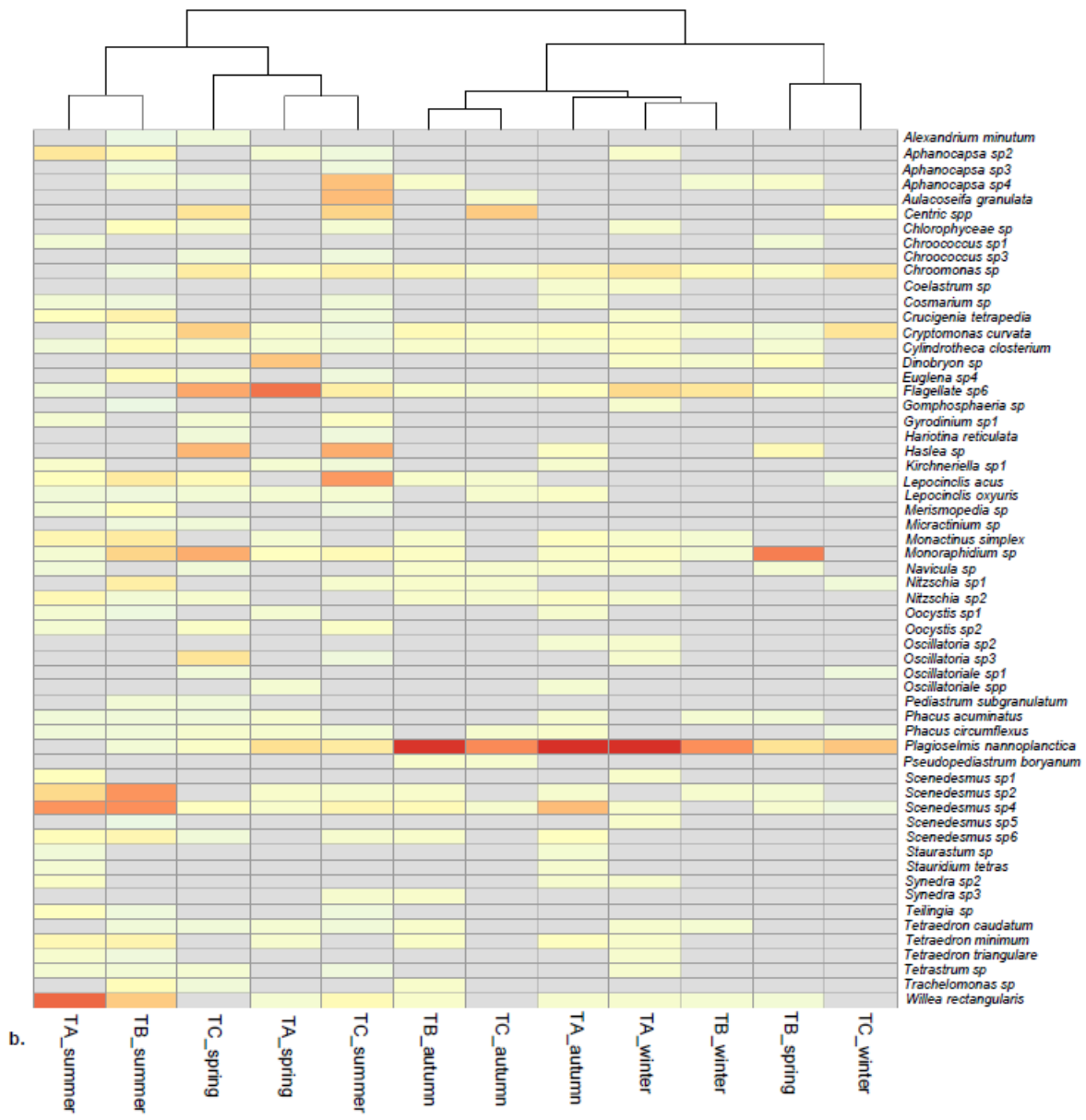
For the metazooplanktonic compartment, 30 and 42 taxa were determined for the Fier d'Ars marsh and the Tasdon marsh, respectively. As for the phytoplanktonic compartment, relative abundances for each taxon were studied per season-station. For the Fier d'Ars marsh (Figure 1.2c), copepods were most abundant with the dominant genus *Acartia* at both FA and FB, especially in autumn. Copepod nauplii were dominant in spring at both FA and FB, as well as in summer at FB. A high abundance of Zoe larvae (*i.e.*, larvae of crab) was also noticed in spring at FA. Considering the distribution of metazooplankton communities between stations and by season, two groups seemed to stand out: a group including both FA and FB in autumn and winter and FA in summer, and a group including both FA and FB in spring and FB in summer.

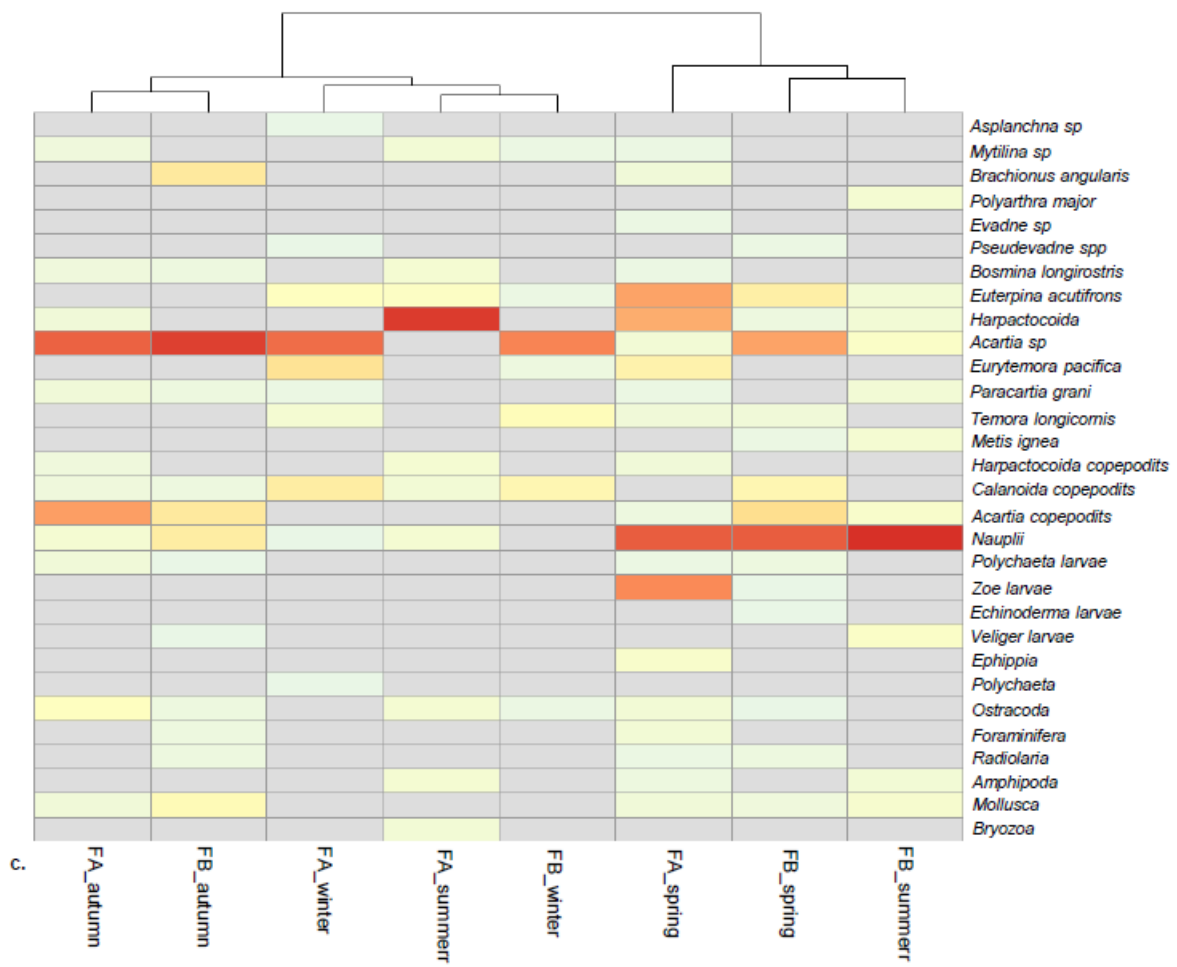
For the Tasdon marsh (Figure 1.2d), Cladocerans were the most abundant, especially *Bosmina longirostris* with highest relative abundances observed in spring at TA and TB as well as in autumn at TA and TC. Cyclopoid copepodite abundances were also high in summer at TA and TB. Rotifers of the genus *Asplanchna* were the most abundant in winter at the three stations, and TC in spring. Nauplii of copepods were the most abundant in summer in TC and in autumn in TB. In addition, two exotic and tropical zooplankton species were found in Tasdon marsh: *Keratella tropica* and *Brachionus falcatus*. Looking at the distribution of mesozooplankton communities between stations and by season, three groups could be distinguished: a first group

including the three stations in winter and TC in spring, a second group including TA in spring and autumn, TB in spring and TC in autumn, and finally a third group including the three stations in summer and TB in autumn gathering the juveniles' forms of copepods (nauplii and copepodites).

Comparing both planktonic communities, the heatmaps showed different station-season's clustering according to the type of planktonic community studied. First, for both study areas, the number of groups resulting from clustering with the relative abundances of microphytoplankton or metazooplankton was different. For the Fier d'Ars data, the majority of station-seasons were grouped in the same way for phyto- and metazooplankton with the exception of FA in spring and winter. For the Tasdon data, more differences were observed: whereas all three stations were grouped together for respectively summer and winter when looking at metazooplanktonic relative abundances, they were only all grouped together for autumn when looking at phytoplanktonic relative abundances. TA and TC in spring were grouped together with TC in summer when looking at phytoplanktonic relative abundances. In contrast, when looking at zooplankton relative abundances, TA and TB in spring were grouped together with TA and TC in autumn, and TC in spring was grouped with all three stations in winter.







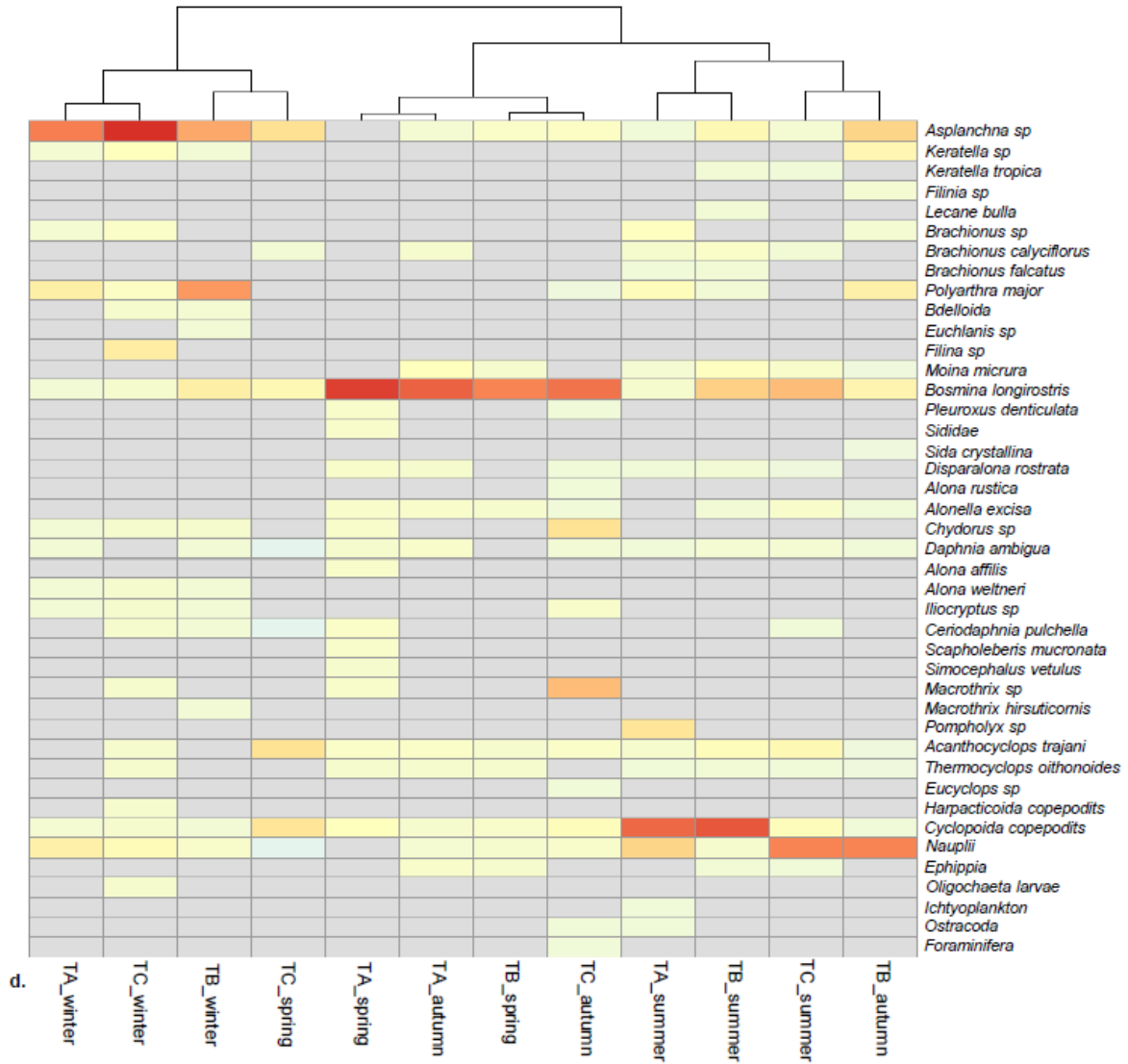


Figure 1. 2: Relative abundances (%) of principal microphytoplanktonic taxa (a,b) and metazooplanktonic taxa (c,d) identified at each sampling station in winter, spring, summer and autumn in the Fier d’Ars marsh (FA, FB) and the Tasdon marsh (TA, TB, TC), The redder the color, the higher the relative abundance for that taxon. Clustering of station-season couples were done using the ward method with euclidean distances.

1.3.2 Spatio-temporal variations of planktonic communities

For the Fier d'Ars marsh, the three axes of the MFA explained around 72% of the variance of data (Figure 1.3). The abundance of heterotrophic prokaryotes (HPT), euglena (EUG), rotifera (RTF), metazooplanktonic larvae (LRV), copepoda (COP), other metazooplanktonic organisms (OTH) and pennate diatoms (DTMp) defined the first axis of the MFA with abiotic variables such as the water temperature (T.w) and salinity (Sal). It was noted that all these variables were in opposition with the dissolved oxygen concentration (O_2). The abundance of cryptophyceae, cladocerans (CLA) and the four other metazooplanktonic groups which already defined the first axis (COP, OTH, LRV, RTF), euglena, as well as the concentration of particulate organic matter (POM) and dissolved silicate (SI), hydrogen potential (pH) and the proportion of active chlorophyll *a* for organisms between 3 and 20 μm defined the second axis. The third axis was explained by the abundance of naked ciliates (CILn) and the concentration of nitrate (NO_3), nitrite (NO_2), phosphate (PO_4) and particulate inorganic matter (PIM). The importance of environmental parameters (especially temperature, salinity, and dissolved oxygen concentration) in the distribution of the data indicated a strong seasonal effect. This observation was confirmed by the representation of station-season individuals with ellipses of confidence via the MFA (Figure 1.4), where especially summer and winter seemed to stand out from the other seasons. Contrary to the seasonal effect, the three management operations included in the MFA as descriptive qualitative variables, were not well represented in the three axes of the MFA.

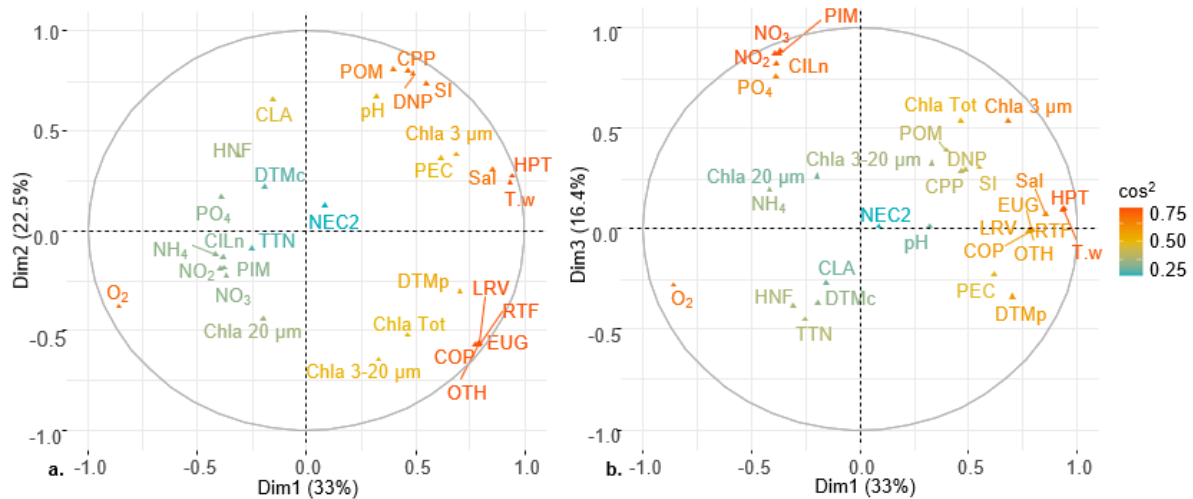


Figure 1. 3: Correlation circle from MFA analysis on the Fier d’Ars marsh data: a. axes 1-2, b. axes 1-3. The quality of the representation of the quantitative variables is indicated by the \cos^2 value.

Details: pH: hydrogen potential, T.w: water temperature, Sal: salinity (ppt), O_2 : dissolved oxygen concentration (mg/l), NO_3 : nitrate concentration ($\mu\text{mol/l}$), NO_2 : nitrite concentration ($\mu\text{mol/l}$), NH_4 : ammonium concentration ($\mu\text{mol/l}$), PO_4 : phosphate concentration ($\mu\text{mol/l}$), SI: silicium concentration ($\mu\text{mol/l}$), PIM: particulate inorganic matter concentration (mg/l), POM: particulate organic matter concentration (mg/l), Chla Tot: proportion of total active chlorophyll a (%), Chla 20 μm : proportion of active chlorophyll a for organisms bigger than 20 μm (%), Chla 3-20 μm : proportion of active chlorophyll a for organisms between 3 and 20 μm (%), Chla 3 μm : proportion of active chlorophyll a for organisms smaller than 3 μm (%), RTF: Rotifera abundance (ind/m^3), CLA: Cladocera abundance (ind/m^3), COP: Copepoda abundance (ind/m^3), LRV: larvae and eggs abundances (ind/m^3), OTH: other metazooplanktonic organisms abundance (ind/m^3), DTMp: pennate diatoms abundance (cell/l), DTMc: centric and chain diatoms abundance (cell/l), TTN: tintinnids abundance (cell/l), EUG: euglena abundance (cell/l), DNP: dinophyceae abundance (cell/l), CPP: cryptophyceae abundance (cell/l), NEC2: nanoeukaryotes abundance determined by flow cytometry (cell/ml), PEC: picoeucaryotes abundance determined by flow cytometry (cell/ml), CILn: naked ciliates abundance (cell/l), HNF: heterotrophic nanoflagellates abundance (cell/l), HPT: heterotrophic prokaryotes abundance (cell/ml). The quality of the representation of the variables on the graph is indicated by the squared cosine of the variables (\cos^2).

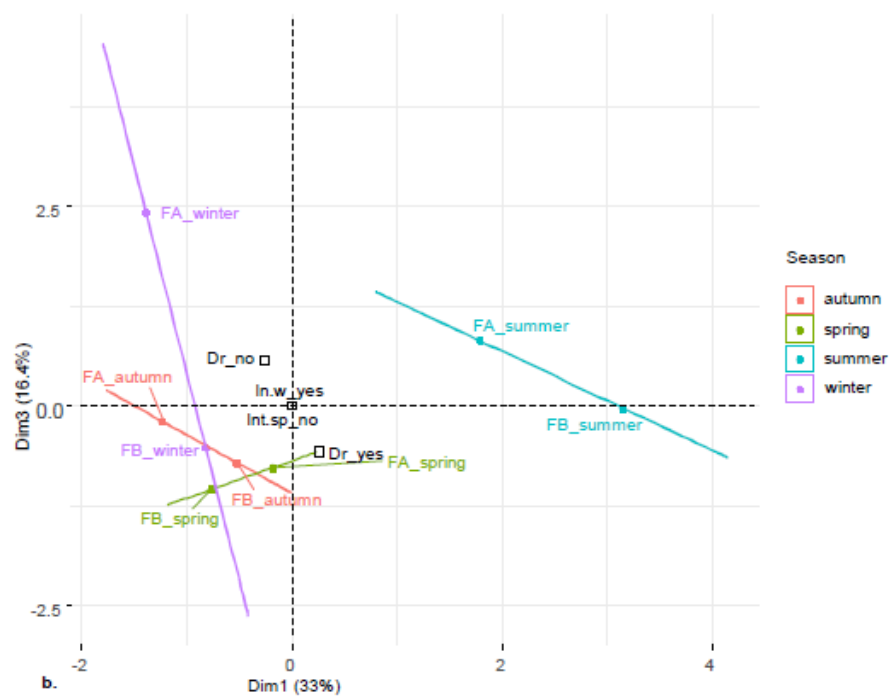
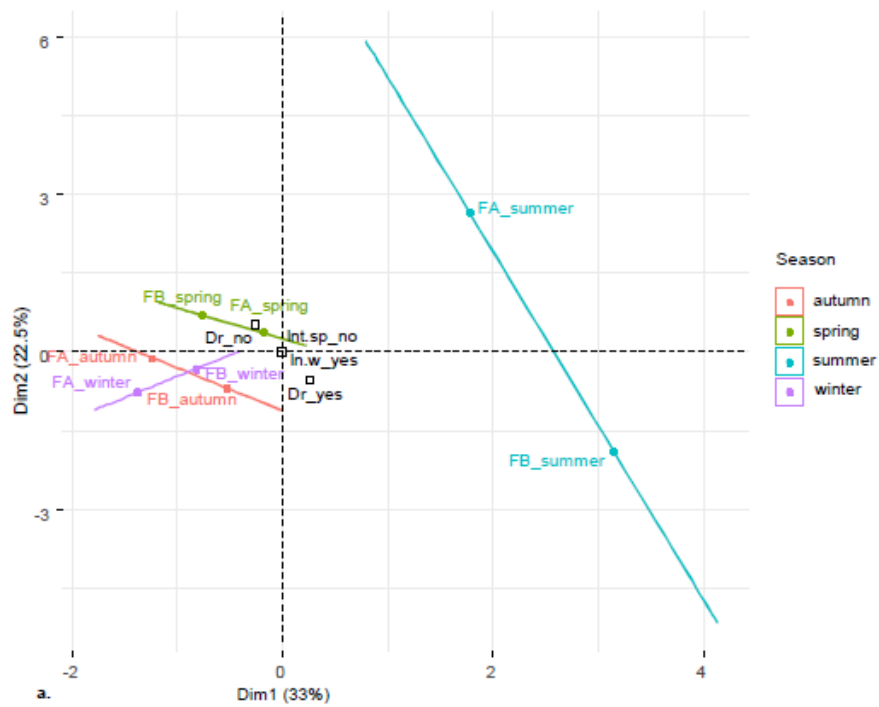


Figure 1. 4: Confidence ellipses on individuals (station-season) from MFA analysis for the four sampling season (spring, summer, autumn, winter) for the Fier d’Ars marsh: a. axes 1-2; b. axes 1-3. Ellipses are represented by straight lines because there are only two sampling stations for this marsh. Dr_no: no annual drought; Dr_yes: annual drought made; In.w_yes: water inlet and renewal made at high tide; Int.sp_no: no introductions of non-native species.

For the Tasdon marsh, around 70% of the variance in the data was explained by the three axes of the MFA (Figure 1.5). The first axis was explained by the abundance of copepoda (COP), cladocera (CLA), metazooplanktonic larvae, heterotrophic prokaryotes, euglena, picoeukaryotes, nanoeukaryotes (NEC1 and NEC2), pennate diatoms and cyanobacteria, as well as the concentration of particular organic matter, silicate. This group was in opposition with nitrates (NO_3) and nitrites (NO_2). Water temperature also positively explained the first axis. The second axis was explained by the abundance of other metazooplanktonic organisms, centric and chain diatoms, as well as the proportion of total active chlorophyll *a* (total and for the three studied size classes), the concentration of particulate inorganic matter, dissolved O_2 , and negatively by salinity and pH. The third axis was mainly determined by the proportion of total active chlorophyll *a* (total and for the three studied size classes), the concentration of phosphate and negatively by the abundance of Rotifera. The abundance of photosynthetic communities on the three size classes was an important factor characterizing the station-month pairs. Furthermore, and similarly to the Fier d'Ars, the importance of environmental parameters (especially temperature and nutrients) in the data distribution indicated a strong seasonal effect. This seasonal effect was revealed by the representation of station-season individuals with ellipses of confidence via the MFA (Figure 1.6), where especially summer seemed to stand out from the other seasons. Water inlet and renewal was represented on the second axis.

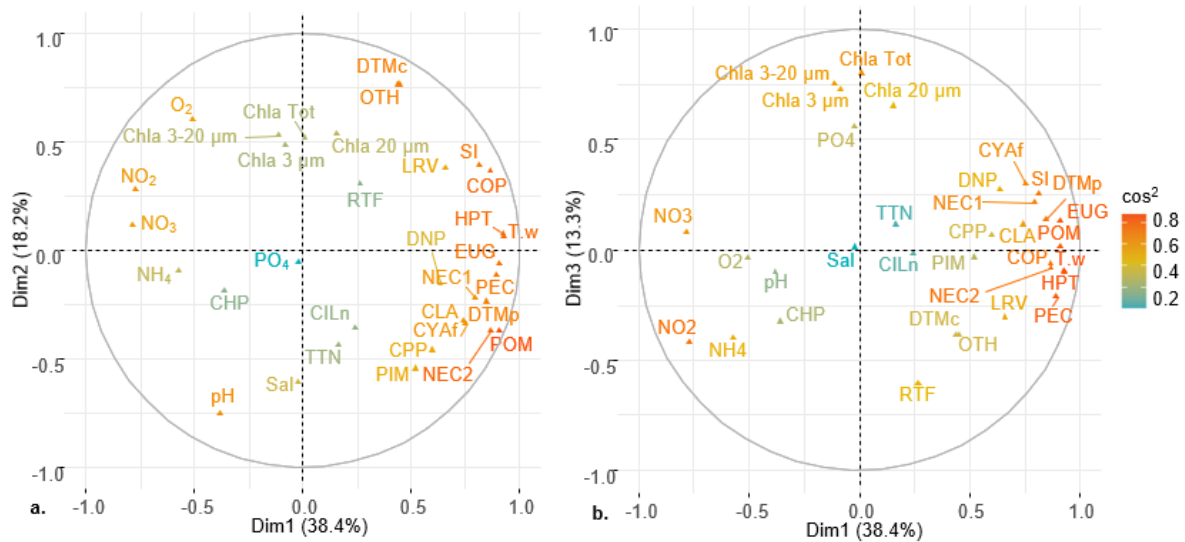


Figure 1. 5: Correlation circle from MFA analysis on the Tasdon marsh data: a. axes 1-2, b. axes 1-3. The quality of the representation of the quantitative variables is indicated by the \cos^2 value.

Details: pH: hydrogen potential, T.w: water temperature, Sal: salinity (ppt), O_2 : dissolved oxygen concentration (mg/l), NO_3 : nitrate concentration ($\mu\text{mol/l}$), NO_2 : nitrite concentration ($\mu\text{mol/l}$), NH_4 : ammonium concentration ($\mu\text{mol/l}$), PO_4 : phosphate concentration ($\mu\text{mol/l}$), SI: silicium concentration ($\mu\text{mol/l}$), PIM: particulate inorganic matter concentration (mg/l), POM: particulate organic matter concentration (mg/l), Chla Tot: proportion of total active chlorophyll a (%), Chla 20 μm : proportion of active chlorophyll a for organisms bigger than 20 μm (%), Chla 3-20 μm : proportion of active chlorophyll a for organisms between 3 and 20 μm (%), Chla 3 μm : proportion of active chlorophyll a for organisms smaller than 3 μm (%), RTF: Rotifera abundance (ind/m^3), CLA: Cladocera abundance (ind/m^3), COP: Copepoda abundance (ind/m^3), LRV: larvae and eggs abundances (ind/m^3), OTH: other metazooplanktonic organisms abundance (ind/m^3), DTMp: pennate diatoms abundance (cell/l), DTMc: centric and chain diatoms abundance (cell/l), TTN: tintinnids abundance (cell/l), EUG: euglena abundance (cell/l), DNP: dinophyceae abundance (cell/l), CPP: cryptophyceae abundance (cell/l), NEC2: nanoeukaryotes abundance determined by flow cytometry (cell/ml), PEC: picoeucaryotes abundance determined by flow cytometry (cell/ml), CILn: naked ciliates abundance (cell/l), HNF: heterotrophic nanoflagellates abundance (cell/l), HPT: heterotrophic prokaryotes abundance (cell/ml). The quality of the representation of the variables on the graph is indicated by the squared cosine of the variables (\cos^2).

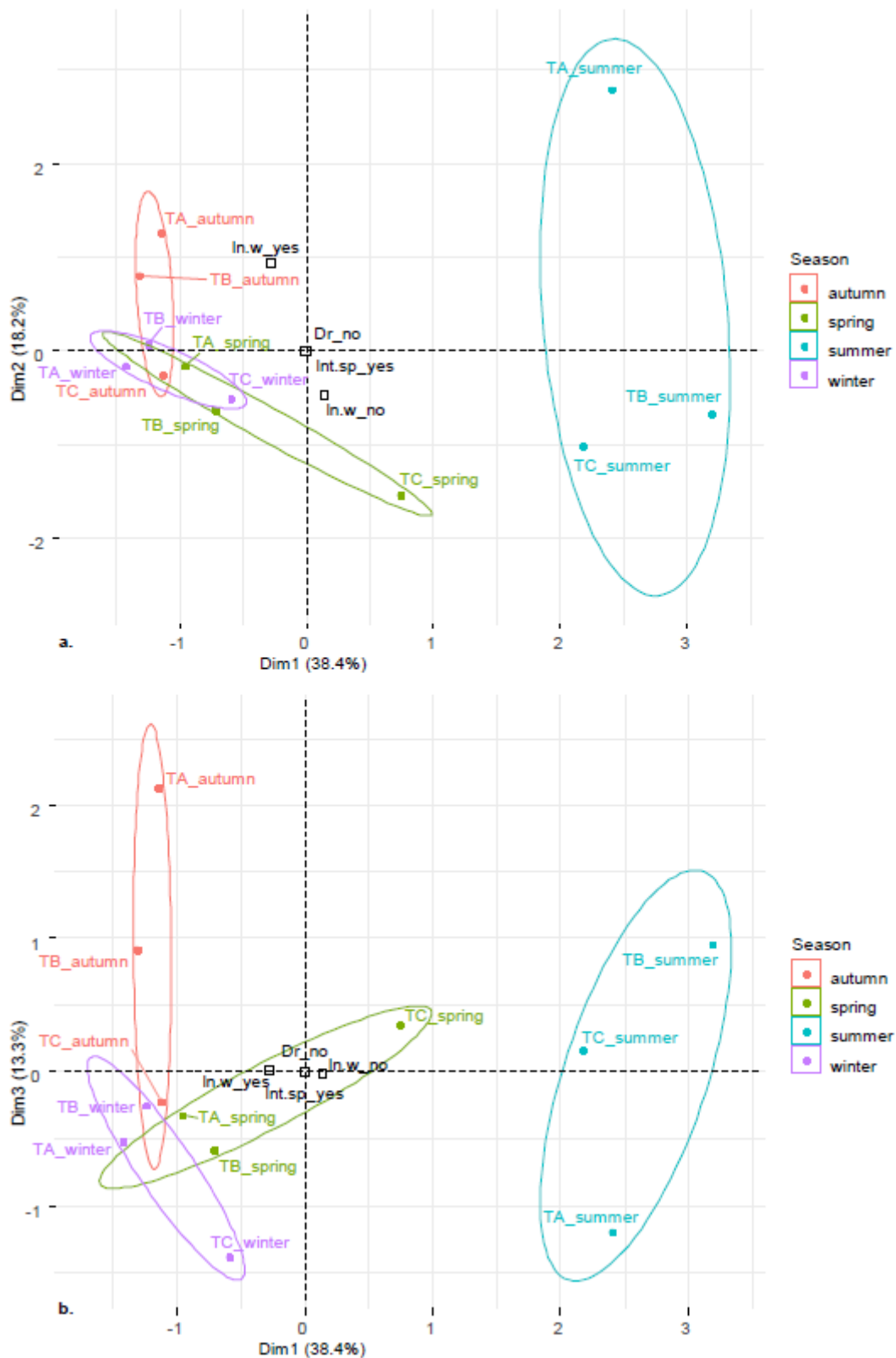


Figure 1. 6: Confidence ellipses on individuals (station-season) from MFA analysis for the four sampling season (spring, summer, autumn, winter) for the Tasdon marsh: a. axes 1-2; b. axes 1-3. Dr_no: no annual drought; In.w_yes: water inlet and renewal made at high tide; In.w_no: no water inlet and renewal made; Int.sp_yes: introductions of non-native species have been made.

1.3.3 Planktonic food web typologies

For the Fier d’Ars marsh, four different food web types were determined during the year of the survey (Figure 1.7). An herbivorous food web (noted FW1, see Figure 1.9), characterized by high abundances of phytoplanktonic communities and high proportion of active chlorophyll *a*, was observed in spring on both FA and FB. A multivorous food web (noted FW2, see Figure 1.9), characterized by high abundances of heterotrophic prokaryotes, micro- and mesozooplanktonic communities, and a medium abundance of phytoplanktonic communities, was observed in summer on both FA and FB. In the case of FA, this food web (FW2, see Figure 1.9) was developing in summer, with an increase in abundance of heterotrophic prokaryotes and phytoplanktonic communities compared to spring, although the abundance of metazooplanktonic communities did not yet increase. The third type of food web, defined as microbial loop (FW3, see Figure 1.9) was observed in autumn on FA, characterized by high concentrations of NH_4 , with average abundance of heterotrophic prokaryotes. The food web “biological winter” (noted FW4, see Figure 1.9) was observed in autumn on FB and in winter on both FA and FB, and was characterized by low abundances of phyto- and zooplanktonic communities, lower abundances of heterotrophic prokaryotes than in the previous season (autumn for FA, summer for FB), as well as an increase of the concentration of NO_2 , NO_3 and PIM.

For the Tasdon marsh, four different food web types were determined, three of which are identical to those identified at the Fier d’Ars marsh (Figure 1.8). As for FA and FB, the herbivorous food web FW1 was observed in spring on TA and TB, and also in winter on TC. The multivorous food web FW2 was observed in summer on all three stations (TA, TB, TC) and in spring on TC. However, this last station was more characterized by FW2 in summer than in spring because the abundances of micro- and mesozooplanktonic communities, phytoplanktonic organisms larger than $20\ \mu\text{m}$ and smaller than $3\ \mu\text{m}$, diatoms and heterotrophic prokaryotes were higher in summer than in spring. The food web FW4 was observed at all three stations in autumn. Another food web identified as “biological winter” (noted FW5, see Figure 1.9) was observed in winter on TA and TB. The main difference between this “biological winter” and FW4 was the higher concentration of NO_2 and NO_3 measured in winter compared to the concentration measured in autumn for these two stations.

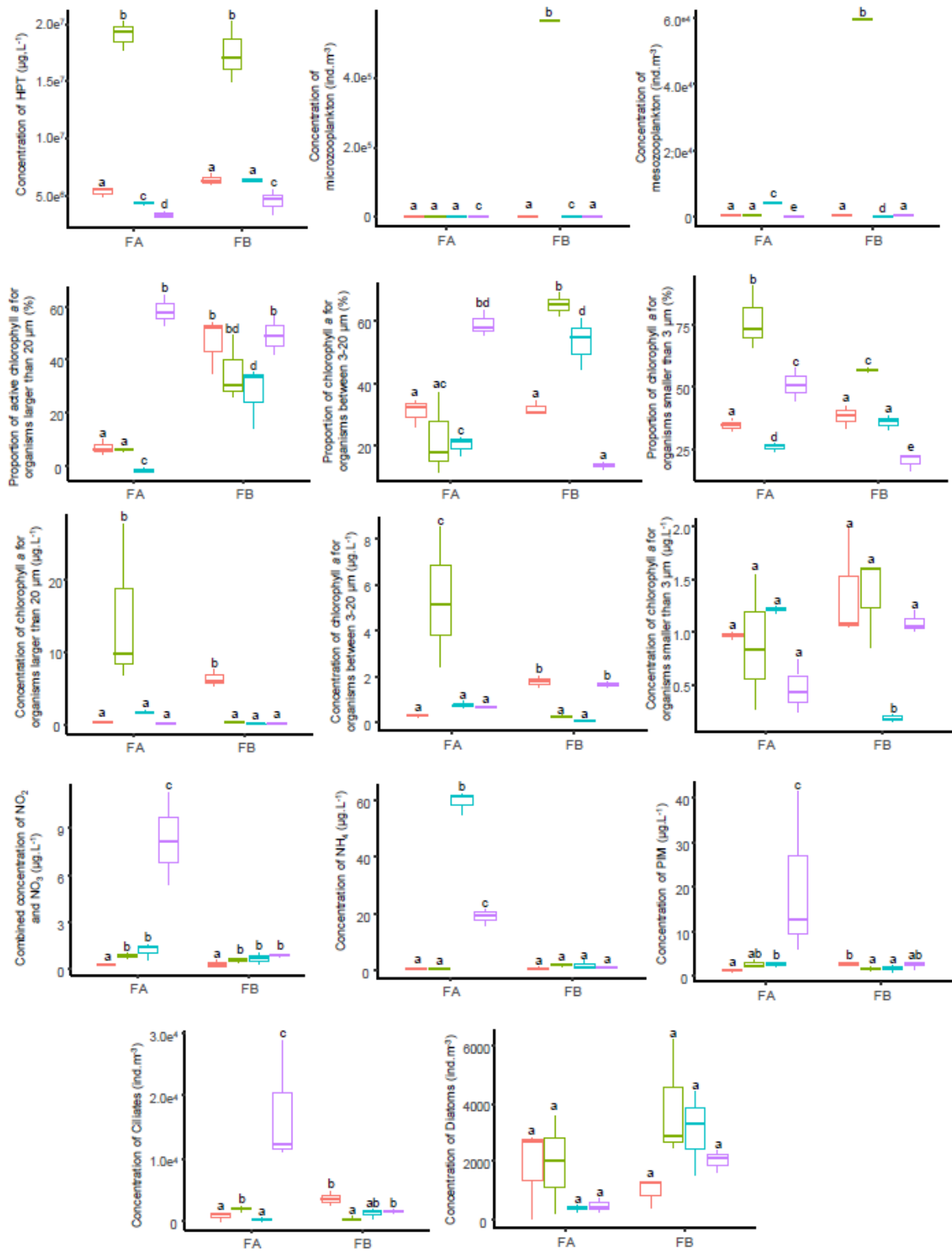


Figure 1. 7: Boxplot showing the median per group for abiotic and biotic parameters per station on the Fier d'Arç saltwater marsh (FA, FB) for each sampling season (red: spring, green: summer, blue: autumn, purple: winter). Results of Permanova analysis for each station per season, showing the significance of differences in values, are represented by the lettering above each box. Boxes for micro- and mesozooplanktonic concentrations are shown as straight lines because the counts were made on the average of the pulled samples (triplicates).

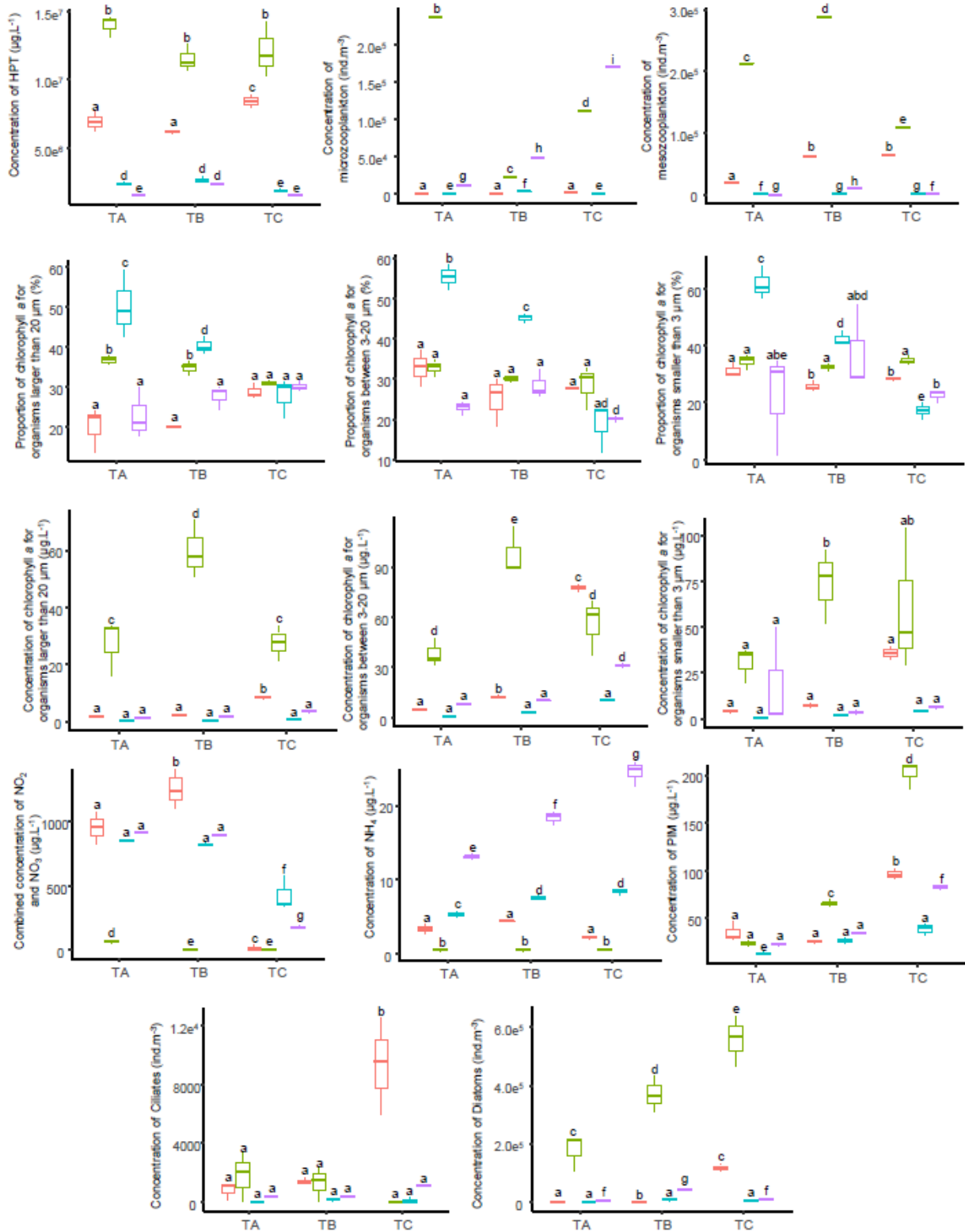


Figure 1. 8: Boxplot showing the median per group for abiotic and biotic parameters per station on the Tasdon freshwater marsh (TA, TB, TC) for each sampling season (red: spring, green: summer, blue: autumn, purple: winter). Results of PerMANOVA analysis for each station per season, showing the significance of differences in values, are represented by the lettering above each box. Boxes for micro- and mesozooplankton concentrations are shown as straight lines because the counts were made on the average of the pulled samples (triplicates).

	Spring	Summer	Autumn	Winter
FA	FW1	FW2	FW3	FW4
FB	FW1	FW2	FW4	FW4
TA	FW1	FW2	FW4	FW5
TB	FW1	FW2	FW4	FW5
TC	Weak	Strong	FW4	FW1






FW1		Herbivorous food web
FW2		Multivorous food web
FW3		Microbial loop
FW4		Biological winter
FW5		Biological winter with high nutrient concentration

Figure 1. 9: Summary of the five different types of food webs (FW1, FW2, FW3, FW4, FW5) determined by the method of Masclaux et al. (2014) in spring, summer, autumn and winter 2019 in the Fier d’Ars marsh (FA, FB) and the Tasdon marsh (TA, TB, TC).

1.4 Discussion

1.4.1 Diversity and trophic functions of microphytoplankton and metazooplankton

Overall, the planktonic diversity was higher in the freshwater marsh of Tasdon (102 taxa) than in the saltwater marsh of the Fier d’Ars (54 taxa). The saltmarsh phytoplanktonic communities were dominated by Cryptophyta in autumn and winter, and by nanoflagellates and Cyanobacteria in summer. Marine copepods (Calanoida and Harpacticoida) characterized the metazooplanktonic communities. The freshwater marsh (Tasdon) was also dominated by Cryptophyta in autumn and winter. However, in summer, Chlorophyta dominated at TA and TB while Euglenozoa, some diatoms and cyanobacteria dominated at TC. In spring, phytoplanktonic communities were dominated by Chrysophyceae, Chlorophyta and undetermined flagellates dominated the and metazooplanktonic communities by Cladocerans and Rotifera.

These differences of planktonic taxa are consistent with planktonic diversity described in different habitats (salt or freshwater) in the literature (*e.g.*, Walkusz et al., 2010; Badsı et al., 2012; Thakur et al., 2013; Grujcic et al., 2018). Focusing on phytoplanktonic species, the data showed similarities in the taxa found in both salt- and freshwater marsh, such as, for example, the presence of Cryptophyta. However, high abundances of cyanobacteria and Euglenozoa were found in addition in the freshwater marsh in summer. This observation is often correlated with high turbidity (up to an average of $223.84 \pm 13.41 \mu\text{g L}^{-1}$ of PIM at TC in summer) and can

cause the seasonal succession of food webs in the marsh (Abrantes et al., 2006). However, Ersanli and Gönülol (2006) concluded that such environmental conditions are an indicator of low water quality.

It has been demonstrated in many aquatic ecosystems that a higher diversity might generate a better stability and resilience (e.g., Ives and Carpenter, 2007; Pennekamp et al., 2018). Although diversity can induce functional redundancy and hence not necessarily additional ecological functions, it can also induce more diversified ecological functions. Indeed, the more different species there are, the higher the probability of having species with different functional traits, and thus of having actors of different ecological functions. It is therefore important to keep a high planktonic diversity in these environments in order to maintain a maximum of ecological functions provided by these communities (Norlin et al., 2006; Chaparro et al., 2019). In this study, the higher diversity of phytoplanktonic communities in the freshwater marsh might produce a higher primary production than in the saltwater marsh, which has lower phytoplanktonic diversity. Some protists (Euglenozoa, Cryptophyta, some of the ciliates) are mixotrophic and can change their trophic regime according to the environmental conditions (Esteban et al., 2010; Cordoba et al., 2021), thus their trophic functions are more difficult to determine. Nevertheless, these communities contribute, with the other autotrophic phytoplanktonic communities, to the fixation of atmospheric carbon through photosynthesis (Yan et al., 2021; Jia et al., 2022; Cohen, 2022). The resulting phytoplankton biomass, which might then be transferred along food web to higher trophic levels via the protists and mesozooplankton in these marshes and as such fuel the supply function (Atkinson et al., 1996).

Focusing on the trophic diets of metazooplanktonic species identified in this study, there was a high proportion of omnivorous species in the Fier d’Ars marsh, such as Harpacticoid copepods, *Acartia* sp., *Temora longicornis*, *Eurytemora pacifica*, *Evadne* spp., *Brachionus angularis* (Rieper, 1982; Kleppel, 1993; Berggreen et al., 1988). Different meroplanktonic larvae were also observed (Polychaeta, Zoe, Echinoderma, veligers), confirming the importance of omnivory in the Fier d’Ars marsh (McEdward, 2020). Furthermore, detritivore species, such as *Mytilina* sp., Ostracoda and Amphipoda (Navarro-Barranco et al., 2013; Galir Balki et al., 2017) were also present.

For the Tasdon marsh, *Asplanchna* sp., *Ceriodaphnia pulchella*, *Acanthocyclops trajani*, *Brachionus calyciflorus*, *Brachionus falcatus*, *Polyarthra major*, *Keratella tropica*, *Lecane bulla*, described as omnivorous species (Amoros, 1984; Abrantes et al., 2009; Santos-medrano et al., 2016; Rahmati et al., 2020), were present. Non-selective filter feeder species as *Bosmina*

longirostris and *Sida cristallina* (Amoros, 1984; Bleiwas and Stokes, 1985) were also present. Detritivore species (Amoros, 1984; Robertson, 1988) in the Tasdon marsh, were *Disparalona rostrata* and *Alonella excisa*.

Since omnivorous and non-selective filter feeder species can feed indifferently on plant or animal organisms, they are more likely to find resources, which explains their high abundance in the marshes. High abundances of these metazooplanktonic communities can provide a significant food source for higher trophic level, and thus support the nursery function (Milstein et al., 2006; Rahmati et al., 2018; Didenko et al., 2020). Detritivore species feed on suspended detrital matter by filtration and are therefore actors of the purification function (Stanachkova et al., 2017). Overall, in both marshes, similar trophic functions were found, which means that similar types of planktonic food web probably exist in both of these marshes.

1.4.2 Seasonal changes of planktonic communities

On both marshes, a strong seasonal effect was observed in the planktonic communities. The environmental parameter most strongly associated with the variability of these communities was temperature, which explains the difference between the confidence ellipses of the stations in summer compared to other seasons (Figures 1.4 and 1.6). Phytoplankton blooms take up nutrients and as such purify the water. At FA station, the NO_2 and NO_3 concentrations were low in all the seasons except in winter, and in parallel, phytoplankton abundance or biomass of chlorophyll were high in spring and summer. Phytoplankton biomass provides resources for herbivorous (e.g., *Paracartia grani* for the Fier d'Ars marsh and *Daphnia ambigua* for the Tasdon marsh), omnivorous and non-selective filter-feeder zooplankton (Timms and Moss, 1984; Landry et al., 2004), thus supporting the entire food web (Costalgo et al., 2020). In addition, for the Fier d'Ars marsh, there was a strong effect of nutrients (NO_2 , NO_3 , PO_4) observed with the MFA analysis, possibly linked to the run-off. For the Tasdon marsh, the MFA analysis showed that phytoplanktonic communities were key actors with the strong correlation of the proportion of active chlorophyll *a* for all three size classes. Apart from TA which can receive freshwater from a connected river according to its seasonal flow, TB and TC are stagnant marshes, without water renewal. It is known that planktonic communities tend to develop better with higher abundances in lentic and stagnant environments than in lotic environments because their residence time in the environment is longer (Baker and Baker, 1979; Koslow et al., 2008). So here also, the considerable phytoplankton presence represents a purification function.

1.4.3 Food web and ecological functions

While the present study does not include flux measurements, the deduction of food web typologies made from biomass data is justified by the fact that solid theoretical basis exists for this approach (Volterra, 1928; Tortajada, 2011; Barbier and Loreau, 2019). Also, several of the food web typologies reported in the marches studied, such as an herbivorous, microbial and mixed loop types have also been found experimentally in other coastal, SPM rich environments, such as brackish and freshwater estuarine reaches (Tackx et al., 2003; David et al., 2006; Van de Meersche et al., 2009; Masclaux et al. 2014; Kimmel et al., 2015; David et al., 2016).

A total of five different types of food web were determined between the two marshes studied (Figure 1.9). The herbivorous food web (FW1) was defined by high abundances of phytoplanktonic communities and sufficiently high abundance of herbivorous zooplanktonic communities to regulate them by grazing (Dupuy et al., 2011; Chenillat et al., 2021). Landry et al. (1995) demonstrated that pigment analyses of zooplankton stomach contents showed a higher concentration of chlorophyll pigments in autumn and spring, and a higher grazing rate especially for microzooplankton. These results are consistent with those published by Masclaux et al. (2014) on the regulation of phytoplankton communities by zooplankton in the herbivorous food-web (FW1). In the Tasdon marsh, the high proportion of active chlorophyll *a* indicated a strong photosynthetic activity from autotrophic organisms during this period, thus a strong contribution to atmospheric carbon fixation in the water column (Copping and Lorenzen, 1980). The data indicated two orders of magnitude higher nutrient concentrations in the Tasdon marsh (see Figures 1.7 and 1.8) than in the Fier d'Ars marsh. This could be explained by the fact that the Tasdon marsh, unlike the Fier d'Ars marsh, is located on an urbanized watershed, and therefore receives more nutrients by leaching during rainfall (Rudy et al., 1994). Thus, the intake of nutrients might have a higher effect on the saltwater marsh studied since their concentrations of NO_3 and NO_2 were initially lower. The efficiency of the purification function in both marshes might be equivalent, since the concentrations of NO_3 and NO_2 tended to decrease significantly between seasons in FA, TA, TB and TC. The difference in the initial concentrations of nutrients in this case is important to consider. Since the decrease of NO_3 and NO_2 concentrations between winter and spring, was significant (p -value = 0.009) at FA but not at FB the water purification function might be more efficient at FA than at FB. It is however clear that more information is needed on nutrient and organic matter inputs to be able to fully assess the importance of purification activities by plankton and prokaryote communities.

The multivorous food web (FW2) was defined by high abundances of heterotrophic prokaryotes and protists, phyto- and metazooplanktonic communities as well as high turbidity linked to a high concentration of particulate organic matter resulting from bacterial degradation and mineralization processes (Kirchman, 1994; Jia et al., 2017), and a low concentration of nutrients (Masclaux et al., 2014). This food web appeared directly after the herbivorous food web: the increase of the abundance of phytoplankton during the previous period induced the increase of available prey for zooplankton which can thus grow in the habitat (Chenillat et al., 2021). A multivorous food web can be qualified as weak or strong depending on the abundances of all planktonic compartments (Masclaux et al., 2014). Therefore, there was a weak multivorous food web in spring at TC compared to all three stations of Tasdon marsh in summer because HPT and mesozooplanktonic abundances were not as high. Moreover, at FA in summer, the multivorous food web identified was beginning because the abundance of micro- and mesozooplankton were just starting to increase compared to their higher abundance in spring. Overall, these high planktonic abundances represented a large pool of resources and food for planktivorous species and thus might indicate a substantial nursery function if they are simultaneously present in these habitats, the case in both marshes during summer, and at TC in spring.

The microbial loop (FW3) was identified only in autumn at FA and defined by high concentration of NH_4 , which is a product of particulate matter recycling in the water column, low concentrations of NO_2 and NO_3 , and high abundances of heterotrophic prokaryotes (Legendre and Rassoulzadegan, 1995; Almuktar et al., 2018). Since the concentrations of nitrite and nitrate were low despite the nutrient input coming from water inlet, the purification function was well shown at FA. The first type of “biological winter” (FW4) was defined by low phytoplanktonic, metazooplanktonic and heterotrophic prokaryote abundances. The second type of “biological winter” (FW5) was similar as FW4 except for the higher concentration of nitrite and nitrate, which may be linked to inlets of water bringing nutrients in the freshwater marsh (Nalubega, 1999). FW5 might correspond to a late state of biological winter close to transition with an herbivorous food web when the temperature increases with phenology (Trombetta et al., 2019).

The herbivorous and multivorous food webs were found in both marshes, as well as the first type of “biological winter” FW4. The microbial loop was only noted in the Fier d’Ars marsh, whereas the second type of “biological winter” FW5 was only revealed in the Tasdon marsh. According to the statistical analyses, the effect of nutrient concentrations in the water column

seemed to have a stronger impact in the saltmarsh than in the freshwater marsh. Again, knowing that the intake of nutrients by water inlets might be more important at Fier d’Ars than Tasdon; sampling the water directly in the channel leading to the marshes and measuring nutrients concentrations during each the season would be necessary to solidify this statement.

It is highly likely that a season is composed of a succession of different food webs; unfortunately, with only one sampling per season, it is possible that we missed some situations. The second type of “biological winter” might have been identified in the saltmarsh if the sampling had been done later in winter, closer to the beginning of spring. It should be noted that the presence and dynamics of some phyto- and zooplanktonic species seem to be directly linked to the season, which correlates with other published studies (Ogbuagu and Ayoade, 2012; Ratnam et al., 2022), therefore the efficiency of their associated ecological functions might be affected as well.

Overall, the seasonal succession of food web types seemed to follow the patterns generally described in the literature (Legendre and Rassoulzadegan, 1995; Masclaux et al., 2014).

The results of the MFA indicated that, during the year studied, the three management operations studied did not impact planktonic communities more than the natural seasonal effect. Angeler and Moreno, 2007 also state that planktonic communities are resilient this type of one-time and infrequently repeated methods applied on coastal marshes. It would be interesting to study whether similar results are found if these same methods are used at higher frequencies, to assess the limit of resilience of planktonic communities. Also, the potential combined effects of different management operations, such as the three actions studied here and sediment resuspension caused by landscapes modelling, should be studied over consecutive years to determine how resilient the communities involved in these ecological functions.

1.5 Conclusion

Overall, this study showed that, although planktonic communities’ composition, abundance and diversity are substantially different, similar planktonic food web types can be found on salt and freshwater coastal marshes. This one-year survey, with a sampling each season, provides a basis of information on the composition and abundance of the planktonic communities in the Fier d’Ars and Tasdon marshes and allows to deduce their most likely trophic pathways and associated ecological functions. Integration into the context of the interdisciplinary project

PAMPAS will allow more detailed analysis of the role of planktonic communities within the total marsh ecosystems.

CRedit authorship contribution statement

Lauriane Bergeon: Conceptualization, Formal analysis, Investigation, Writing – Original Draft, Writing – Review & Editing, Visualization. Frédéric Azémar: Conceptualization, Resources, Writing – Review & Editing, Supervision. Claire Carré: Resources, Data Curation, Writing – Review & Editing. Bénédicte Dubillot: Methodology, Validation, Investigation, Resources. Claire Emery: Investigation, Resources, Data Curation. Hélène Agogué: Investigation, Resources, Data Curation, Writing – Review & Editing. Philippe Pineau: Investigation, Resources, Data Curation. Thomas Lacoue-Labarthe: Project administration, Funding acquisition, Writing – Review & Editing. Marc Bouvy: Resources, Data Curation, Writing – Review & Editing. Michèle Tackx: Conceptualization, Validation, Writing – Review & Editing, Supervision. Christine Dupuy: Conceptualization, Methodology, Validation, Investigation, Resources, Data Curation, Writing – Review & Editing, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Chapitre 2 : Impact of changing the management of an urban wetland on its planktonic ecological functions (Tasdon marsh; Atlantic coast of France)

En 2020, le marais de Tasdon a été restauré dans le but de préserver sa biodiversité, plus précisément recréer des habitats refuges propices pour les oiseaux limicoles migrateurs. Cette étude compare des échantillonnages saisonniers réalisés un an avant restauration (2019-2020) et un an après restauration (2021-2022) afin d'évaluer l'impact de cette restauration sur les communautés planctoniques et leur fonctions écologiques associées. La méthodologie de suivi et les hypothèses liées aux premiers résultats ont été présentés à l'oral au colloque international ECSA 58 – EMECS 13 « Estuaries and coastal seas in the Anthropocene Structure, functions, services and management ». Les résultats de ce chapitre ont été présentés sous forme de présentation orale, en parallèle des résultats sur l'étude de l'ichtyofaune par Mireia Kohler dans ce même marais, au colloque national pluridisciplinaire « Restauration et reconnexion des marais littoraux ».

Impact of changing the management of an urban wetland on its planktonic ecological functions (Tasdon marsh; Atlantic coast of France)

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Abstract

Wetlands can provide many ecosystem services linked to their biodiversity, such as water purification, buffering against flooding, carbon sequestration and recreational area. Adaptive management of wetlands is therefore crucial in order to preserve their assets. The suburban Tasdon wetland (Atlantic coast of France) is since recently subject to several parallel restoration efforts: watercourse rectification, landscape remodeling and reconnection to coastal marine waters (ecological continuity from upstream to downstream). The objective of this restoration efforts is to increase biodiversity, more specifically to increase nesting and migratory areas for shorebirds. The aim of this study is to determine the impact of these restorations on the biodiversity and ecological functioning of the wetland, focusing on planktonic communities

and CO₂ fluxes. Four seasonal samplings were conducted both before and after the restoration. Results showed that the new management impacted planktonic communities by shifting their diversity, affecting their trophic function, and lowering global abundances of planktonic communities. However, some species observed only before the restoration works tended to reappear a year after (e.g., *Bosmina longirostris*, *Brachionus calyciflorus*). The proportion of heterotrophic organisms compared to autotroph organisms was higher after the restoration works. Nonetheless, the carbon fluxes showed lower pCO₂ values after the restoration works, potentially improving the carbon sink function of the marsh. Only two of the four types of planktonic food web determined before the restoration were found after (multivorous and transition state between biological winter and herbivorous food web).

Keywords: wetland; restoration; planktonic diversity; water pCO₂ and water air-fluxes; ecosystem functions

2.1 Introduction

Wetlands are typically ecosystems sheltering a high biodiversity and ecological service reserves found across the globe. They are among the most productive ecosystems in the world (Hammer and Bastian, 1989). The Ramsar convention in 2020 stated that wetlands account for approximately 6% of emerged environments. According to their type and management, they provide different ecosystem services (Bullock and Acreman, 2003). Freshwater marshes (natural or artificial) are coastal areas temporary disconnected from the sea and represent shelter habitats for various catadromous species, such as *Anguilla anguilla* (Daverat and Tomas, 2006), reservoirs of biodiversity (Maltby and Baker, 2009) or stopovers for birds (Beauchard et al., 2012; Shraddha et al., 2017). They are also used as grazing area or for grass farming (Kakuru et al., 2013; Biro et al., 2020). Saltmarshes are natural or artificial areas which are generally separated from the sea by a dike and/or floodgate allowing the regulation of water inflow (Doody, 2008). These productive areas are privileged zones for migratory shorebirds and as nesting areas (Schekkerman et al., 1994; Saintilan, 2009) and important reservoirs of biodiversity of several organisms, going from invertebrates to birds (Maltby and Baker, 2009). Based on their high productivity, these systems can be exploited for food production. For example, in the south of Spain, some saltmarshes contain a large diversity of macroinvertebrates and thus are used for aquaculture of the seabream *Sparus aurata* (Guerra-Garcia et al., 2023). Several freshwater marshes are also used for crayfish farming (Holdich, 1993).

Another main role of coastal wetlands is their role as a carbon sink by absorbing and sequestering atmospheric CO₂ (Tang et al., 2018; Wang et al., 2021). Brevik and Homburg (2004) studied the accumulation of organic carbon sequestered in a coastal area in southern California and found overall between 1.7 and 88.2 kg/m³ organic carbon content in the sediments of the different sampling sites. In addition, these ecosystems act as buffer against flooding (Sheng et al., 2021; Ahlen et al., 2022) and allow water purification by sedimentation of the particles present in the water column, phytoremediation by the vegetation and bacterial activity in the sediments (Nichols, 1983; Verhoeven et al., 2006; Lin and Mendelsohn, 2009; Song et al., 2022).

While the attractiveness of coastal areas leads to a strong increase in the population on the coasts (Burak et al., 2004; Le Berre et al., 2016), wetlands, both salt and freshwater, have long been considered as unhealthy places sites where animal and plant debris accumulate in stagnant water producing a foul-smelling mud (Meindl, 2000; Huisman, 2017). Many of these marshes were drained and backfilled to develop farming or to expand nearby cities (Rojas et al., 2019). Other wetlands were not managed and therefore tended to fill in and silt up, before invasive vegetal species became established (Ehrenfeld, 2008). These processes led to habitat fragmentation reducing ecological continuity (Lowe and Peterson, 2014; Gilby et al., 2020).

In recent years, people started to realize the importance of preserving wetlands and the ecosystem services they can provide. Thus, several actions are now realized in order to restore these environments for diverse purposes such as returning to a more natural hydrology to recreate a buffer zone (Mitsch, 2005), and preserve biodiversity and ecosystem services (Kumari et al., 2019). These actions include restoration of the tidal hydrology (Maris et al., 2007), retreat of dikes (Mazik et al., 2010), restoration of biological corridors (Mathias and Moyle, 1992; Sun et al., 2023) sediment decontamination (Mulligan et al., 2001), removal of invasive species (Gratton and Denno, 2006; De Meester and Richter, 2009), revegetation (Rodrigo, 2021), and/or development of refuge for migratory birds (Wilson, 2010; Fournier et al., 2021). Some initiatives focus on creation of new wetlands to enhance and/or protect biodiversity (Kim et al., 2011). Other focus on restoration by replanting macrophytes or epiphytes (Nishihiro et al., 2006; Palma and Laurance, 2015; Rodrigo, 2021). The actions taken by managers depend on what ecological functions and ecosystem services they want to preserve and develop.

Among key actors of ecological functions in marshes, planktonic communities are the basis of aquatic food webs by being primary producers and consumers (Kobayashi et al., 2014; Verma

and Prakash, 2020). Beyond its role as a food resource, plankton is also an important actor in the biogeochemical cycles. Through photosynthesis, phytoplankton uses quantities of carbon dioxide (CO₂) and contributes to the aeration of the water (Boyd et al., 2017). Moreover, phytoplankton also represents a form of fixed organic carbon and, in some cases, carbon as calcium carbonate which settles in the sediments (Sayers et al., 2021). This phenomenon is enhanced by metazooplankton predation on phytoplankton, and nychthemeral migration which accelerates the flow of matter to the sediments (Avois-Jacquet et al., 2005). Thus, planktonic communities have an important role in carbon sequestration. In addition, planktonic species also represent good bioindicators to detect perturbations and pollutants in the water column (Parmar et al., 2016; Zaghoul et al., 2020). Hemraj et al. (2017) showed how some phytoplanktonic (*e.g.*, Dinoflagellates) and zooplanktonic species (*e.g.*, *Acartia* sp.) can be used to follow fluctuation of salinity and nutrient concentration in the water column in coastal lagoons. Despite the importance of planktonic communities in ecosystem functioning, few studies concerning wetland restoration have included monitoring of these communities (Dodson and Lillie, 2001) and no study concerned simultaneously measurements of CO₂ data and plankton communities. The literature shows more studies concerning planktonic resilience in wetlands subject to natural or anthropogenic disturbances (Stevic et al., 2013; Yang et al., 2019; Kahsay et al., 2022). A few studies have studied the dynamics of the plankton in newly created wetlands (Calero et al., 2015; Rodrigo and Segura, 2020). A more complete description of the planktonic communities and their ecological role is given in the second part of the general introduction of this manuscript.

The aim of this study was to quantify the impact of a freshwater coastal marsh restoration on CO₂ fluxes, diversity and abundance of planktonic communities as well as planktonic food webs. This study focused on a coastal freshwater marsh, a suburban marsh on the west Atlantic coast of France. Monitoring of CO₂ flux (atmosphere/water) and planktonic communities before and after restoration works was done to compare abundances and diversity taking into consideration the changes of management. For memory, restoration measurements taken in the Tasdon marsh were essentially watercourse rectification, landscape remodeling and periodical reconnection to coastal waters (salinization of a part of freshwater marsh). More details are given in the Material and Methods section.

Considering the nature of these works, multiple hypotheses on their impact are proposed: the restoration might change the CO₂ fluxes on a short term. New species might become dominant while native species might not be able to cope with the modifications of their habitat (*e.g.*, effect

of current, saltwater intake). Intake of saltwater in a freshwater environment might enhance CO₂ fluxes and modify planktonic diversity. Moreover, all these changes might affect the structure and the succession of planktonic food webs in the marsh.

2.2 Material and Methods

2.2.1 Study area

The freshwater marsh of Tasdon is a suburban marsh of 124 ha located on the west coast of France near the cities of La Rochelle and Aytré (Figure 2.1). It was initially a saltmarsh since the Middle Ages and exploited until 1935 and then became an area for cattle grazing between 1935 and 1960. Thereafter, a dam was built in 1962 on the river passing through this marsh, causing disconnection with the sea. Due to expansion of the cities nearby, partial backfilling was carried out around 1970. Since then, the marsh was progressively invaded by vegetation. Following a recent from La Rochelle Agglomeration wish to preserve the general biodiversity and restore the ecological functions provided by the marsh, its managers decided in 2020 to carry out restoration works. These works included watercourse rectification, landscape remodeling and periodical reconnection to coastal waters. The sampling for monitoring planktonic communities and carbon (water pCO₂ and atmospheric fluxes) took place in 2019 and 2021, thus before and after these restoration works.

The first station (TA: N 46° 08' 56.4"; W 01° 07' 26.4") has freshwater conditions, with a maximum depth of 1.35 m (Figure 2.1). The only restoration works done was replanting of vegetation on the shores to help maintain their structure and integrity. The second station (TB: N 46° 9' 3.6"; W 1° 8' 9.599") was originally a stagnant freshwater pond with a maximum depth of 0.8 m before the restoration. Landscape remodeling and watercourse rectification have been done in 2020: the riverbed has been re-dug. For now, the river is passing through this station after wet meadow. The third station (TC: N 46° 08' 49.2"; W 01° 08' 13.2") was in a long stagnant freshwater pond with a maximum depth of 1 m, which is reconnected, since 2020, to coastal water via a floodgate letting saltwater in- and outflow according to tidal levels. Since the first spring after the restoration works, an inflow of seawater reaches station TC every two weeks: the floodgate stays open between 2 or 3 days depending on the initial water level of the marsh to avoid overflow. During the rainy seasons (mid-autumn to late winter), there was no saltwater inflow. Landscape remodeling was also done to provide islets used as nesting areas for migratory shorebirds.

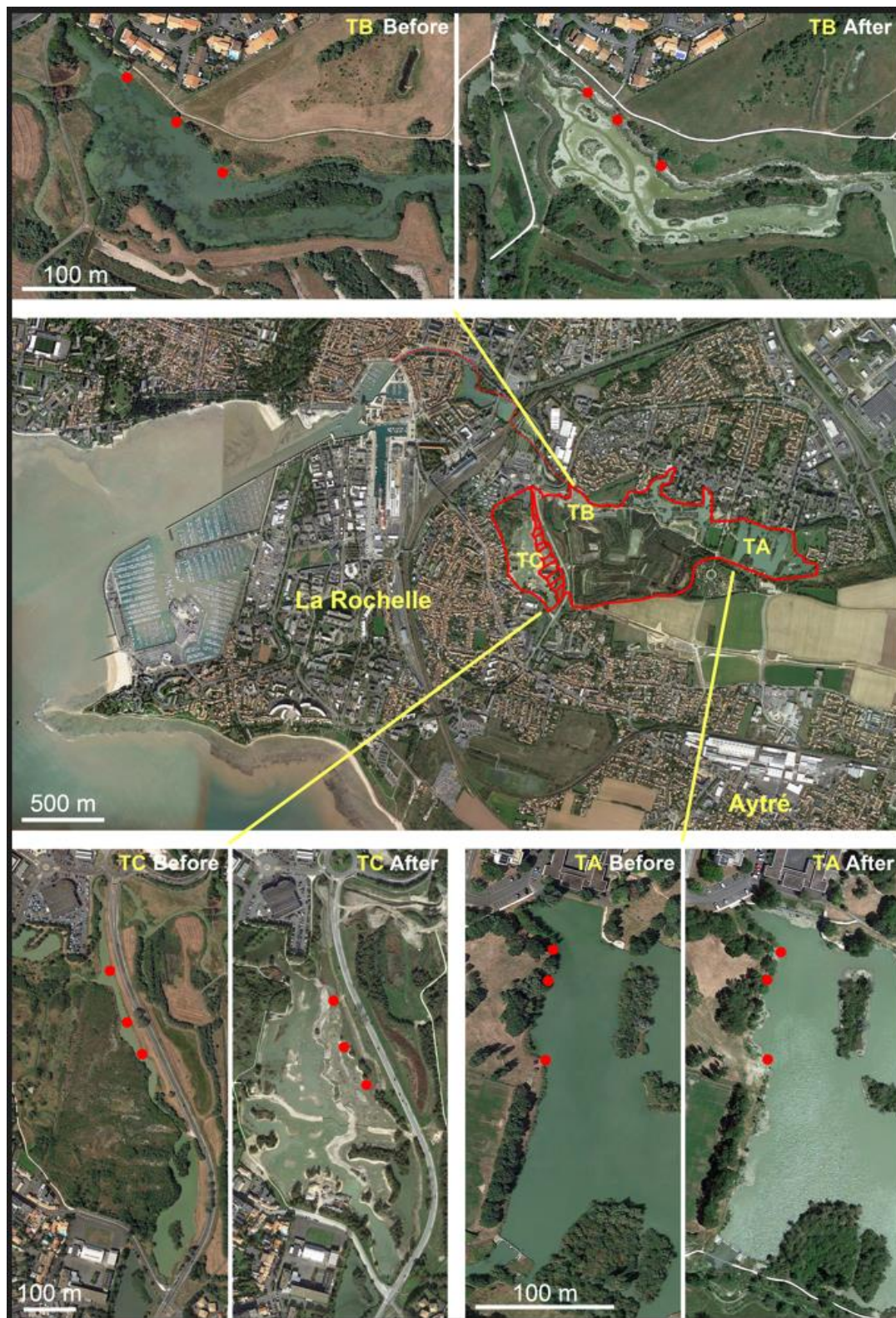


Figure 2. 1: Satellite vision of the Tasdon marsh located in the west coast of France near La Rochelle and Ayré (outlined in red), with a focus on each sampling station (TA, TB, TC; TC corresponds to the red hatched area) before and after the restoration, The red dotted line on the overall map indicates the path the saltwater follows since the reconnection to the sea. The red dots indicate the sampling points (triplicates) for each sampling station. Coordinates of the sampling stations: TA: N 46° 8' 56.4"; W 1° 7' 26.4"; TB: N 46° 9' 3.6"; W 1° 8' 9.599"; TC: N 46° 8' 49.2"; W 1° 8' 13.2". Picture taken in 08/2018 (TA, TB, TC Before), 04/2022 (TC After), and 05/2022 (TA and TB After).

2.2.2 Sampling methods and abiotic parameter measurements

Four seasonal samplings were conducted both before and after the restoration, respectively in 2019 and 2021. A multiparametric probe (VWR™) was used to measure the temperature, salinity, pH, and dissolved oxygen concentration. All water samplings were made in triplicate at each station at 0.5 m depth, using a bucket. These samples were used for quantifying different parameters: Suspended Particulate Matter (SPM), Particulate Inorganic Matter (PIM), Particulate Organic Matter (POM), nutrients (NO₂, NO₃, NH₄, PO₄, Si), chlorophyll *a* and phaeopigments concentrations, as well as diversity and abundances of different planktonic compartments (see after). For bacterial and eukaryotic molecular diversity analyses (see after), a pool of the triplicate at each station was done.

These samples were preserved from light in opaque black plastic bags until return to the lab (15 minutes of travel).

To estimate the abundance of heterotrophic prokaryotes (HPK) and pico-nanophytoplankton, 1.5 mL of water was directly preserved with a mixture of glutaraldehyde (final concentration 0.2%) and poloxamer (final concentration 0.001%) and was frozen in liquid nitrogen and then stored at -80°C in the lab until the analysis. The abundance of heterotrophic prokaryotes, pico- and nanophytoplankton were determined by flow cytometry analyses performed with a FACS CantoII flow cytometer according to the method described in Marie et al. (1999). FlowCam analyses were conducted on living microplankton for each replicate directly upon return to the laboratory. The abundance of microplanktonic groups (microphytoplankton and heterotrophic protists) and the diversity were determined by FlowCam analyses following the methodology of Buskey and Hyatt (2006).

Metazoan microzooplankton was sampled by filtering 6L of water through a 63 µm mesh and then fixed with buffered formaldehyde (final concentration of 4%). Mesozooplankton was done by horizontal hauls at each station with a standard WP2 (200 µm mesh net) coupled with flow meter (Mechanical Flow Meter with back-run stop, Model 438 115). The content of the net collector was fixed with buffered formaldehyde (final concentration of 4%). Micro- and mesozooplanktonic organisms were identified and counted with binocular microscope observations using the method of Postel et al. (2000). Identification of micro- and mesozooplankton was performed to the species level whenever possible (genus or order if damaged) (Amoros, 1984; Pourriot and Francez, 1986; Dussart and Defaye, 2001). Crustaceans were dissected and observed with an optical microscope (x400) when necessary to achieve

species level identification. All copepodite stages were regrouped according to each copepod order. Planktonic larvae were identified to order directly under a stereomicroscope (x120) without prior dissection.

2.2.3 *In situ* CO₂

In the subsurface waters (0.5 m depth) of each station, partial pressures of CO₂ (pCO₂) and associated biogeochemical parameters were autonomously measured every minute by *in situ* underwater probes during six 24-hour cycles (spring and autumn 2019 before restoration and spring, summer, autumn 2021 and winter 2022 after restoration) to record temporal (diurnal and seasonal) and spatial variations over the Tasdon marsh. At each season, measurement cycles were performed at one-day intervals over each station. A C-sense™ probe (PME/Turner Designs) was deployed to measure continuously water pCO₂ and an EXO2 multiparameter probe (YSI) was deployed to measure simultaneously temperature, salinity, turbidity, dissolved oxygen concentration (DO) and pH. The measurement range of the C-sense probe is 0-4000 ppmv with an absolute accuracy of 120 ppmv (3% of the full scale; Turner Designs). The C-sense probe was calibrated by the manufacturer before the study. A water pCO₂ correction was applied taking the total dissolved gas pressure, the atmospheric pressure during the calibration (1009 hPa) and the measured pCO₂ values into account, following Mayen et al. (submitted 2022). The EXO2 probe was used to measure temperature ($\pm 0.01^\circ\text{C}$), salinity (± 0.5 salinity unit), turbidity (± 0.3 NTU), DO concentration ($\pm 3.1 \mu\text{mol L}^{-1}$), DO saturation level ($\pm 1\%$) and pH (± 0.01 pH unit). Before each 24-h cycle, the pH was calibrated using three YSI buffer solutions (pH 4.01, pH 7.00 and pH 10.01) according to the National Institute of Standards and Technology (NIST).

2.2.4 Sample analyses

The concentration of nitrate (NO₃), nitrite (NO₂), ammonium (NH₄), phosphate (PO₄) and silicate (Si) was determined on filtered water (0.7 μm GF/F glass fiber membrane, Whatman) using a SEAL AA3 autoanalyzer with the detection limit of: 0.02 $\mu\text{mol.L}^{-1}$ (NO₃), 0.003 $\mu\text{mol.L}^{-1}$ (NO₂), 0.06 $\mu\text{mol.L}^{-1}$ (NH₄), 0.01 $\mu\text{mol.L}^{-1}$ (PO₄), 0.04 $\mu\text{mol.L}^{-1}$ (Si) according to the methodology of Aminot and K erouel (2004).

SPM were measured according to the methodology of Aminot and K erouel (2004). After SPM measurement, filters were calcinated and measurement of PIM was made by weighing filters again. POM was calculated as the difference between SPM and PIM weight. The concentration of chlorophyll *a* and phaeopigments was determined for each replicate for three size classes:

microphytoplankton ($> 20 \mu\text{m}$), nanophytoplankton (between 3 and 20 μm) and picophytoplankton ($< 3 \mu\text{m}$). Then, a triplicate filtration was first performed on a 20 μm nylon fiber membrane (Millipore). Then, a fraction of the resulting filtrate was filtered onto a 3 μm Nuclepore membrane (Whatman) and the rest of the filtrate onto a 0.7 μm GF/F glass fiber membrane (Whatman). Chlorophyll *a* and phaeopigments (*i.e.*, concentration of degraded chlorophyll pigments) concentrations were quantified by fluorimetry according to the methodology Lorenzen (1966). The proportion of active chlorophyll *a* was measured by calculating the ratio of concentration of phaeopigments to phaeopigment plus chlorophyll *a* initially measured.

To analyze the molecular diversity of bacteria and eukaryotes, between 100 ml and 200 ml (depending on the water turbidity) of sample were filtered through polycarbonate membrane (0.22 μm pore size, 47 mm diameter, GVWP04700; Millipore). The filters were then kept in sterile tubes and stored at -80°C . DNA extractions were conducted using the PowerWater DNA Isolation Kit (Mo Bio Laboratories) with a modified methodology to optimize the DNA extraction efficiency. After adding the PW1 solution on the filter, a heat-shock phase alternating 30 s in liquid nitrogen with 2 min at 60°C was repeated three times. Then, the tubes were incubated at 65°C during 10 min and 330 μl of 24:25:1 phenol-chloroform-isoamyl alcohol was added (Melayad et al 2020). Samples were afterwards submitted to a bead-beating methodology consisting of two phases of 40 s at a speed setting of 6.0 m/s interspersed with a 30 s break (FastPrep-24, MP Bio). The DNA's manufacturer methodology was then followed until the end. After DNA extraction, samples were paired-end sequenced by next-generation sequencing by using Illumina Miseq platform (Novogene). Sequencing targeted V4-V5 region of Bacterial 16S rRNA gene using 515F-Y (5'-GTGYCAGCMGCCGCGGTAA-3') and 926R (5'-CCGYCAATTYMTTTRAGTTT-3') (Parada et al, 2016), and Eukaryotic V4 region of 18S rRNA gene with the primer set TAREuk454FWD1 (5'-CCAGCASCYGC GGTAATTCC-3') and TAREukREV3 (5'-ACTTTCGTTCTTGATYRA-3') (Stoeck et al. 2010).

2.2.5 Statistical analysis

For variables measured continuously for 24 hours, the data did not respect a normal distribution. Shapiro-Wilk tests and non-parametric comparison tests such as the Mann-Whitney and Kruskal-Wallis tests were carried out with 0.05 level of significance. A Dunn test was used to perform a post-hoc multiple comparison of the Kruskal-Wallis test to detect significant differences among groups. Spearman correlation matrix of the biogeochemical and physicochemical parameters was performed with the GraphPad Prism 7 software. Temporal

graphs and linear regressions were performed with the GraphPad Prism 7 software. Since pCO₂ and turbidity before the restoration works were only measured for spring and autumn, these variables were not considered in the statistical analysis describing the ecosystem in 2019. However, there were used as qualitative information to interpret the analysis. These two variables were considered in the analysis after restoration works since than they have been measured for all seasons.

In addition, the abundance of planktonic communities was converted into biomass per carbon unit (see Appendix 2.2). The ratios between autotrophs (picophytoplankton, nanoflagellates counted by flow cytometry, diatoms) and heterotrophs (heterotrophic prokaryotes, dinoflagellates, ciliates, nanoflagellates counted by FlowCam) organisms' biomass was calculated to investigate potential correlation between carbon fluxes and planktonic activity. Mixotrophic organisms were considered as heterotrophic organisms in the calculation of this ratio (Flynn et al., 2012). To distinguish between temperature and non-temperature effects on *in situ* pCO₂ variations at the diurnal scale, TpCO₂ (pCO₂ variations related to temperature physical effects, in ppmv) and NpCO₂ (pCO₂ variations related to non-temperature effects, in ppmv) were calculated following the methodology of Takahashi et al. (2002). Whereas TpCO₂ is only associated with the physical pump, NpCO₂ is associated with biological processes, tidal advection and benthos-pelagos couplings that may be important in shallow coastal systems (Cotovicz et al., 2015, Polsenaere et al., 2022). For each 24h cycle, the gas transfer velocity (k₆₀₀) and hourly CO₂ fluxes (FCO₂) at the air-water interface were estimated following formula from Ribas-Ribas et al. (2011) and Polsenaere et al. (2022) for coastal environments. Water pCO₂ (ppmv) were measured by the in-situ C-Sense probe and atmospheric CO₂ concentrations (ppm) were obtained from the National Oceanic and Atmospheric Administration (NOAA) at the Mauna Loa Observatory in Hawaii (<https://gml.noaa.gov/ccgg/trends/>) (411, 413, 419, 414, 416 and 419 in April 19, November 19, April 21, August 21, December 21 and March 22, respectively). The CO₂ solubility coefficient (α) was calculated according to Weiss (1974) considering water temperature and salinity. The gas transfer velocity (k) significantly controls air-water FCO₂ since it directly takes turbulence processes at the air-water exchange interface into account (Polsenaere et al. 2013). In this study, k (or k₆₀₀) was calculated according to Raymond & Cole (2001).

The gas transfer coefficients normalized to a Schmidt number of 600 (k₆₀₀) obtained with the RC01 parametrization were then converted to the gas transfer velocity of CO₂ at the in-situ temperature and salinity (k) according to Jähne et al. (1987).

Statistical analyses on planktonic abundances were done using R software (version 4.2.2). Since the data did not follow a normal distribution, a non-metric multidimensional scaling (nMDS) was conducted on data collected before and after restoration works (R: package *vegan*). Shepard plots were previously made to assess the number of dimension where the stress value was the lowest. Following nMDS, ANOSIM were conducted to assess if there were a significant effect of station and/or season (p -value < 0.05). In addition, planktonic food web before and after the restoration works were determined following the methodology of Masclaux et al. (2014) and Bergeon et al. (2023) (R: packages *ade4*, *psych*, *clue*, *ggplot2*, *ggdendro*): station-season couples are regrouped thanks to an Ascending Hierarchical Clustering (AHC) to determine the potential number of different types of planktonic food web. Then, the values of selected abiotic and biotic parameters are plotted (boxplots) and compared between these groups to be able to determine the type of planktonic food web for each group (see Bergeon et al., 2023). For an example, if high concentrations of nutrients (NO_2 , NO_3) and high abundances of phytoplankton smaller than 20 μm are observed, in addition to low abundances of other planktonic compartments, we can deduce the presence of an herbivorous-type planktonic food web. This type of planktonic food web reflects high photosynthetic activity on the part of phytoplankton, and therefore a high level of atmospheric carbon uptake. This methodology is used to establish the link between observed planktonic food webs and the ecological functions associated with planktonic communities. The differences in values described in results between before and after restoration are those that statistical tests have shown to be significant (p -value < 0.05). Trends were assessed by a Spearman-Rank correlation (p -value < 0.05).

2.3 Results

To help understanding the variation of data on all variables, Table 2.1 summarizes the general trends before and after the restoration.

Table 2. 1: Summary of the principal changes after vs before restoration works observed at each station in abiotic and biotic parameters. The differences indicated are significant according to the statistical tests done (p -value < 0.05).

Station	TA	Season observed	TB	Season observed	TC	Season observed	Comments
Environmental parameters							
pCO ₂	decreased	Spring and autumn	decreased	Spring and autumn	decreased	Spring and autumn	No sampling in summer and winter before restoration)
Temperature	No differences	All four seasons	No differences	All four seasons	No differences	All four seasons	x
Salinity	No differences	All four seasons	No differences	All four seasons	Slight Increase	Especially in summer 2021	TC receives periodical saltwater intakes
pH	No differences	All four seasons	No differences	All four seasons	No differences	All four seasons	
Dissolved O ₂ concentration	Higher after restoration	All four seasons	Higher after restoration	All four seasons	Higher after restoration	All four seasons	Only slightly higher in spring in all three stations
Nutrient concentration	Higher global concentrations	All four seasons	Higher global concentrations	All four seasons	Higher global concentrations	All four seasons	Global: NO ₃ , NO ₂ , NH ₄ , PO ₄
Biotic parameters							
General HPT abundance	Higher	All four seasons, especially in summer and autumn	Lower	All four seasons, especially in summer and autumn	Higher	All four seasons	x
General Phyto abundance	Variations depended on the season	Similar in spring, lower in summer and winter, higher in autumn	Variations depended on the season	Lower for all four seasons except in autumn (similar)	Lower	All four seasons	TA less affected by the restoration works than TB and TC; TB is now affected by the current effect
Phyto diversity	More Euglena and Cryptophyceae after restoration	All four seasons	More Euglena and Cryptophyceae after restoration	All four seasons	More Euglena and Cryptophyceae after restoration	All four seasons	Some species observed before restoration tended to reappear in winter 2022; More different taxa identified before restoration
Chlorophyll a concentration	Depending on season	Similar in spring, lower in summer and higher in autumn and winter	Depending on season	Lower in spring and summer, higher in autumn and winter	Depending on season	Lower in spring and summer, higher in autumn and winter	Total including all three size classes
General metazooplankton abundances	Lower	All four seasons	Lower	All four seasons	Variations depended on the season	Lower for all four seasons except in autumn (similar)	x
Metazooplankton diversity	Less herbivorous species, more detritivorous species until winter	All four seasons	Less herbivorous species, more detritivorous species until winter	All four seasons	Less herbivorous species, more detritivorous species until winter	All four seasons	Some species observed before restoration tended to reappear in winter 2022; More different taxa identified before restoration
Planktonic food web	Four types determined before restoration, only two after	See Figure 7	Four types determined before restoration, only two after	See Figure 7	Three types determined, only two after	See Figure 7	x

2.3.1 Environmental parameters

Focusing on the variations of environmental parameters measured continuously for 24 hours after the restoration works (Figure 2.2). As in the material and methods section, environmental parameters before restoration works were only measured continuously during spring and autumn (2019). To give a full overview of variations of these parameters during all seasons, we first describe the continuous measurement of the water temperature, the turbidity, the dissolved oxygen concentration and saturation, and the $p\text{CO}_2$ after the restoration, which were carried out in all four seasons.

At all stations, temperature generally increased to a maximum by the end of the day, except at TA, where temperature was rather constant throughout the 24 hours during summer, autumn and winter.

Turbidity showed important variations only at station TB during spring, with high values at night, and at TC where it increased during daytime towards a maximum, at the end of the day, to decrease during the night. Dissolved Oxygen concentration increased during daytime and decreased during nighttime. This trend was more pronounced at TB and TC than at TA. Saturation at TA generally remained above 100 %, except during summer, where it was below even during the daytime. At TB and TC, oxygen saturation was above 100 % during the day, to decrease during the night and often below 100 % at the end of the night. At all stations, and in all seasons, TpCO_2 varied little during the day, and variation in total $p\text{CO}_2$ was mainly caused by NpCO_2 (*i.e.*, variation of $p\text{CO}_2$ mainly induced by planktonic communities, not the temperature). The non-parametric comparison tests showed that, for the environmental parameters measured only in spring and autumn before the restoration works, most values were higher before the restoration works compared to the measurements done for the same season after these works, especially concerning $p\text{CO}_2$ values. However, the DO values were similar and the mean turbidity values observed in TB were lower before the restoration works (Table 1).

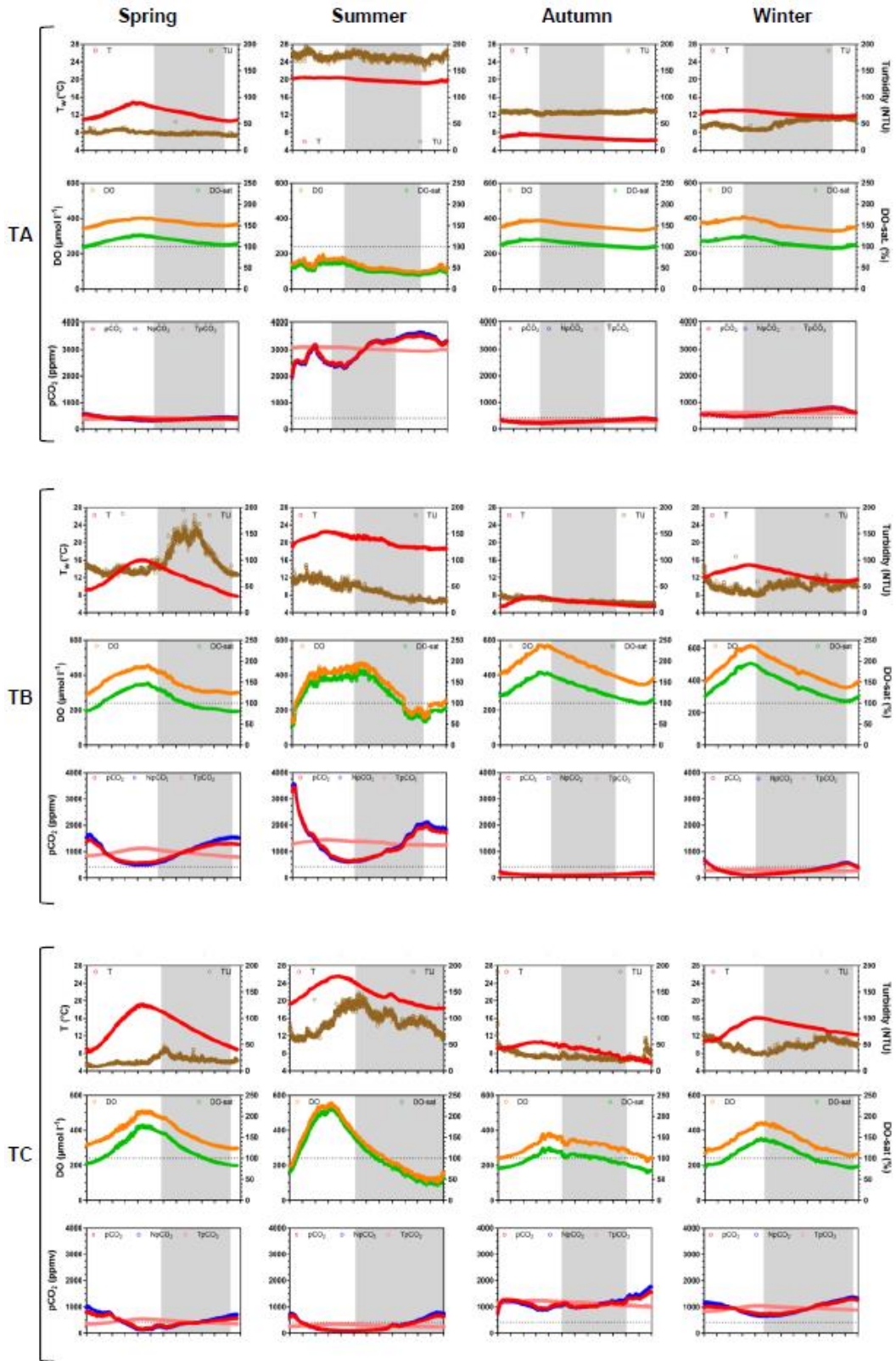


Figure 2. 2: Continuous measurements during 24h for each season (spring, summer, autumn, winter) and station (TA, TB, TC) in the Tasdon marsh after restauration works: of water temperature (T in °C), turbidity (NTU), dissolved oxygen concentration (DO in μmol/l), saturation level of dissolved oxygen concentration (DO-sat in %), partial pressure of carbon dioxide (pCO₂ in ppmv), part of pCO₂ induced by planktonic communities (NpCO₂ in ppmv), part of pCO₂ induced by temperature (TpCO₂ in ppmv). The darker background represents nighttime and the lighter background represent daytime.

2.3.2 Abundance, diversity and biomass of planktonic communities

2.3.2.1 Counts and identifications

A total of 65 phytoplanktonic and protist taxa and 34 metazooplanktonic taxa were identified in 2019 before restoration. In spring for phytoplankton (Figure 2.3a), heterotrophic flagellates were highly dominant in TA and TB, with a high abundance of *Dinobryon* sp. In TB. In TC, Dinophyceae, *Cryptomonas curvata* and *Cylindrotheca closterium*, were the most abundant taxa for this season. In summer, Chlorophyceae were overall very abundant in TA and TB, but not with the same group of dominant species: in TA, *Willea rectangularis* and *Scenedesmus* sp. Were dominant in the water column. In TB, these two species were also abundant, together with two other Chlorophyceae species: *Monoraphidium* sp. and *Monactinus simplex*. In addition, nanoflagellates such as *Lepocinclis acus* were also abundant in this station. In TC, *Lepocinclis acus* was the most abundant taxa. Diatoms such as *Centric* spp. and heterotrophic flagellates were also abundant. In autumn and winter, *Plagioselmis nannoplanctica* was the most abundant phytoplanktonic taxa among all in all three stations, with also *Centric* spp. in autumn. *Chroomonas* sp., another nanoflagellate taxon, was also abundant in TA. Flagellates were dominant in winter in TB. In TC, *Chroomonas* sp. and *Cryptomonas curvata* were abundant.

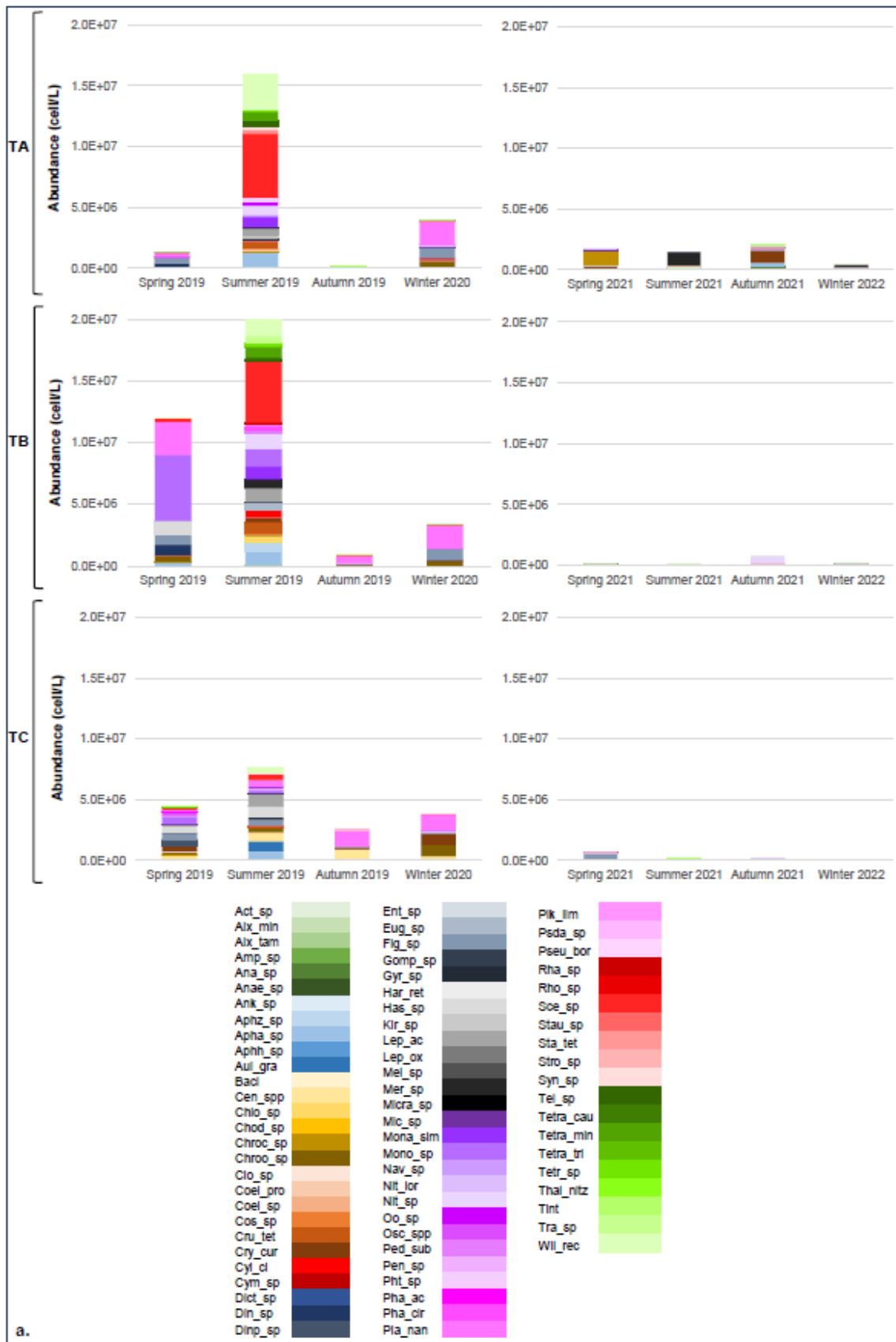
Among the metazooplanktonic species identified (Figure 2.3b), three were subtropical nonindigenous species: one Cladocera (*Moina micrura*) and two Rotifera (*Brachionus falcatus*, *Keratella tropica*). In spring, *Bosmina longirostris* was abundant mesozooplanktonic species and *Asplanchna* sp. was the dominant microzooplanktonic species in all three stations. *Polyarthra major* was also abundant in TB. In TC, *Acanthocyclops trajani* and Cyclopoids copepodites were even more present than Cladocera. In summer, *Bosmina longirostris* was still abundant but only dominant in TC. In both TA and TB, Cyclopoids copepodites were dominant mesozooplanktonic taxa. For metazoan microzooplankton, Nauplii of Copepods were dominant in TA and TC. *Asplanchna* sp. and *Polyarthra major* were also abundant in TA. In TB, *Asplanchna* sp. and *Brachionus calyciflorus* were more abundant than Nauplii of Copepods. In autumn, *Bosmina longirostris* was again the most abundant mesozooplanktonic species in all three stations and *Macrothrix hirsuticornis* specifically in TC. Concerning the microzooplankton, the abundances were overall higher in TB where Nauplii of Copepods and *Asplanchna* sp. were dominant. In TC, they were also dominant. In TA, a dominance of ephippia was observed in the water. In winter, Cyclopoid copepodites were the dominant mesozooplanktonic taxa in TA. In TB, *Bosmina longirostris* and *Chydorus* sp. were the dominant mesozooplanktonic taxa. In TC, *Chydorus* sp., *Bosmina longirostris* and Cyclopoid

copepodites were dominant. For the microzooplankton compartment, *Asplanchna* sp. is the dominant taxa in all three stations. *Polyarthra major* was the second dominant taxa in TA and TB. In TC, the two taxa with higher abundances after *Asplanchna* sp. were *Filinia* sp. and *Keratella* sp.. Overall, the highest metazooplanktonic abundances were determined in summer. The metazooplanktonic diversity was higher in spring and summer compared to autumn and winter.

After restoration, a total and 50 phytoplanktonic and protist taxa and 22 metazooplanktonic taxa, were identified in 2021 for all the stations. For phytoplankton (Figure 2.3a) in spring in TA, the nanoflagellates *Cryptomonas curvata* were most abundant. In TB and TC flagellates were most abundant. In summer, two Chlorophyceae taxa were most abundant in TA: *Ankistrodesmus* sp. and *Willea rectangularis*. In TB, diatoms of the genus *Nitzschia* were the most abundant, followed by dinoflagellates such as *AlexandriumI* sp.. In TC, *Ankistrodesmus* sp. and *Nitzschia* sp. were most abundant for this season. In autumn, *Cryptomonas curvata* was dominant in TA. In TB, flagellates were dominant for the same season. In TC, the nanoflagellates taxa *Plagioselmis nannoplanctica* was the most abundant. In winter, the most abundant taxa for each station were the same identified for each in autumn: *Cryptomonas curvata* in TA, flagellates in TB, and *Plagioselmis nannoplanctica* in TC.

Concerning metazooplankton (Figure 2.3b) in spring, *Daphnia magna*, a species newly reported for the Tasdon marsh, was the most abundant mesozooplanktonic species in TA and TC. In TB, Cyclopoid copepodites were most abundant. For the metazoan microzooplanktonic compartment, Nauplii of Copepods were dominant in all three stations. In summer, for the mesozooplanktonic compartment, *Daphnia magna* was most abundant in TA and TB. In TC, *Acanthocyclops trajani* was the most abundant mesozooplanktonic taxa. For the microzooplanktonic compartment, rotifera of the genus *Asplanchna* were most abundant in TA. In TB, another rotifera was the most abundant: *Polyarthra major*. In TC, benthic Foraminifera were dominant. In autumn, *Bosmina longirostris* was the most abundant mesozooplanktonic species in TA and TB. In TC, Cyclopoid copepodites were most abundant. Concerning the metazoan microzooplanktonic compartment, *Brachionus calyciflorus* and Nauplii larvae were the most abundant in TA. In winter, *Bosmina longirostris* was still the most abundant mesozooplanktonic species in TA and TB. In TC, mesozooplanktonic species were very low in abundance: the two Copepods identified were *Acanthocyclops trajani* and *Thermocyclops oithonoides*. For the microzooplanktonic compartment, Nauplii of Copepods were most

abundant in TA and TB. In TC, three species were equally abundant: *Asplanchna* sp., *Polyarthra major* and *Brachionus calyciflorus*.



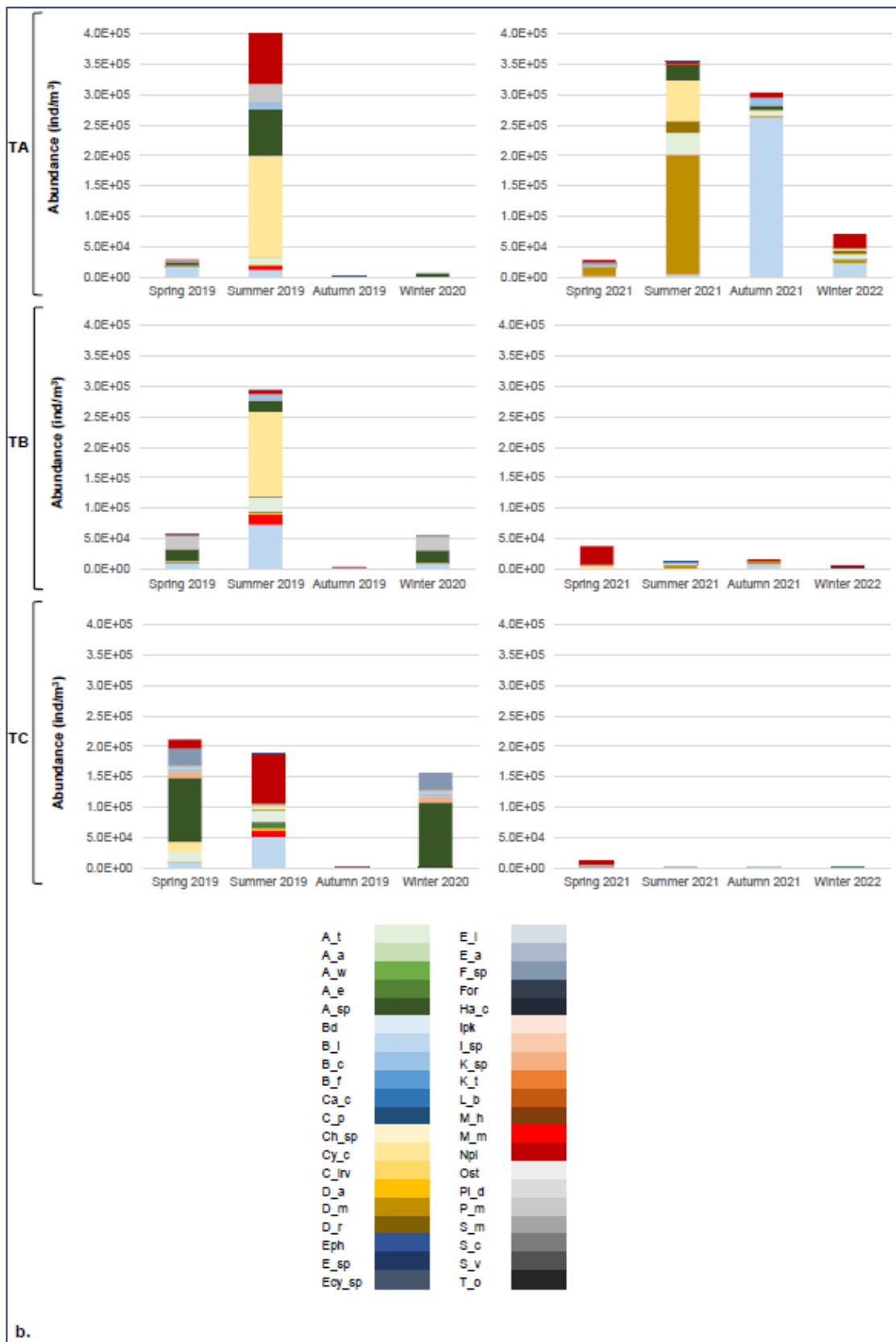


Figure 2. 3: Abundance of a. phytoplanktonic taxa class (cell/L) and b. metazooplanktonic (taxa ind/m³) in the three stations (TA, TB, TC) in the Tasdon marsh before (2019-2020) and after (2021-2022) restoration. The link between the name of each taxon and the abbreviations used in the legends is specified in Appendix 2.1.

2.3.2.2 DNA analyses

Concerning the relative abundances of bacterial taxa (Figure 2.4a), 23 bacterial classes (>0.6 % of total abundance) were selected between before and after the restoration. Different assemblages of bacterial communities were observed between the three sampling stations before the restoration works. In TA, *Actinobacteria* and *Gammaproteobacteria* were highly present in all four seasons, with a higher proportion of respectively *Actinobacteria* in summer and *Gammaproteobacteria* in winter. *Cyanobacteria* were also abundant in spring in this station. In TB, *Actinobacteria* were highly present in spring and were still observed in summer, autumn and winter. *Gammaproteobacteria* were mainly observed in autumn, while *Cyanobacteria* represented almost 50 % of the bacterial communities determined in summer. In TC, the proportions of the different bacterial communities observed were similar between all four seasons: the most dominant taxa overall were again *Actinobacteria*, *Gammaproteobacteria* and *Cyanobacteria*, as well as *Clostridia* specifically in spring and summer.

After the restoration, an increase of *Actinobacteria* and a decrease of *Gammaproteobacteria* relative abundances were observed in TA in all seasons. *Alphaproteobacteria* relative abundance also increased specifically in summer. In TB, the relative abundances of *Alphaproteobacteria* tended to increase compared to the proportion observed before the restoration. *Verrucomicrobiae* were highly observed in spring right after the restoration in TB. The most significant variations in the proportions of relative abundance of bacterial communities were observed in TC: once again, the relative proportion of *Alphaproteobacteria* (mainly the orders *Sphingomonadales* and *Rhodobacterales*) increased, contrary to the relative abundances of *Bacilli* and *Closteria* which tended to decrease after the restoration. Concerning the relative abundances of eukaryotic communities (Figure 2.4b), 15 eukaryotic classes (>1% of total abundance, metazoan taxa excluded) were selected before and after restoration. Some data were not present. However, these results still showed some differences in the composition of taxa before and after the restoration. In TA and TB, the *Perkinsidae* taxa present in spring before the restoration works were not found afterwards. In addition, in TA, the proportion of *Cryptophyceae* significantly increased and replaced *Chlorophyceae*. In TB, *Charophyceae* and *Bacillariophyceae* were observed only after the restoration. In TC, while the composition of eukaryotic communities was like those of TA and TB before the restoration, significant differences were observed afterward: the relative abundances showed a consequent decrease of *Cryptophyceae* and *Chlorophyceae* in favor of *Bacillariophyceae* and *Mediophyceae* in autumn, and *Mediophyceae* and *Dictyophyceae* in winter.

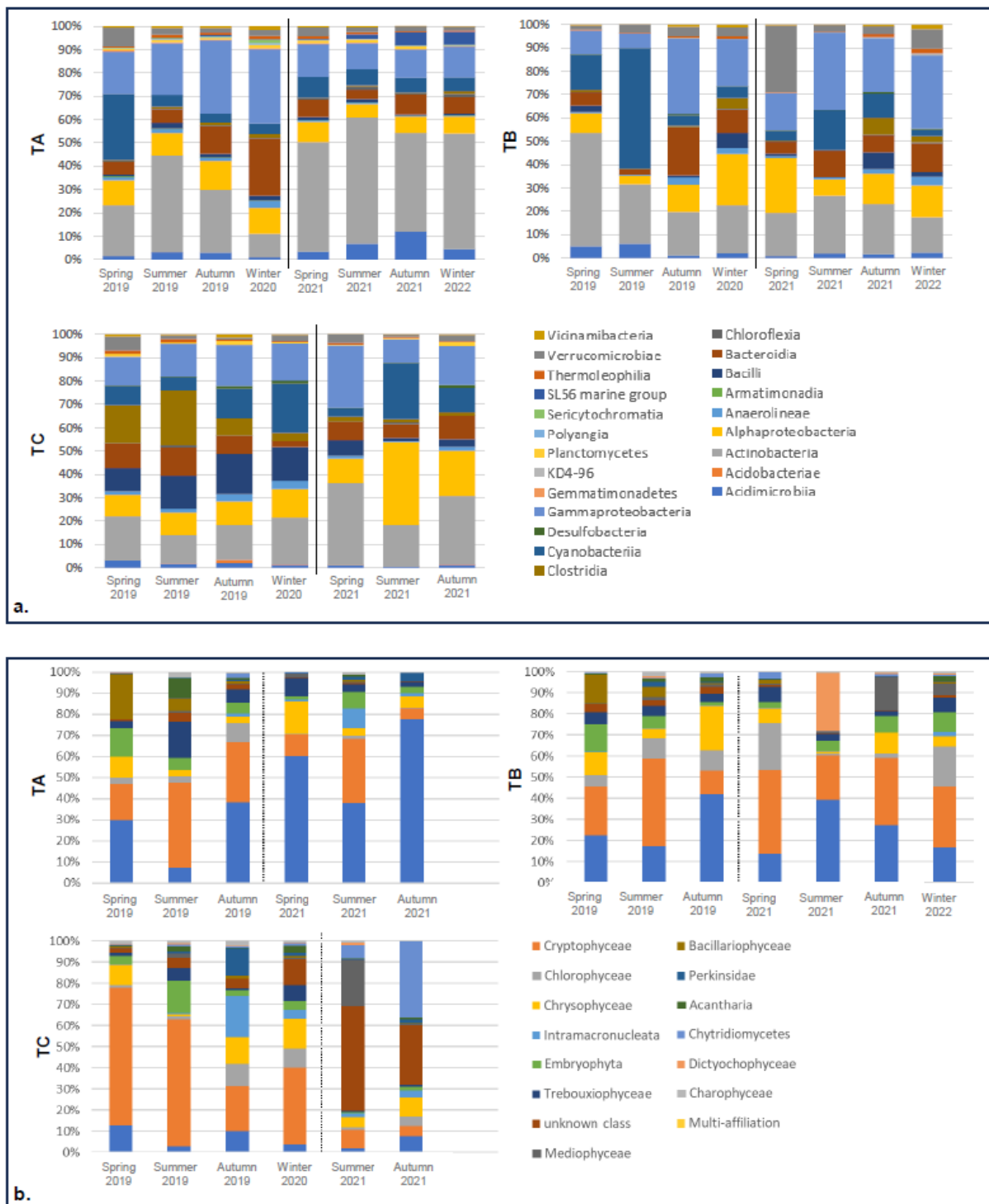


Figure 2. 4: Relative abundance (% of sequences) of a. bacterial class (>0,6% of total abundance) and b. eukaryote class (>1% of total abundance) in the three stations (TA, TB, TC) before (2019-2020) and after (2021-2022) restoration. Some data are missing due to too little DNA on the analyzed filter.

2.3.2.3 Ratio of biomasses

Biomass of autotrophic and heterotrophic communities were determined to assess the mean ratio between them before and after the restoration works for each station/season couple (Figure 2.5). Before the restoration works (Figure 2.5a), heterotrophic communities' biomass was higher than autotrophic communities' biomass in two stations (TA, TB) in all four seasons except in TC where heterotrophic communities' biomass was higher only in summer (0.72 ± 0.12); autotrophic communities' biomass was higher than heterotrophic communities' biomass and increased the ratio from summer to winter (from 1.08 ± 0.18 to 2.27 ± 0.16). After the restoration works (Figure 2.5b), heterotrophic communities' biomass was higher than autotrophic communities' biomass in TA and TC in all seasons except winter, and in TB in summer and autumn. The highest mean ratio values were found in winter in TC (7.12 ± 0.04) and TA (3.09 ± 0.01). Overall, the mean ratio values were higher in autumn and winter after restoration works. On the contrary, the mean ratio values were lower in summer after the restoration works.

Overall, the ratio between autotrophic communities' and heterotrophic respective biomasses showed that autotrophic communities were highly present after the restoration works during the autumn in TB (ratio = 1.76 ± 0.016 ; autotrophic biomass multiplied by 9.6 between before and after the restoration, heterotrophic biomass multiplied by 1.3 between before and after the restoration), and winter in TA (ratio = 3.09 ± 0.001 ; autotrophic biomass multiplied by 91 between before and after the restoration, heterotrophic biomass multiplied by 85.3 between before and after the restoration) and TC (ratio = 7.12 ± 0.04 ; autotrophic biomass multiplied by 1.5 between before and after the restoration, heterotrophic biomass multiplied by 1.6 between before and after the restoration).

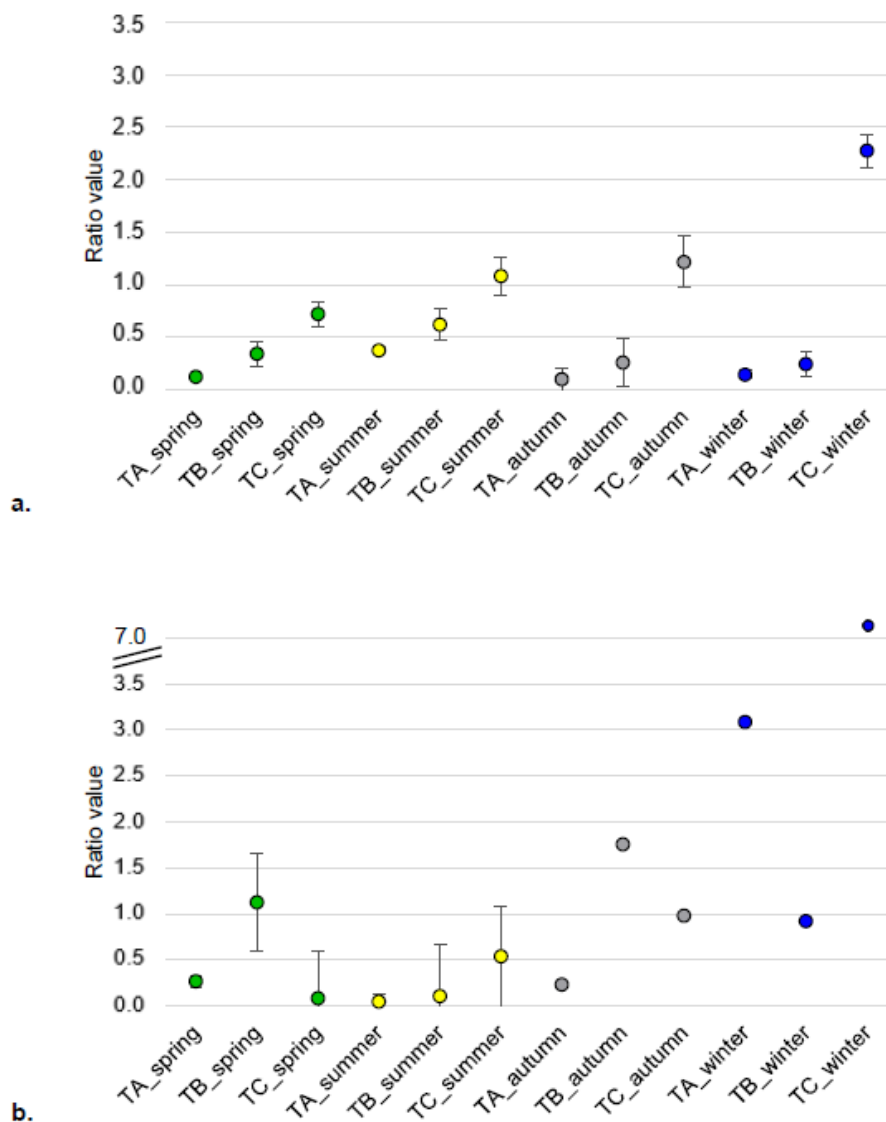


Figure 2. 5: Mean ratios of autotrophic communities' biomass ($\mu\text{g C/l}$) on heterotrophic communities' biomass ($\mu\text{g C/l}$), with standard deviation, determined in the Tasdon marsh (green: spring, yellow: summer, gray: autumn, blue: winter) a. before and b. after the restauration works for each station-season. Values superior to 1 mean that autotrophic community's biomass was higher than heterotrophic communities' biomass and vice versa. The standard deviation not visible on the graphs were below 0.01.

2.3.3 Differences before and after restoration works

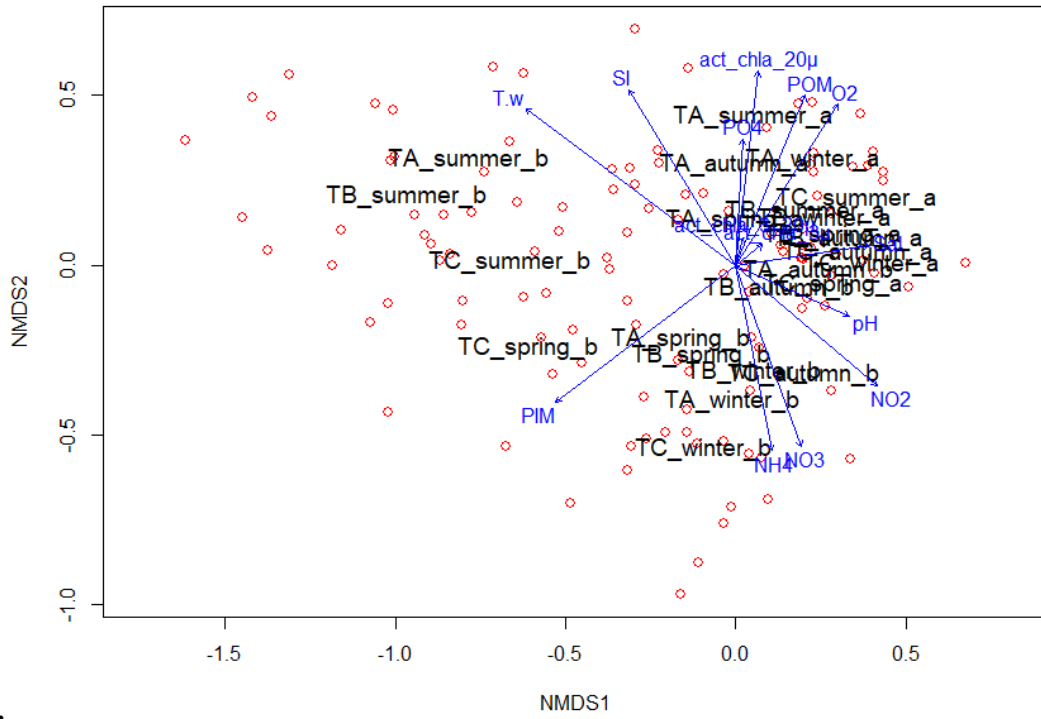
Several analyzes were done to study the Tasdon marsh before and after the restoration works. First, all the data collected before and after the restoration were analyzed to evaluate the potential effect of the restoration works, as well as a potential effect of the station and/or the seasons. Then separated analyzes were done to evaluate specifically to see the potential effect of station and/or seasons before and then after the restoration to assess the variability of these two factors only on the year the data were collected.

The first nMds representing the data distribution before and after the restoration works was done on two dimensions (Figure 2.6a), which was robust according to Shepard plot (non-metric fit, $R^2 = 0.989$; linear fit, $R^2 = 0.960$; stress value = 0.104). Looking at the station-season couples, two data groups were observed: a first one including almost all data collected before the restoration works (observed on the left on the nMds figure), and a second one including all data collected after the restoration works as well as TA and TB in autumn (observed on the right on the nMds figure). In the first group, all three stations in summer were associated with water temperature while they were associated with the concentration of NO_3 , NH_4 and PIM in spring, winter for TA, TB and TC, and specifically in autumn for TC. In the second group, TA in all four seasons after the restoration was associated with the concentration of PO_4 , dissolved O_2 and POM, and the proportion of active chlorophyll *a* for the three size classes. Concerning TB and TC in all four seasons after the restoration as well as TA and TB in autumn before the restoration, the data was associated with the salinity, the pH and the proportion of active chlorophyll *a* for organisms smaller than 3 μm . The ANOSIM showed once again no significant effect of station (significance = 0.502). However, it also showed a strong significant effect of season (significance = 0.0001) and a light significant effect of the restoration (significance = 0.049).

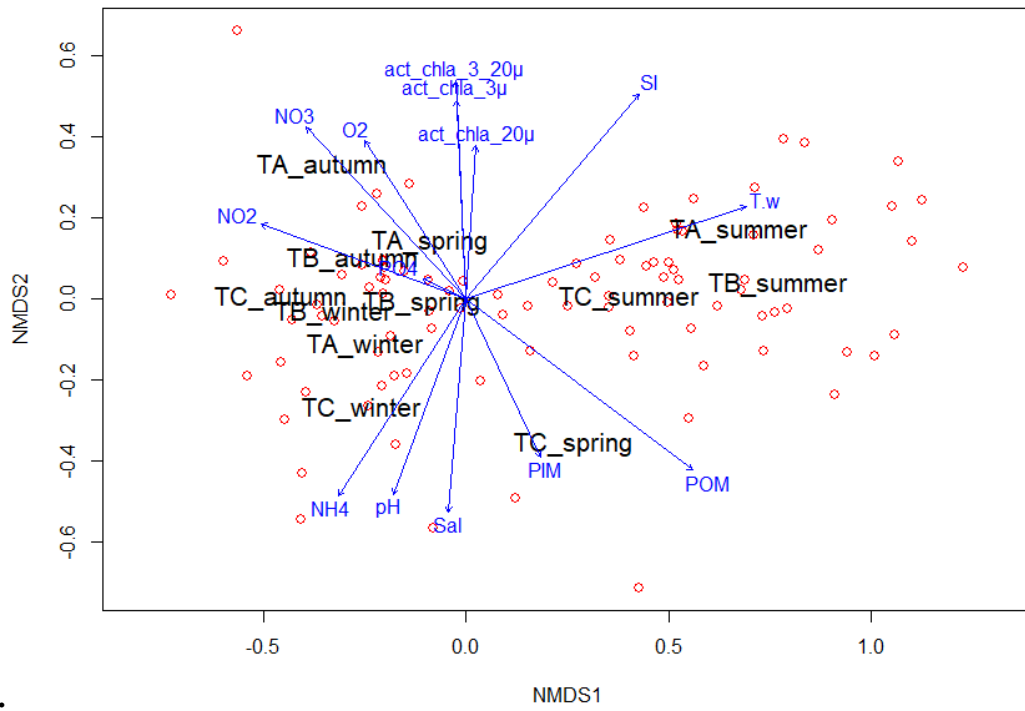
The second nMds representing the data distribution before restoration works was done on two dimensions (Figure 2.6b), which was robust according to the Shepard plot (non-metric fit, $R^2 = 0.995$; linear fit, $R^2 = 0.979$; stress value = 0.071). Looking at the station-season couples, all three stations in summer were similar and linked mainly by the temperature. TA and TB were similar in both autumn and spring and linked mainly by the concentrations of NO_2 and NO_3 , as well as the concentration of O_2 in TA. The proportion of active chlorophyll *a* for each class of size seemed to be especially linked to TA in spring. The three stations in winter were mainly linked by the concentration of NH_4 and the pH, especially in TC. Contrary to the similarity of TA and TB in spring, TC was mainly affected by the concentration of PIM and POM. The ANOSIM showed that there was no significant effect of station (significance = 0.910), but there was a strong significant effect of seasonality (significance = 0.0001). This effect was well represented on the nMds plot, even though the three stations in spring were not as close as their representation for the other seasons on the plot.

The third nMds representing the data distribution after restoration works was also done on two dimensions (Figure 2.6c), which was robust enough according to the Shepard plot (non-metric fit, $R^2 = 0.982$; linear fit, $R^2 = 0.898$; stress value = 0.135). Looking at the station-season

couples, they were all regrouped: TA in spring was the most dissimilar point where high abundance of Ciliates (c_2) was observed. TA in summer and autumn were induced by the concentration of PO₄ and the proportion of active chlorophyll *a* for organisms larger than 20 μm. TA in winter was mainly related to turbidity. TB in summer and spring was associated to the proportion of active chlorophyll *a* for organisms lower than 20 μm, and the concentration of NO₃ and PIM. TB in autumn and TC in spring were mainly influenced by the concentration of NO₂. TC for the three other season (summer, autumn, winter) was mainly influenced by salinity, as well as pCO₂ and the concentration of POM and O₂ in summer. The ANOSIM showed no significant effect of station (significance = 0.164), nor for the seasons (significance = 0.116).



a.



b.

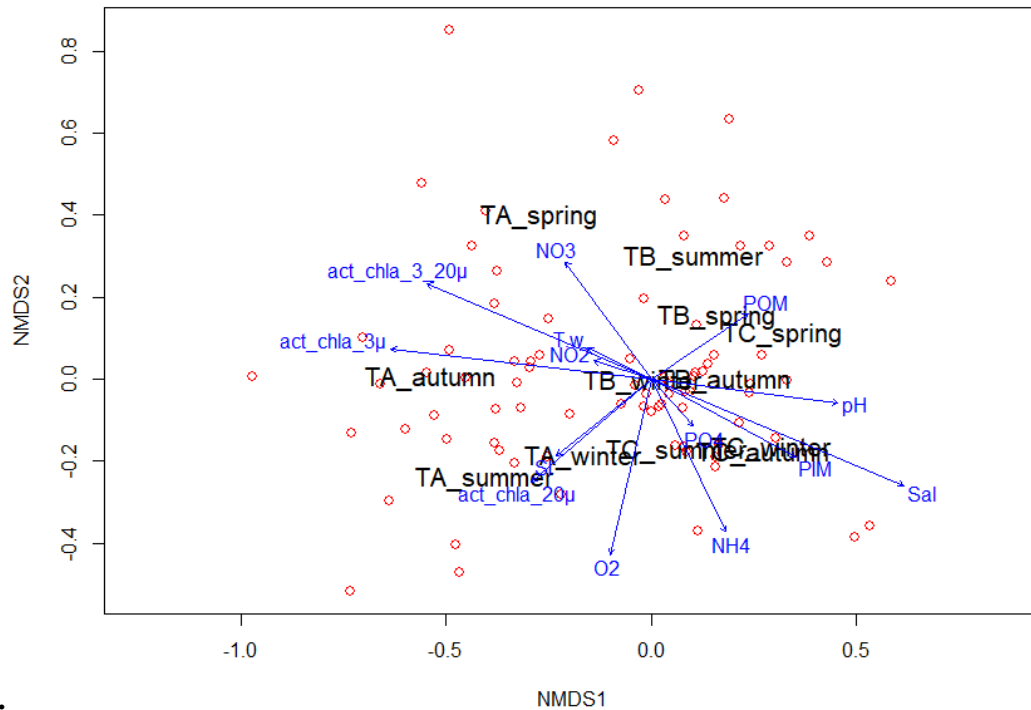


Figure 2. 6: Non-Metric dimensional Scaling plot on two dimension (stress value = 0.071) representing the data distribution of the Tasdon marsh a. before and after restoration, b. before restauration works, c. after restauration works, works for each station-season couple (TA, TB, TC; spring, summer, autumn, winter). The variables in red represent the abundances of phyto- and metazooplanktonic taxa (see Appendix 2.1), The variables in blue represent environmental parameters: pH: potential hydrogen, T.w: water temperature ($^{\circ}\text{C}$), Turb: turbidity (NTU), Sal: salinity, O_2 : dissolved oxygen concentration (mg/l), pCO_2 : partial pressure of carbon dioxide (ppmv), NH_4 : ammonium concentration (mg/l), NO_3 : nitrate concentration (mg/l), NO_2 : nitrite concentration (mg/l), PO_4 : phosphate concentration (mg/l), SI: silicium concentration (mg/l), PIM: particulate inorganic matter concentration (mg/l), POM: particulate organic matter concentration (mg/l), act_chla_20 μ : proportion of active chlorophyll a for organisms bigger than 20 μm (%), act_chla_3_20 μ : proportion of active chlorophyll a for organisms between 3 and 20 μm (%), act_chla_3 μ : proportion of active chlorophyll a for organisms smaller than 3 μm (%). Concerning plot c., the mention “_b” refers to data collected before the restoration works, and the mention “_a” refers to data collected after the restoration works.

2.3.4 Planktonic food web topologies

Before the restoration, four types of food web were determined for the Tasdon marsh (Figure 2.7a). The first type of food web (FW1) was determined as an herbivorous food web since the concentration of chlorophyll *a* for organisms in all three size classes was high, as well as the proportion of active chlorophyll *a* for these organisms and the concentration of nutrients (NO_2 , NO_3 , NH_4). On the contrary, the biomasses of heterotrophic prokaryotes and meso- and microzooplanktonic metazoan organisms were low. FW1 was determined in spring in TA and TB, and in winter in TC. The second type of food web (FW2) was determined as a multivorous food web since the different planktonic communities (*i.e.*, phytoplankton, heterotrophic

prokaryotes, metazooplankton) were abundant in the water column. FW2 was determined in spring in TC and in summer on all three stations. The third type of food web (FW3) was determined as a “biological winter” since the abundances of the different planktonic communities were low, and the concentration of inorganic particulate matter (PIM) was higher compared to FW1 and FW2. FW3 was determined in autumn in TA, TB and TC. The fourth type of food web (FW4) was determined as different type of “biological winter” than FW3 since the concentration of NO_2 , NO_3 and NH_4 in the water column were significantly higher than their concentrations observed for FW3. FW4 was determined in winter in TA and TB.

After the restoration, three types of food web were determined in the Tasdon marsh (Figure 2.7b). One of these food web types was as one of those determined before: FW2, the multivorous food web, was clearly determined in summer in TA and TC, based on the same arguments as mentioned for before restoration. A weaker multivorous food web was also determined in spring and autumn in TA and TC, and in summer in TB. In this case, the concentration of chlorophyll *a* was variable but all the different planktonic communities were present, even though their abundances were as high as observed in summer in TA and TC. Thus, two of the three types of food web determined after restoration were considered as slightly different stages of a multivorous food web. The third type of food web (FW5) was determined as a transitional food web between a “biological winter” and the installation of a weak herbivorous food web. The concentration of NO_2 and NO_3 were high and there were also variable abundances of microzooplanktonic organisms and phytoplanktonic organisms between 3 and 20 μm . FW5 was observed in winter on all three stations, as well as in autumn and spring in TB.

	Spring	Summer	Autumn	Winter
TA	FW1	FW2	FW3	FW4
TB	FW1	FW2	FW3	FW4
TC	FW2	FW2	FW3	FW1

a.

	Spring	Summer	Autumn	Winter
TA	FW2	FW2	FW2	FW5
TB	FW5	FW2	FW5	FW5
TC	FW2	FW2	FW2	FW5

b.

Figure 2. 7: Summary of the different types of planktonic food webs determined in the Tasdon marsh a. before, and b. after the restoration. FW1: herbivorous food web (green), FW2: multivorous food web (orange), FW3: “biological winter” (gray), FW4: “biological winter” with high concentrations of nutrients (blue), FW5: transitional food web between biological winter and weak herbivorous (yellow).

2.4 Discussion

2.4.1 Changes in carbon fluxes

Measuring the $p\text{CO}_2$ of water in relation to that of the atmosphere is essential to determine whether the ecosystem acts as a source or sink of atmospheric carbon (Figure 2.8). Apart from the high $p\text{CO}_2$ value in TA in summer after restoration, the values for summer and winter in all three stations were also low after the restoration. Variations of $p\text{CO}_2$ were directly affected by the communities in the water column; the temperature did not affect it (see Figure 2.2). The increase of the CO_2 sink might come from different sources: the increase of turbidity in the water column might induce reduced development of the autotrophic communities due to the reduction of the light penetration in the water column (James et al., 2001). The dead planktonic organisms might then sink to the sediments, thus bringing carbon to the benthic layers (Howard et al., 2017). The higher concentration of suspended matter seemed to have increased the turbidity, thus the microbial activity by heterotrophic prokaryotes might have increased (Muylaert et al., 2003). However, an increase in the microbial activity also means that the respiration might increase, which seemed not to have affected the carbon sink since the $p\text{CO}_2$ values decreased after the restoration. It might be possible that the increase of photosynthesis activity from autotrophic communities, and hydrophytes vegetation bordering the marsh,

consumed more CO₂ than the part produced by the respiration of planktonic communities. The literature shows that the sequestration of CO₂ in a wetland type of environment is mainly due to the photosynthesis of autotrophic communities (Morant et al., 2020) and the degradation of organic matter by heterotrophic prokaryotes (Kayranli et al., 2010). Since there were no significant differences between the percentage of active chlorophyll *a* for the three class of size studied between before and after the restoration works, the microbial activity might be the factor influencing the increase of carbon sequestration in the water column. Furthermore, the ratio of autotrophic and heterotrophic communities showed that autotrophic communities were not dominant in 2021, confirming the impact of heterotrophic bacteria linked to the restoration. Unfortunately, flux measurements could not be done in this study to verify this hypothesis. Nonetheless, the results have showed that, especially in TC, the Tasdon marsh is more often a sink than a source of carbon throughout the year after the restoration. In TC, the periodic intake of saltwater coming from the sea might explain the lowest pCO₂ mean values observed after the restoration works since pCO₂ values are generally lower in saltwater than in freshwater (Mayen, 2020). This management operation imitated the effect of a rising tide and the associated horizontal fluxes (*i.e.*, the exchanges of carbon with saltwater masses).

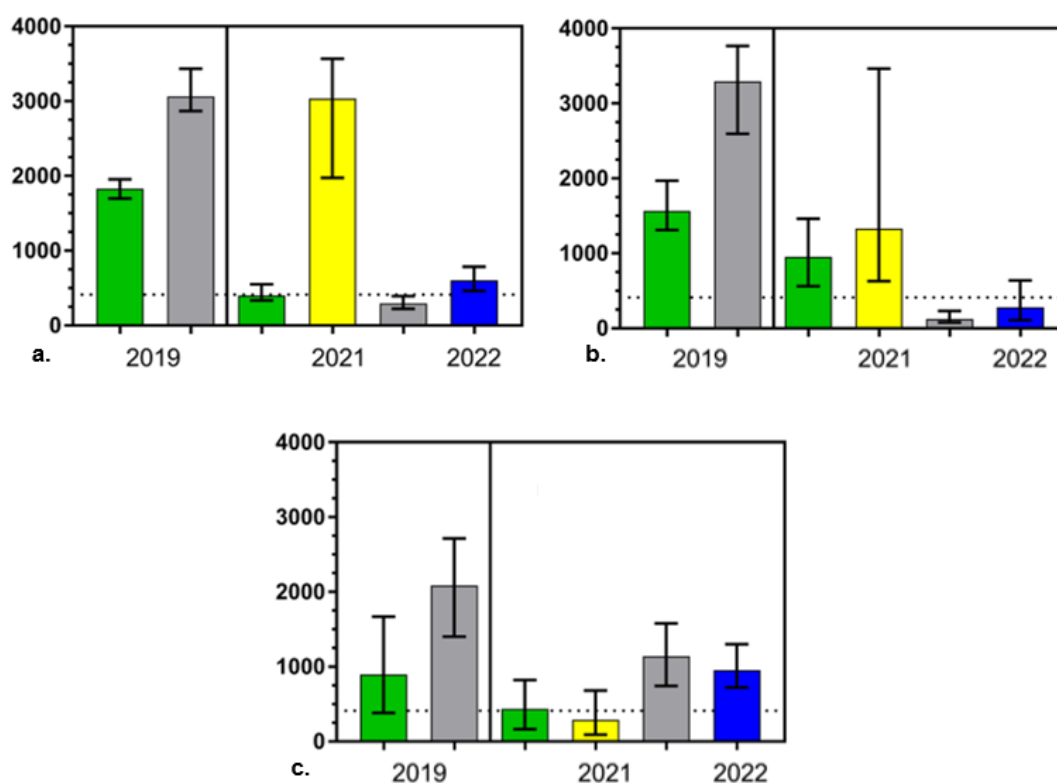


Figure 2. 8: Compared means with standard deviation of pCO₂ (ppmv) measured in different seasons in the Tasdon marsh (green: spring, yellow: summer, gray: autumn, blue: winter) before (2019) and after (2021-2022) the restoration works for a. TA, b. TB, c. TC. The dotted line indicates the under which the environment is considered to sink more CO₂ than it releases.

2.4.2 Diversity and ecological functions

Focusing on the diversity, abundance and biomasses of planktonic communities, the study showed that autotrophic communities, specifically phytoplankton, were more abundant before the restoration works than after, except in winter. Heterotrophic (and sometime mixotrophic organisms) communities such as *Euglena* and *Cryptophyceae* were more abundant after the restoration works, indicating a lower quality of water. Concerning the metazooplanktonic communities, the dominant species present before the restoration works were herbivorous species, such as *Bosmina longirostris* and *Daphnia ambigua*, and after the restoration works the dominant species were detritivores and non-selective filter feeders, such as *Daphnia magna* and *Chydorus* sp.. During spring and summer in 2021, most of the herbivorous mesozooplanktonic species were not observed. However, their complete disappearance in the water column could not be affirmed since it was possible that their abundances were too low during the sampling. The same deduction could be made for species such as *Daphnia magna*, which were not observed before the restoration works. In the case of Cladocerans, the literature shows that they can produce ephippia (*i.e.*, type of eggs capable of remain dormant in the sediment if the environmental conditions are not suitable for their development), which might be another hypothesis to explain not observing this species in the Tasdon marsh before.

In addition, some missing species, which were present in all four seasons before restoration in 2019 but not observed in spring and summer in 2021, reappeared in autumn and winter 2021, especially in TC: the main reason might be the fact that there was no intake of saltwater during two months between autumn and winter because the water level was high due to the rainfall. Thus, the station did not receive salinity nor suspended matter input: the detritivores planktonic species might have been short on nutrition. Between the three stations studied, TC was the most impacted one after the restoration works: at this station the lowest global abundances of planktonic communities during each season were observed, compared to those determined before restoration works. The periodical intake of water, inducing several perturbations in the water column is likely to have influenced the planktonic communities, sensitive to changes of salinity (Sarma et al., 2006; Toruan, 2012), temperature (Baird et al., 2001), or turbidity (David et al., 2005; Modéran et al., 2010). In TC, approximately 50 % of female Cladocera observed were carrying ephippia instead of normal egg when the sampling was done two to three days after the intake of saltwater, contrary to when the sampling was done at least five days after. This observation showed that these intakes induced stress for some metazooplanktonic species which prepared a bank of egg in the sediment (Carvalho and Hughes, 1983; Bailey et al., 2004)

ready to hatch when the environmental parameters in the water column returned to a suitable habitat for them. Although some marine species were occasionally determined in TC after the restoration works (*e.g.*, Calanoid copepodites, Cypris larvae), they so far did not develop in the environment. The main reason might be the too low salinity for them to survive in the former freshwater marsh (Kimmel and Bradley, 2001).

2.4.3 Changes in planktonic communities

Looking overall at all three stations, the nMDS and associated ANOSIM tests the station effect was not significant before (p -value = 0.913) and after (p -value = 0.161) the restoration. The seasonal effect was significant only before the restoration (p -value = 0.0001). The effect of the restoration works was lightly significant (p -value = 0.049) thus to be interpreted with caution, as the seasonal effect seems to remain the factor with the greatest impact on plankton community dynamics at the three stations studied. Even though the bacterial communities seemed to be affected by the restoration, discerning seasonal variations, spatial variations and station-specific restoration works are difficult. Concerning the fact that stations did not differ, effect of station, it could be explained by the fact that each station receives water from the same source (*i.e.*, the river passing through the marsh), so planktonic communities were similar on each station. At the station TC, which periodically receives saltwater after the restoration works, the salinity did not increase as much as expected (see Appendix 2.3). So, marine plankton might not be able to settle in this environment while freshwater species remained dominant. Since the overall planktonic diversity between TA, TB and TC was similar, the non-significant effect of the seasonality might come from the shift of management influencing the environmental parameters after the restoration works. Since plankton profits from long residence times (Sierszen et al., 2006; Lucas et al., 2009), The change of TB from a stagnant pool to a small current has probably decreased planktonic development. Concerning TC, the periodic intake of saltwater might be able to modify several environmental parameters every two weeks: it could bring loads of organic and inorganic matter through resuspension of part of the sediments (Vernberg and Vernberg, 2001), which might influence the activity of heterotrophic prokaryotes in the water column, as well as a reduction of the euphotic zone (Goosen et al., 1999) leading to a lower development of autotrophic planktonic communities. This hypothesis might be directly linked to the mean ratio values of autotrophic and heterotrophic biomasses, which were only higher after the restoration works in autumn and especially in winter, right after a stop of management operations for 3 months. Thus, autotrophic communities' biomass was only higher when the potentiality of the resuspension of organic and/or inorganic matter was lower. The

watercourses rectification and landscapes remodeling might have also caused resuspension of sediments (Vernberg and Vernberg, 2001); thus, TA could be affected as well even though this station was the least affected by the restoration works.

2.4.4 Planktonic food web topologies

The type and succession of planktonic food webs in the Tasdon marsh were affected by the restoration. The herbivorous food web and “biological winter” were not clearly determined after the restoration, even in TA which was the least affected station by the restoration works. In the case where these types of food webs would not reappear in a long-term monitoring, it might induce a shift of some ecological functions provided by planktonic communities. On the other hand, this new management inducing a longer multivorous food (weak and strong, and not a classical one) web in the marsh throughout the year might enhance other ecological functions: an overall increase of planktonic communities’ biomasses (biomasses multiplied between 1.2 and 3.0 between before and after restoration) through the year might allow more feeding resource for the juvenile of fish or shorebirds, thus enhancing the nursery function (Milstein et al., 2006; Didenko et al., 2020). However, even if planktonic biomass becomes more abundant after restoration, the quality of food available for the nursery function could be diminished as herbivorous zooplanktonic species have been replaced by non-selective detritus feeders and non-selective filter feeders. For example, in TA, Cryptophyceae were highly abundant post-restoration works due to the increase of turbidity, decreasing the euphotic zone thus not allowing other phytoplanktonic taxa to develop as well as before. Cryptophyceae are known to be bioindicators of poor water quality (El-Kassas and Gharib, 2016; Dembowska, 2021): therefore, the nursery function should be specifically enhanced for non-selective feeder predators. The fact that the transitional type of food web FW5 was observed in winter right after an interruption on the new management operation for three months indicates that the management resulting of the restoration tends to enhance a multivorous food web by, for example, providing more nutrients and particulate matter (higher values observed two to three days after saltwater intakes) with periodical intakes of saltwater (Scott et al., 2014).

An additional study monitoring the different planktonic communities and their food webs for several years might allow to confirm the changes in the structure and seasonal succession of these communities. If the salinity tends to increase more than 4.3, which is the higher value of salinity observed in this study, there might be more changes in the diversity of planktonic communities. Analyzing the sediments to look for a potential planktonic egg bank might as well be interesting to verify the type of resting stages present and evaluate the potential structure of

planktonic communities and their trophic function in the Tasdon marsh, thus their potential associated ecological functions that could be affected by this restoration on the long-term.

2.5 Conclusion

Overall, this study showed that the management operations issued from the restoration works in the Tasdon marsh quickly affected the planktonic communities: their abundance/biomass and their diversity, thus their ecological functions, seemed to be modified indirectly by the change of key environmental parameters, such as turbidity or temperature, caused by these works. This new planktonic community's structure induced changes in the carbon fluxes in the environment by directly affecting the net primary production and the carbon sequestration function. Since planktonic communities tend to have a short resilience to changes in their environment, a long-term monitoring of all three station would be needed to evaluate how this ecosystem will evolve with this new management, and what ecosystem services they could provide. A comparative study with a saltmarsh going through restoration works might also be useful to see the different, or not, benefits.

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Chapitre 3 : Impact of short-term marine submersion on planktonic communities: an *in situ* simulated experiment

A ce jour, la majorité des études sur ce sujet sont réalisées en laboratoire dans des conditions contrôlées (mésocosmes) ou par le biais de modèles statistiques. Le but de ce dispositif est d'offrir une première approche de l'étude d'impact de la submersion sur le réseau trophique aquatique dans des conditions plus proches de la façon dont les paramètres environnementaux évolueraient en milieu naturel. Le protocole expérimental ainsi que les premiers résultats ont été présentés sous forme de poster lors du colloque international ECSA 59 « Using the best scientific knowledge for the sustainable management of estuaries and coastal seas ». Les résultats spécifiques aux communautés zooplanctoniques ont été présentés sous forme de poster au colloque international de l'ASLO « Resilience and Recovery in Aquatic Systems ».

Impact of short-term marine submersion on planktonic communities: an *in situ* simulated experiment

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Abstract

Due to climate change, natural disasters such as marine submersion tend to become more frequent. These phenomena can have a significant impact on coastal ecosystems and the ecosystem services they provide. Several laboratory experiments have been carried out to study the potential impact of marine submersion, but few in the natural environment. This study carried out between February and April 2022 presents an simulated *in situ* experiment studying the potential impact of marine submersion on the diversity and abundance of planktonic communities (phytoplankton, metazooplankton, heterotrophic prokaryotes and heterotrophic protists) of a coastal saltmarsh, together with the planktonic community metabolism and abiotic parameters (temperature, oxygen concentration, salinity, turbidity and concentration of suspended matter: organic and inorganic). Following three days of submersion, these communities were monitored during two months in three control and three submerged ponds. After the simulated submersion, some abiotic parameters confirmed that the submersion was well simulated. Later most environmental parameters measured fluctuated through time, although variability between the three control and the three submerged ponds was not significantly different. The only abiotic parameters which differed significantly between the two treatments right after the submersion was the saturation of dissolved oxygen. High abundances of Ciliates were observed in all the ponds, contrary to Diatoms and Dinoflagellates abundances. Metazooplanktonic abundances were dominated by Copepods, especially *Eurytemora pacifica* in all six ponds. There were no significant differences in the assemblage

of planktonic communities between all six ponds. The variability between the ponds did not allow to dissociate the potential effect of short-term submersion from the seasonal effect. The methodology of this new type of *in situ* experiment need improvement to confirm these first results.

Keywords: saltmarsh, pond, short-term flood, plankton, biodiversity

3.1 Introduction

Marine submersion refers to the temporary flooding of coastal areas by the sea under extreme weather conditions. Different types of marine submersion exist, from short-term flooding episodes with little seawater input to more intense submersion episodes where coastal areas are flooded for several days or even weeks. One example of frequent, short-term periodic marine submersion is the "Acqua alta" that occurs every year in Venice (Italy) in autumn (Caporin and Fontini, 2016). This annual period of high tide, varying in intensity from year to year, floods several parts of the city for a few days. On the other hand, an example of an intense and violent marine submersion phenomena is the one caused in New Orleans (USA) by the Katrina hurricane (Dolfman et al., 2007; Olshansy, 2008). Waves of up to eleven meters in height inundated the city, causing almost 2,000 deaths and heavy material damage. This kind of intense marine submersion phenomena, more violent but also rare, are often induced by storms causing high swell and surge (Chaumillon et al., 2017). The combined effect of change of atmospheric pressure and wind can locally cause an increase in sea level (Dobson, 1971; Pirazzoli, 2000). For example, the 1953 North Sea flood was a combination of a storm and marine submersion phenomenon (Maspataud et al., 2013): at the time it occurred, the theoretical tide level was 6.70 m, but the storm surge reached 1.30 m, and the swell effect was added. The result was a sea level of 8.50 m, significantly higher than the expected theoretical level, causing thousands of human casualties (<https://www.environmentandsociety.org/arcadia/north-sea-flood-1953>; <https://www.britannica.com/event/North-Sea-flood>) in England, the Netherlands and Belgium. In the South Netherlands, this event gave rise to extensive dike building to protect the lowlands (polders) against flooding along the Schelde – Maas Delta (<https://www.rijkswaterstaat.nl/en>). Submersion phenomena can be even more intense if the tide level is initially high (Chaumillon et al., 2017). The integrity of coastal areas is often affected by marine submersion, which can accentuate erosion phenomena in the littoral zone, making it more vulnerable to future episodes of submersion (Suarez et al., 2007; Chaib et al., 2020). Due to climate changes, marine submersion might tend to become more frequent all over the world (Almar et al., 2021) and

coastal ecosystems might become more and more vulnerable to the point of no longer being able to provide their ecosystem services (Simas et al., 2001; De Wit, 2011).

Coastal marshes are often used as buffer zones between the sea and the land in the event of flooding or marine submersion (Kennish, 2001; Temmerman et al., 2023), and as such can be heavily affected by these phenomena. Despite the disappearance of these environments in the last century due to urbanization of the littoral (Kennish, 2001; Wu et al., 2017; Faccini et al., 2021), coastal wetland restoration plans have been increasingly adopted in recent years (Zhao et al., 2016). Contrary to the dike building policy favoured at the second half of the twentieth century, the fact that coastal marshes constitute natural buffer zones between the sea and the land is more and more realised and used as a strategy for flood protection. As such, one of the most frequently performed actions seen in the change of management to restore coastal marshes is depoldering (Esteves, 2014; Warner et al., 2018). Even though these new managements tend to protect these ecosystems and the ecosystem services that they provide, a gradual rise in sea level and flooding episodes in coastal areas might affect this potential. For example, biodiversity could be affected by a lack of time to adapt to the new flooding frequency, or by the violence of the phenomena, especially for changing the salinity in freshwater marshes (David et al. 2020). For example, Lorrain-Soligon et al. (2021) showed that, after an extreme event of marine submersion on the west coast of France, changes in the composition of amphibian communities were observed (mainly due to the increase in salinity) although these communities showed of resilience in the long term. Several studies using modelling tried to assess the overall impact of frequent marine submersion on the aquatic food web of coastal wetlands (Spencer et al., 2016; Debue et al., 2022), as well as the potential economic value impact (Kuhfuss et al., 2016). Statistical models usually show that a significant proportion of coastal zones will eventually disappear due to frequent flooding and sea level rise, and that new management actions must be done to preserve these coastal environments.

At the base of the aquatic food web are planktonic communities. Although planktonic communities might be resilient to some environmental perturbations (Toruan, 2012; Ginatullina et al., 2017; David et al., 2020), an increase of marine submersion episodes might compromise their adaptation capacity, thus having a strong bottom-up effect on the aquatic food web. Many abiotic parameters are directly impacted by marine submersion phenomena: studies try to assess the impact specific environmental parameters such as salinity (Hall and Lewandowska, 2022), turbidity (Llames et al., 2009), or temperature (Lewandowska and Sommer, 2010) in controlled mesocosm experiments. However, to the best of our knowledge, no studies have so far tried to

evaluate the potential effect of marine submersion on marine planktonic communities and aquatic food web directly in the field, in a natural environment. David et al. (2020) did monitor on planktonic communities in freshwater marshes when marine submersion occurred after the Xynthia storm, but not in saltwater marshes.

The aim of this study is to suggest a protocol to simulate an *in situ* marine submersion on a saltwater coastal marsh to determine its potential effect on planktonic communities (phytoplankton, metazooplankton, heterotrophic prokaryotes, heterotrophic protists). The type of marine submersion chosen was a short-term submersion of three days. The planktonic communities in the study site were subsequently monitored for two months after the marine submersion. This experience was done in winter, to have the best set up with the climate and conditions in which submersion phenomena occur most often naturally (Rothenbücher and Schaefer, 2006; Kaniewski et al., 2021). Hypothesis were that an increase of turbidity might occur, inducing a low development of phytoplanktonic communities (*i.e.*, low abundances observed), as well as an increase of nutrient and dissolved organic carbon (DOC) by shoreline washing. Low phytoplanktonic abundances would represent less prey availability for metazooplankton, thus low abundance of metazooplanktonic communities might be observed. This cascading effect might offset the seasonal succession of planktonic communities. On the other hand, a significant input of nutrient in the water column might increase heterotrophic prokaryote and phytoplankton development when the turbidity starts to decrease. In this study, the term “submersion” will be used to characterize the short-term submersion simulated in this experiment.

3.2 Methods

3.2.1 Study area

The L’Houmeau marsh (N 46° 12’ 9.69”; W 1° 12’ 0.96”), located on the west coast of France, is a 7 ha experimental area of the French “Centre National de Recherche Scientifique” (CNRS) with several ponds of different sizes, all fed directly by seawater (Figure 3.1). Comprising several types of ponds of various size and levels, this versatile setup allows a large possibility of experiments thanks to the possibility to control the tidal cycles with floodgates and the possibility of *in situ* replicates.

Since 1985, this experimental marsh is indeed used for several experiments and monitoring on various organisms (*e.g.*, bivalves, bass) (Mustafa et al., 1991; Dupuy et al., 2000; Barbarin et

al., 2022). Among these ponds, eight measure 200m² and are located next to an adjacent channel supplying them with seawater through pipes in phase with the tides. The end of this channel has a floodgate which can be used to prevent the water drain from the channel. Six of these ponds were selected for this experiment (Figure 3.1): three of them were used as control ponds (CR1, CR2, CR3), and the other three were submerged (IR1, IR2, IR3). Before the beginning of the experiment, all six ponds were drained and left to dry for one month (December 2021). They were then all refilled up to the same water level (70 cm) with sea saltwater, and several multiparameter probes were submerged in the ponds to measure water height, temperature, dissolved O₂ saturation and pH. On February 3rd, 2022, when tidal range was around 6.30 m, the floodgate was closed for three days to allow the water from the adjacent channel to overflow into the ponds to be submerged. The control ponds received no water intake during this period. At the end of the third day, the ponds were restored to their original water level (around 70 cm).

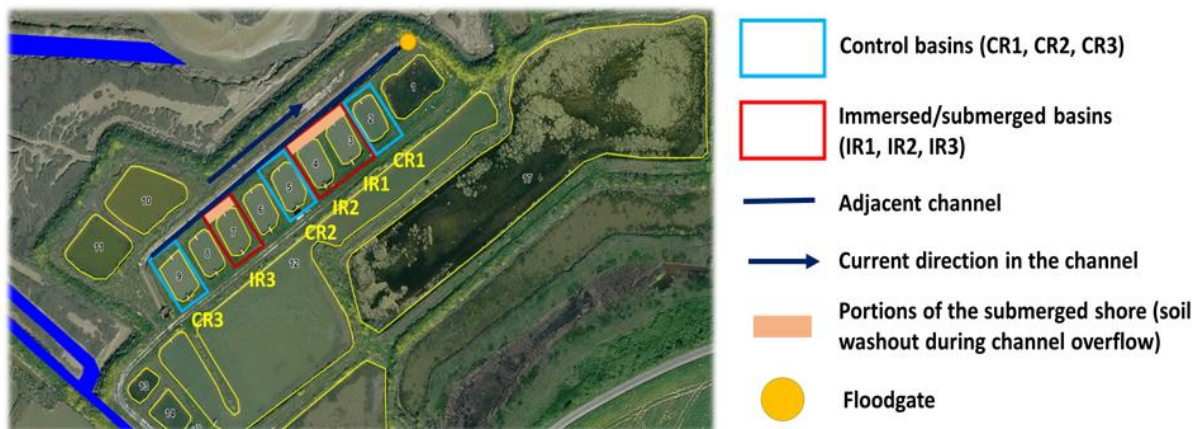


Figure 3. 1 : Aerial view of the experimental marsh of CNRS L'Houmeau (France). Schematic presentation of the experimental design of the in situ submersion experiment.

3.2.2 Sampling method

The experimental design is based on the BACI (Before-After-Control-Impact) method to test the potential before-after submersion effect between the two treatments (Green, 1979; Underwood, 1991). Prior to the experimental submersion, sampling was carried out to inventory planktonic species present in the marsh. Monitoring of abiotic parameters, heterotrophic prokaryotes, heterotrophic protists, phytoplankton and metazooplankton was done during two months after the simulated submersion (twice per week the first month, then biweekly during the second month; see Table 3.1). In addition, an Ysi probe was set up in each pond to continuously measure temperature, turbidity, salinity and of dissolved oxygen proportion in the

water column. Two sensors (NKE) were added to two of the ponds (CR2 and IR2) to measure the height of the water level during the whole experiment by measuring the pressure exerted by the water column, which enabled to calculate the water height using the hydrostatic hypothesis.

Concerning abiotic parameters, in addition to the punctual measurements of environmental parameters (water temperature, pH, salinity, dissolved oxygen concentration) a with multiparametric probe (VWR™), at each sampling occasion, 5L of water were carefully sampled with a bucket to avoid resuspension of sediment and stored in bottle to quantify Suspended Particulate Matter (SPM), Particulate Inorganic and Organic Matter (respectively PIM and POM), nutrient concentrations (NO₂, NO₃, NH₄, PO₄, Si, DOC). The bottles were kept in the dark in a cool environment until the return to the laboratory. Immediately upon arrival in the laboratory, samples were filtered in triplicate on pre-weighed GFC filters for SPM and PIM and the filtrates were used for nutrient quantification. For chlorophyll *a* and phaeopigment concentrations, three size classes of organisms were separated by filtration: (microphytoplankton: > 20 μm, nanophytoplankton: between 3 and 20 μm, picophytoplankton: < 3 μm).

1.5 mL of water was transferred in cryotubes with a mixture of glutaraldehyde (final concentration: 0.2 %) and poloxamer (final concentration: 0.001%) to evaluate the abundance of heterotrophic prokaryotes and phytoplankton (pico- and nano-). These samples were frozen liquid nitrogen and then stored at -80°C in the laboratory. For metazoan microzooplankton, 6 L of water was filtered with a 63 μm mesh stainless-steel sieve: the filtrate was then fixed with buffered formaldehyde (final concentration: 4%). For metazoan mesozooplankton, horizontal hauls were done in each pond with a standard WP2 (200 μm mesh net). Depending on eye assessment of plankton abundance in the collector, the distance of the hauls varied from 5 to 40 m to obtain enough organisms to have a solid community composition determination. Horizontal hauls were considered sufficient to sample planktonic communities in the water column; thus, no additional vertical hauls were done (Semyalo et al., 2009; Das et al., 2020). Apart from the cryotubes, all planktonic samples were kept at 4°C in a cold-storage room at the laboratory until analyses.

Table 3. 1: Correspondence of the abbreviation used in the analyses and the dates where the sampling was done.

Date	Abbreviation	
24/01/2022	T0	} Before submersion
08/02/2022	T1	
11/02/2022	T2	} First month after submersion
14/02/2022	T3	
18/02/2022	T4	
22/02/2022	T5	
28/02/2022	T6	
15/03/2022	T7	} Second month after submersion
18/03/2022	T8	
29/03/2022	T9	

3.2.3 Sample analyses

The concentration of nitrate (NO₃), nitrite (NO₂), ammonium (NH₄), phosphate (PO₄) and silicate (Si) was determined on filtered water (0.7 µm GF/F glass fiber membrane, Whatman) using a SEAL AA3 autoanalyzer with the detection limit of: 0.02 µmol/L (NO₃), 0.003 µmol/L (NO₂), 0.06 µmol/L (NH₄), 0.01 µmol/L (PO₄), 0.04 µmol/L (Si) according to the methodology of Aminot and K erouel (2004). For Si analyzes, tests were made with a calibration solution with a known concentration of silicate (between 35 et 40 µmol/L). The concentration of this unfiltered calibration solution was compared with 100 mL and 2 liters of the same solution filtered on glass fiber filters. The results showed that differences between filtered and unfiltered solution oscillate between 0.4 and 0.8 µmol/L more with filtration on GF/F. These differences were not significantly different according to the volume of water filtered in this experiment, thus this methodology for silicate was considered suitable and sufficiently accurate for this study. SPM were measured according to the methodology of Aminot and K erouel (2004). After

SPM measurement, filters were calcinated and measurement of PIM was made by weighing filters again. POM was calculated as the difference between SPM and PIM weight. Phytoplanktonic pigments (chlorophyll *a* and phaeopigments) were determined for each replicate for three size classes: microphytoplankton (> 20 µm), nanophytoplankton (between 3 and 20 µm) and picophytoplankton (< 3 µm). A first filtration was done on a 20 µm nylon fiber membrane (Millipore). A fraction of the filtrate was then filtered onto a 3 µm nucleopore membrane (Whatman). The second filtrate was filtrated onto a 0.7 µm GF/F glass fiber membrane (Whatman). Chlorophyll *a* and phaeopigments (*i.e.*, concentration of degraded chlorophyll pigments) concentrations were quantified by fluorimetry according to the methodology of Lorenzen (1966). The proportion of active chlorophyll *a* was measured by calculating the ratio of concentration of phaeopigments to phaeopigment plus chlorophyll *a* initially measured. Water was also sampled in glass bottle of 125 mL to evaluate the metabolic activity of planktonic communities on T0, T2, T4 and T6: the net community production (NCP), the community respiration (CR) and the gross primary production (GPP) were determined following the methodology of Navarro et al. (2004).

Following the methodology of Marie et al. (1999), the abundance of heterotrophic prokaryotes, pico- and nanophytoplankton communities were determined by flow cytometry (FACS CantoII). The abundance and diversity of microphytoplankton and heterotrophic protists were determined by FlowCam analyses according to the methodology of Buskey and Hyatt (2006). Metazooplanktonic organisms (micro- and meso-) were identified and counted with binocular microscope observations following the methodology of Postel et al. (2000). Identification of metazooplanktonic organisms was performed to species level, when possible, otherwise to genus or order (Amoros, 1984; Pourriot and Francez, 1986; Dussart and Defaye, 2001). Copepods were dissected and observed with an optical microscope (x400) to achieve species level identification. All five copepodite stages were regrouped according to each copepod order.

3.2.4 Statistical analyses

The continuous measurement of environmental parameters from the probes and sensors, are represented as curves in time graphs to observe the dynamic of these parameters through the two months of experiment. Unfortunately, some of the sensors on some of the Ysi probes did not work properly, thus data were not available for all six ponds. However, continuous measurements were recorded successfully for both treatment (control and submerged) for temperature, turbidity, salinity and the saturation of dissolved oxygen in the water column. Spearman rank tests were done to assess the potential difference between the continuous

measurements. In addition, multivariate statistical analysis was done with R software (version 4.2.2). A Redundancy Analyse (RDA) was performed (package *vegan*) on the database containing punctual environmental parameters (water temperature, salinity, pH, concentration in O₂, suspended particulate matter, particulate inorganic matter, organic particulate matter, NO₃, NO₂, NH₄, PO₄, Si, DOC, chlorophyll *a* total and for the three size's classes, active chlorophyll *a* total and for all three size's classes) and planktonic abundances for each sampling (Table 1). Since metazoan microzooplanktonic organisms were nearly absent in the samples, mesozooplankton and microzooplankton were regroup in the analysis under "Metazooplankton" label. Concerning phytoplanktonic diversity, organisms were divided in five groups: heterotrophic ciliates (*i.e.*, *Didinium* sp., *Lohmaniella* sp., Petrichida, *Strombidinopsis* sp., *Strombidium* sp., *Tintinnopsis* sp. and other naked ciliates), autotrophic ciliates (*i.e.*, *Myrionecta rubra*), diatoms (*i.e.*, *Entomoneis* sp. and other pennate diatoms), dinoflagellates (*i.e.*, *Gymnodinium sanguineum*, *Gyrodinium* sp. and other naked dinoflagellates), and other algae (*i.e.*, *Euglena*, *Cryptophyceae*, *Skeletonema* sp. and nanoflagellates' colonies). Anova tests were performed on RDA axes to determine their significance, as well as the significance of the potential effect environmental parameters on planktonic communities between control ponds and submerged ponds. The metabolism measurements for the first month of the experiment were plotted: Permanova tests were performed to assess the potential difference between the two treatments. For all statistical tests, differences in trends and values were considered significative when p-value < 0.05.

3.3 Results

3.3.1 Environmental parameters

The data on recorded water height in both CR2 and IR2 ponds (Figure 3.2) showed that the water height in the submerged pond nearly doubled during the simulation of submersion. The water height in the control pond did not vary significantly. The sharp variations in measurements between January 29 and February 3 corresponded to a recalibration of the sensors in relation to the water level in the ponds and were therefore not considered in this study. The same variations were observed between the control and the submerged ponds for water temperature (Figure 3.3a): an increase in water temperature was observed between the start and the end of the submersion. Afterwards, temperature oscillated around 12°C before increasing around 15°C, to then decrease around 9°C. For turbidity, no significant differences were recorded between the two treatments during the submersion (Figure 3.3b). The overall

turbidity was slightly higher in the submerged ponds than in the control ponds: the second replica for each treatment (CR2 and IR2) were often the ponds with the higher value of PIM along the monitoring (see Appendix 3.A). Salinity decreased in both treatments during the three days of submersion (Figure 3.3c). Even though the overall variations in time were similar on this period, a variability between control pond was clearly significative between CR3, where the salinity was lower (salinity around 27.5), and CR1 (salinity around 29). The daily variations in the saturation of dissolved oxygen in the water were relatively stable for two months in the control ponds (around 90 ± 20 % through a day) (Figure 3d). However, in the submerged ponds, the values increased when the simulated submersion happened (mean 90 ± 20 % during the first day to 140 ± 20 % during the last day) and dropped to 40 ± 20 % the following month before stabilizing to similar values than those of the control ponds. Between the beginning and the end of the two months monitoring, the value of DOC did approximately double in both treatment (see Appendix 3.A). The values of the concentration of nutrients (NH_4 , NO_3 , NO_2 , PO_4 , Si) followed the same evolution in all six ponds (see Appendix 3.A): despite the variability of values measured between the ponds, NO_3 concentrations were the higher of the nitrogen nutrients during the two months, especially the firsts two weeks. PO_4 concentrations values were always around $1 \mu\text{mol/L}$. Si concentrations were widely variable between all the ponds, but the values were overall between 20 and $30 \mu\text{mol/L}$ during the first month, then increased up to around $100 \mu\text{mol/L}$ at the end of the second month.

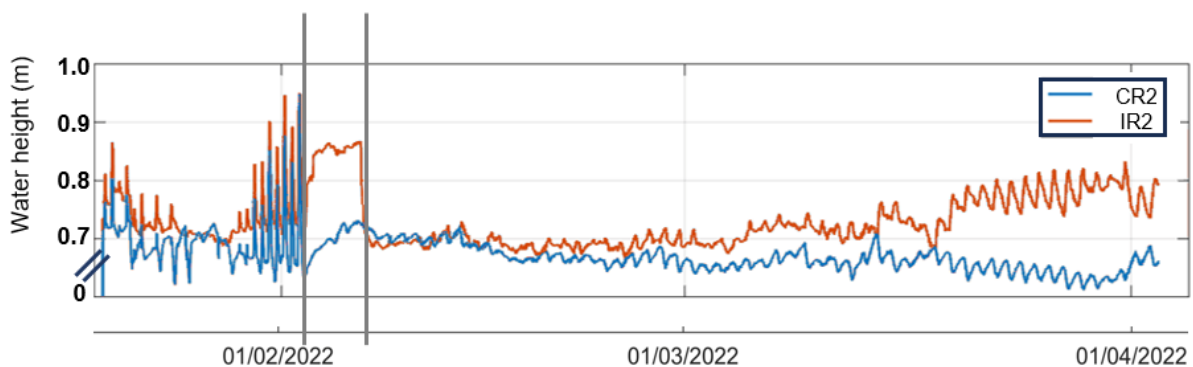


Figure 3. 2: Water height values (m) recorded continuously for two months in the CR2 and IR2 ponds in the l’Houmeau marsh (NKE sensors). The grey lines indicate when the 3 days of submersion began and ended.

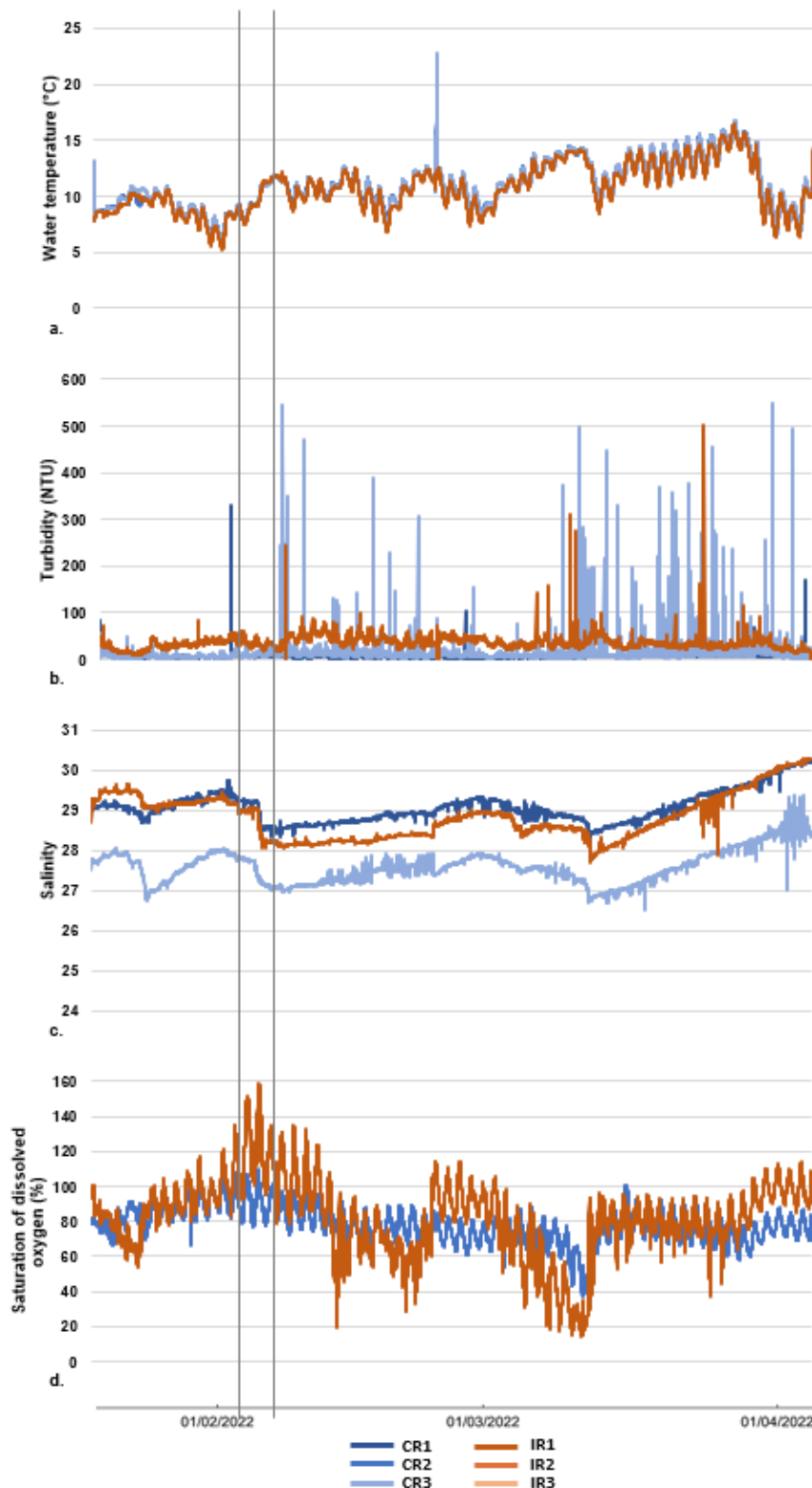
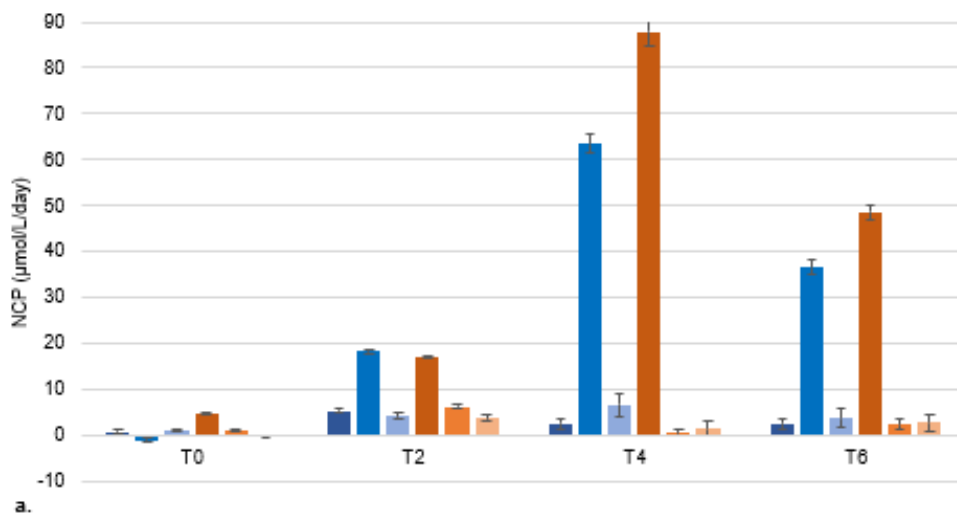


Figure 3.3 : Continuous measurements of water temperature (°C; CR1, CR2, CR3, IR1, IR2, IR3), turbidity (NTU; CR1, CR3, IR1, IR2), salinity (CR1, CR3, IR1) and saturation of dissolved oxygen (%; CR1, CR3, IR1, IR2) for two months in control (CR1, CR2, CR3) and submersed (IR1, IR2, IR3) ponds in the l’Houmeau marsh (Ysi probes). Some data are missing for some of the ponds due to the lack of available probe sensor for this experiment, as well as deficiency from some sensor during the experiment. Data are also sometimes stacked between different ponds. The grey lines indicate when the 3 days of submersion began and ended.

3.3.2 Planktonic metabolism analyses

The variability of the values between the six ponds was high despite the low values of the standard deviations (Figure 3.4). Concerning NCP, the values measured were often between 0 and 20 $\mu\text{mol/L/day}$ through the whole first month, except for T4 and T6 where CR2 and IR1 NCP values were between 35 and nearly 90 $\mu\text{mol/L/day}$. CR values were between 2 and 30 $\mu\text{mol/L/day}$ and seemed to increase through the first month for most of the ponds, except CR3 and IR2. GPP values were overall stable between 0 and 25 $\mu\text{mol/L/day}$ for four of the six ponds: CR2 and IR1 values did drastically increase up to respectively around 85 $\mu\text{mol/L/day}$ and 105 $\mu\text{mol/L/day}$ at T4, before decreasing at T6. No significant differences were found in planktonic community's metabolism determined on the first month following the submersion between the two treatments. Although an overall view seemed to show that the control pond might have higher values for net community's production, community's respiration and gross primary productivity, one of the submerged ponds (IR1) showed higher values for the same three parameters. Once again, the variability between the ponds in a same treatment did not allow detection of a statistically significant difference between the control ponds and the submerged ponds according to Permanova tests.



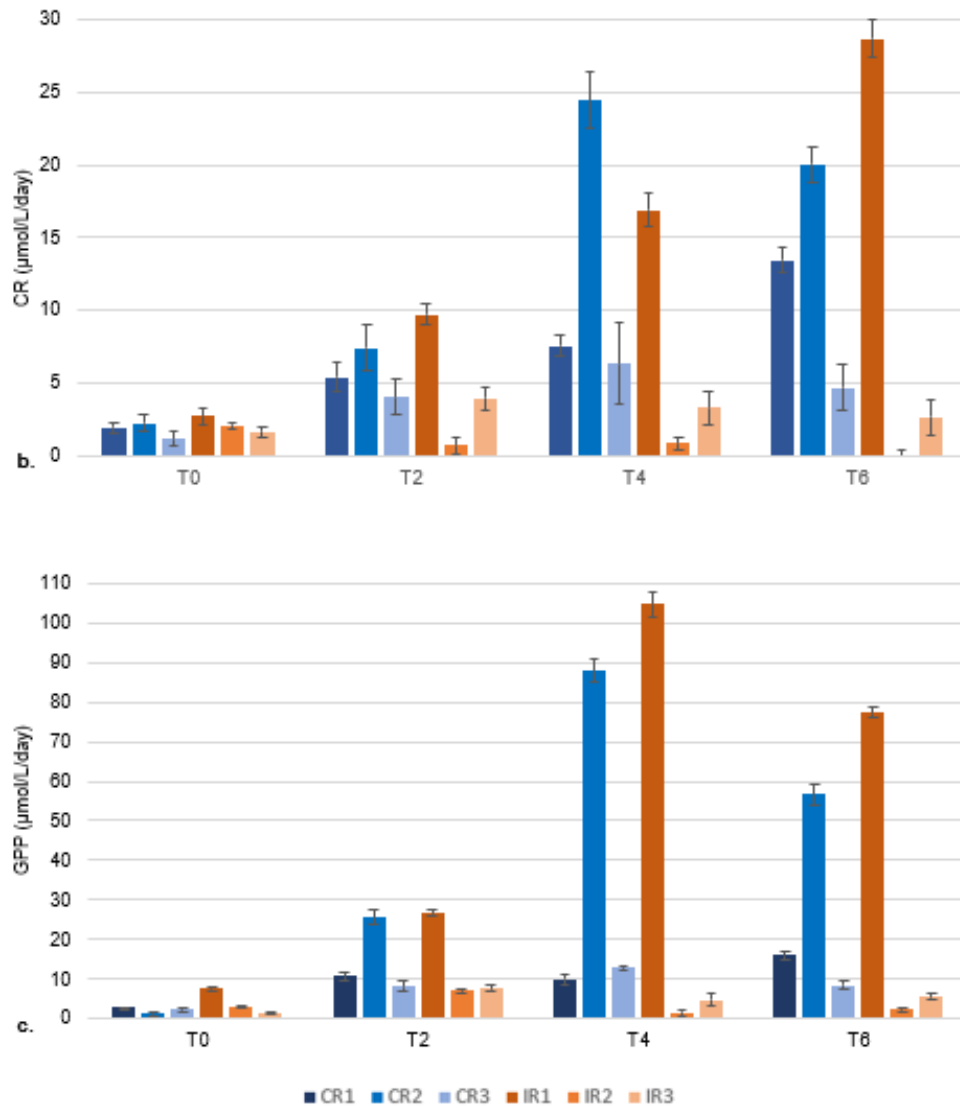


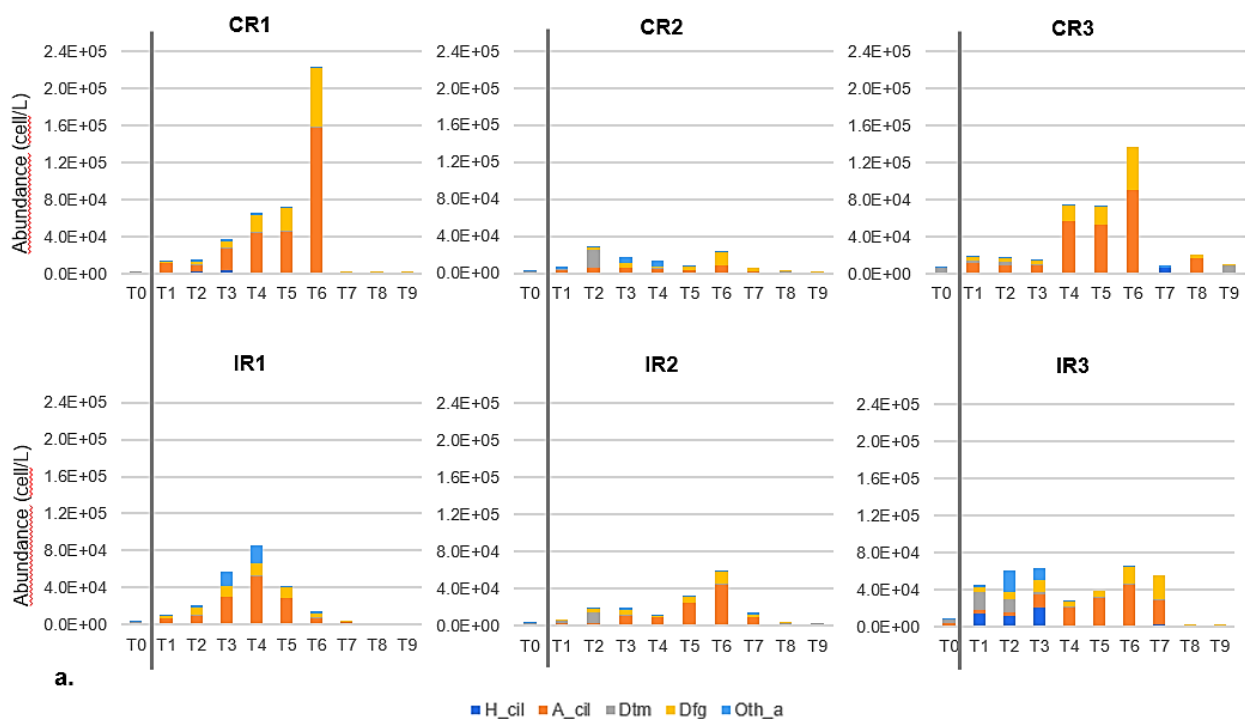
Figure 3. 4: Measurement of the planktonic community's metabolism in control (CR1, CR2, CR3) and submerged (IR1, IR2, IR3) ponds in the l'Houmeau marsh for the first month of the in-situ experiment: a. net community's production ($\mu\text{mol/L/day}$), b. community's respiration ($\mu\text{mol/L/day}$), c. gross primary production ($\mu\text{mol/L/day}$).

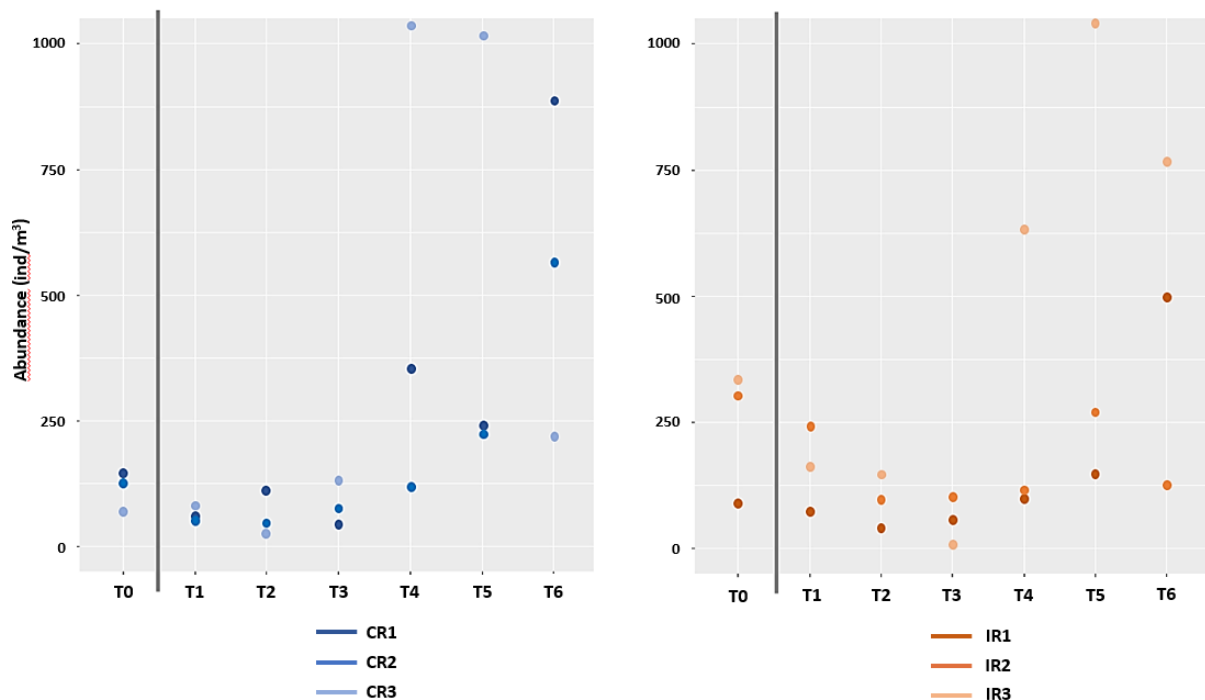
3.3.3 Planktonic diversity and abundance

Phytoplanktonic and protists abundances were variable between the six ponds (Figure 3.5a). However, looking at the diversity, it appeared that during the first month (T0 to T6) autotrophic protists (*i.e.*, *Myrionecta rubra*) were dominant in all ponds. *Myrionecta rubra* abundance highly decreased the second month (T7 to T9), and mostly diatoms were remaining. Overall, it seemed that the initial variability in the ponds for each treatment did not allow a potential vision of the effect of the simulated submersion, in addition to the likely seasonality effect. Initial metazooplanktonic abundances before submersion were also variable in each pond (Figure

3.5b). It was therefore difficult to distinguish a potential effect of submersion compared to the effect of the seasonality in this marsh. From the second month of the experiment, the global metazooplanktonic abundances were over 20 000 ind/m³ and were increasing throughout this month. Calanoid copepods were dominant in all six ponds, especially *Eurytemora pacifica*. No significant tendencies in the assemblage of diversity of metazooplankton were observed between the two treatments due to the variability in each pond.

Although no significant difference in turbidity was measured in the submerged ponds compared to the control ponds, few organisms of the benthic macrofauna (*i.e.*, *Corophium volutator*) were found in the water column right after the submersion (T1, T2, T3) in two of the three submerged ponds (IR2, IR3) only (not in the control ponds). It should be noted also that, in the submerged ponds, the proportion of *Ostracoda* to total zooplankton abundances were slightly higher right after the submersion (T1 and T2). These observations were made directly on the field during the sampling.





b.

Figure 3. 5: Abundance of a. phytoplanktonic and b. metazooplanktonic organisms determined during the simulated submersion on the l’Houmeau marsh in control (CR1, CR2, CR3) and submerged (IR1, IR2, IR3) ponds. For the metazooplanktonic abundances values were not represented here after T6 in all ponds because they were over 20 000 ind/m³. Concerning phytoplanktonic abundances: H_cil: heterotrophic ciliates, A_cil: autotrophic ciliates, Dtm: Diatoms, Dfg: Dinoflagellates, Oth_a: other algae. The grey lines indicate when the submersion happened.

3.3.4 Treatment comparison

A Redundancy analyse (RDA) was performed to evaluate if there was an overall significant effect on the planktonic communities and environmental parameters between the control ponds and the submerged ponds. Only the two first axes of the RDA were significant (RDA1: p-value = 0.001; RDA2: p-value = 0.008). On the RDA plot (Figure 3.6), most data are concentrated along the second axis RDA2. Only two environmental variables seemed to significantly affect the distribution of data: the time (p-value = 0.008), representing the seasonality, and the concentration of chlorophyll *a* for organisms smaller than 3 μm (p-value = 0.001), which is correlated to the abundance of picophytoplanktonic communities. Even though heterotrophic prokaryotes (HPT) abundances seemed to slightly stand out in the analyse, the values were not significantly different between the two treatments and were between of $2.5e^9$ and $1.1e^{10}$ cell/L along the two months of monitoring for all six ponds. The rare sampling points apart from the data gathered along RDA2 corresponded to samples

collected during the second month of monitoring. This analyse showed no significant effect of treatment between the control ponds and the submerged ponds.

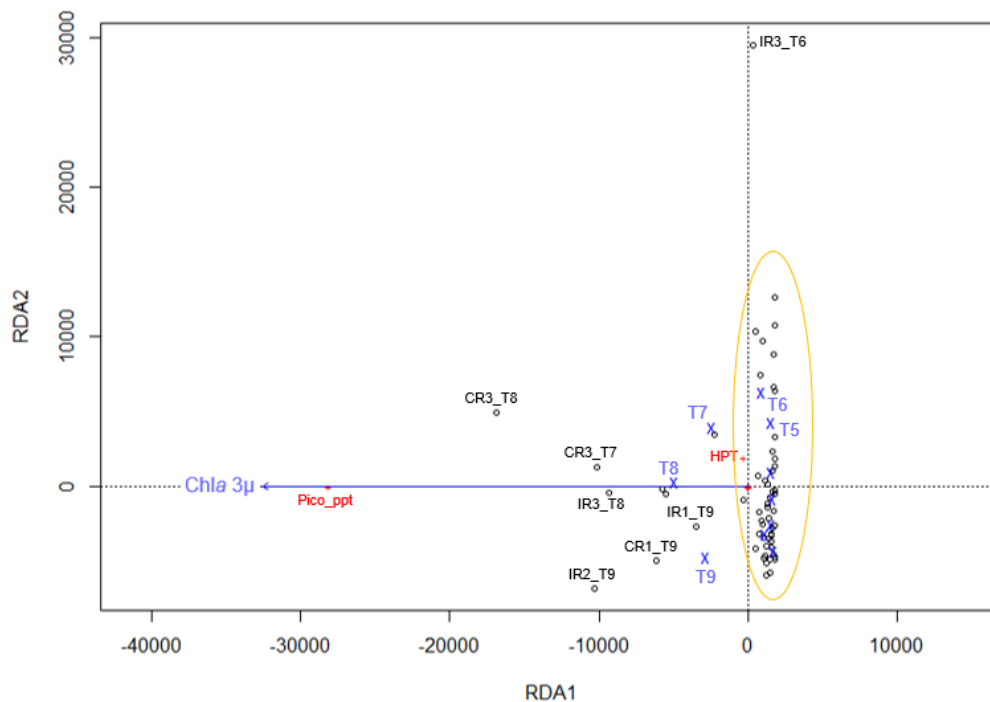


Figure 3. 6: RDA plot representing the significance of abiotic variables on plankton communities in control (CR1, CR2, CR3) and submerged (IR1, IR2, IR3) ponds in the l’Houmeau marsh. Abiotic parameters are indicated in blue, planktonic communities are indicated in red and ponds are indicated in dark. Data were essentially regrouped in the yellow ellipse. Since very few variables were significant, only data that stands out were labelled for greater clarity. Data were essentially regrouped in the yellow ellipse. Chla 3µ: concentration of chlorophyll *a* for organisms smaller than 3 µm. Pico_ppt: picophytoplanktonic communities. HPT: heterotrophic prokaryotes communities.

3.4 Discussion

3.4.1 Environmental parameters

Thanks to the NKE sensors, it was confirmed that during the short-term simulated marine submersion the control ponds did not receive additional water and the submerged ponds did receive inlets of water for three days. Thus, even though it was not a natural marine submersion phenomenon, the simulation *in situ* did work successfully. However, the continuous measurement did not show significant differences of abiotic parameters recorded between experimental and control ponds, except for the saturation of dissolved oxygen in the water column. The increase of the saturation of dissolved oxygen might be caused by reoxygenation of the water in the ponds through turbulences when the adjacent channel overflowed into them (Karstens et al., 2015). The 3 days submersion was started in winter which is the season were

marine submersion tend to appear more often (Rothenbücher and Schaefer, 2006; Kaniewski et al., 2021). However, an increase in temperature was observed in all ponds during the 3 days of submersion (Figure 3.3a). This was explained by an increase of air temperature during the same period (data not shown). The afterward evolution of temperature corresponded to the progressive increase of temperature following the transition from winter to spring. It was expected that the stretch of land between the channel and the ponds, would to be a source of SPM import during the submersion (Figure 3.1). However, this stretch had only a width of about 2 m, which might explain that too little soil was eroded to increase the turbidity significantly in the submersed ponds compared to the control ponds. Concerning the salinity, since the ponds were initially refilled with sea water after the drought and the simulated marine submersion brought additional saltwater from the sea, it seems coherent that salinity fluctuated the same way between the two treatments.

3.4.2 Planktonic diversity and abundance

Since the experimental setup was *in situ*, it seemed logical to have a higher variability of both phyto- and metazooplanktonic abundances between the six ponds than in mesocosm experiments done in laboratory since the interaction between environmental parameters cannot be totally controlled in a natural environment. Even though the results did not allow to isolate the seasonal variation from the possible impact of the simulated submersion, it allows to evaluate the variability and changes in environmental parameters and planktonic communities to be considered in such natural environment experiments. The non-significative differences in planktonic abundances between the control treatment and the submerged treatment might be influenced by the season: Winter is the season where metazooplanktonic abundances are generally low (Abrantes et al., 2006; Bergeon et al., 2023). As such, variability of results of organism abundance by whatever method is high. In addition, this study simulated a short-term submersion for three days, which might cause few perturbations on planktonic communities due to their resilience (David et al., 2020). The inflow of water in all the ponds was from the same source as the water used to refill the ponds after the drought (*i.e.*, seawater). This seemed logical with the fact that no new planktonic species were found after the submersion. If the ponds were refilled with freshwater instead of seawater, the planktonic freshwater species might be affected by the sudden increase of salinity and a shift of planktonic diversity might occur over the time (Bailey et al., 2004; Sarma et al., 2006; Nche-Fambo et al., 2015).

3.4.3 Effect of short-term submersion on planktonic communities' succession

Compared to another study monitoring planktonic communities in the same experimental marsh (Moncelon, 2022), the simulated submersion did not seem to affect the seasonal dynamics and succession of phyto- and metazooplankton significantly. It might be directly linked to the type of submersion chosen in this study. Tortajada et al. (2011) and David et al. (2020) showed that, after the Xynthia storm, several freshwater coastal marshes were highly submerged and few of them could not drain the intake of seawater. Even so, the monitoring of planktonic communities showed that planktonic communities returned to their pre-submersion status in about three weeks. In our experiment, the submersion lasted only for three days, and the additional water was drained afterward. The high resilience of planktonic communities shown in the literature (David et al., 2020) might explain why no significant effect was observed following this apparently low perturbation in our study. During an overflow, the sediments in marshes tend to release nutrients such as nitrogen and phosphorus, as well as dissolved inorganic matter, especially if the marshes go through episodes of drought (Kobayashi et al., 2009). Despite the absence of sediment analyses in this experiment, the no significant difference of nutrient variations measured between the two treatments indicates it was not the case at the marsh of l'Houmeau.

3.5 Conclusion

Overall, this first *in situ* experiment seemed to show no significant impact of a short-term marine submersion on the planktonic communities of a suburban marine marsh. To confirm these first results, the experimental *in situ* set up might be done under different conditions (*e.g.*, in a freshwater marsh, on another season than winter) to specify the resilience of planktonic communities in various situations. It would also be interesting to repeat this experiment multiple times on the same marsh to evaluate the impact of repeated marine submersion phenomena to mimic its increase of frequency in the context of climate change. Sediment samples might also be taken to assess the potential nutrient release caused by the submersion. If similar results are found in these set ups, it might then show that the resilience of planktonic communities is strong enough to compensate the perturbations caused by short-term marine submersion, and that the base of aquatic food web in coastal marshes might be able to resist the increase frequency of this phenomenon due to climate change.

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Discussion générale

1. Importance des réseaux trophiques planctoniques dans l'étude des fonctions écologiques fournies par les communautés planctoniques

Il est à noter que ces résultats, notamment ceux présentés concernant l'impact de la restauration du marais de Tasdon, sont directement liés à la temporalité d'échantillonnage sur un an (avant et après travaux), donc sur une courte période. Cependant, les résultats trouvés dans ces études sur la dynamique saisonnière des communautés planctoniques et les typologies de réseaux trophiques planctoniques concordent avec les quelques études antérieures réalisées sur des marais des Pertuis-Charentais (Tortajada et al., 2011 ; Masclaux et al., 2014 ; David et al., 2020). En effet, des réseaux trophiques planctoniques similaires à ceux trouvés dans ces études ont été déterminés dans les marais du Fier d'Ars et de Tasdon : le réseau herbivore, le réseau multivore et l'« hiver biologique ». Le réseau microbien correspond à ce qui a été observé dans une étude antérieure réalisée par Legendre et al. (1995) en milieu marin.

A ce jour dans la littérature, peu d'études traitent du lien entre les réseaux trophiques planctoniques et leur fonctions écologiques associées dans les marais côtiers (Rinehart et al., 2023). Certaines études se focalisent plus spécifiquement sur la structure des communautés planctoniques dans ces milieux, voire l'impact d'un changement de gestion ou de mesures de restauration sur la diversité planctonique sans évaluer un potentiel changement dans les fonctions écologiques et/ou services écosystémiques fournis (Badosa et al., 2010 ; Cabrera et al., 2019). D'autres études se focalisent spécifiquement sur une fonction écologique clé liée aux communautés planctoniques, comme la production primaire du phytoplancton (Hassan et al., 2011), la quantité de nourriture disponible pour les niveaux trophiques supérieurs (souvent l'ichtyofaune) (Joyeux et al., 2017 ; Colombano et al., 2021), ou encore la fonction épuratrice dans l'étude de la qualité des eaux (Atkinson et al., 2011). Lorsque les études se concentrent sur la biodiversité des marais côtiers, le compartiment planctonique n'est pas nécessairement étudié ; dans le cas où il est pris en compte, cela est souvent lié à la fonction nourricière par évaluation de l'abondance planctonique, et non pas l'étude des réseaux trophiques planctoniques (Carlson, 1978 ; Herbold et al., 2014). Enfin, une partie des études sur la préservation et le fonctionnement des marais côtiers se focalisent sur les services fournis par l'écosystème du marais dans son ensemble (Barbier et al., 2011 ; Rezek et al., 2017), par exemple en tant que zone tampon contre les inondations (Shepard et al., 2011 ; Van Coppenolle et al., 2018), zone de régulation par traitement des eaux usées (Karstens, 2017), milieu propice à la captation du carbone atmosphérique (Harding et al., 1986), ou encore comme espace culturel touristique et de loisirs (Purcell et al., 2020).

L'atout principal de mes travaux de thèse est donc dans l'apport d'études sur l'importance de la biodiversité « non-visible » dans les marais côtiers par l'étude des réseaux trophiques planctoniques comme indicateurs des fonctions écologiques qu'ils fournissent, selon la typologie des ces marais (marais salés ou d'eau douce), en évaluant l'impact à court terme d'un plan de restauration sur ces communautés et fonctions associées. Entre le marais du Fier d'Ars et de Tasdon, il a été observé des réseaux trophiques planctoniques similaires pour certaines saisons. Néanmoins, une des stations du Fier d'Ars était la seule à présenter un réseau trophique microbien. Dans le cadre d'un plan de gestion visant à préserver certaines fonctions écologiques présentes dans les marais côtiers, l'étude des réseaux trophiques planctoniques est un indicateur efficace pour identifier ces fonctions, et ainsi mettre en œuvre des mesures adéquates pour les préserver. L'utilité pour la gestion de ces systèmes est explicitée plus en détails dans la troisième partie de cette discussion générale.

2. Impact de la submersion marine sur les communautés planctoniques

Concernant l'étude de l'impact potentiel d'un phénomène de submersion marine court et modéré sur les communautés planctoniques d'un marais côtier salé, l'expérience *in situ* réalisée à l'Houmeau a montré que les communautés planctoniques semblent être résiliente à ce phénomène. Ces résultats concordent avec ceux de Tortajada et al., (2011) qui avait noté un retour à l'état initial des communautés planctoniques de différents marais de la côte Atlantique en environ trois semaines après la tempête Xynthia en 2010. Cependant, ces résultats sont à prendre avec précautions car dépendant de plusieurs facteurs. Parmi ces facteurs, il y a le type de submersion choisi : il est possible que des résultats différents soient observés sur l'abondance et la diversité des communautés planctoniques dans le cas d'un phénomène plus intense de submersion sur une plus longue durée. Par exemple, une submersion induisant un lessivage de la berge plus important pourrait induire une plus forte concentration en matière organique et inorganique particulaire dans la colonne d'eau, affectant le développement de certains taxa planctoniques (Wang et al., 2016). Notre étude n'a pas démontré un apport significatif de cette matière organique et inorganique dans les bassins, ce qui pourrait directement être lié à la faible intensité du type de submersion simulé. En outre, la diversité et l'abondance des communautés planctoniques auraient probablement été modifiées si la submersion avait été simulée sur un marais côtier d'eau douce. La littérature montre que la salinité est un des facteurs clés, avec notamment la turbidité et la température, modelant l'assemblage des communautés planctoniques (Aladin, 1991 ; Toruan, 2012). Dans notre dispositif d'étude, il était

logistiquement complexe d'alimenter les bassins en eau douce pour simuler ce type de submersion, c'est pourquoi il a semblé plus judicieux de simuler une submersion marine sur des bassins correspondant à un modèle de marais côtiers salés. Un dernier élément à prendre en compte est que les résultats issus de l'expérience réalisée à l'Houmeau représentent la résilience des communautés planctoniques sur un événement modéré de submersion ponctuel. Dans le contexte du changement climatique, ces événements modérés tendraient à devenir plus fréquent (Herbert et al., 2015). Selon une publication d'Almar et al. (2021), il a été évalué une augmentation de presque 50 % des risques d'aléa de submersion entre 1993 et 2015 à l'échelle du globe. Il serait donc nécessaire de répéter cette expérience sur le même site, afin de tester si la résilience des communautés planctoniques serait conservée. Dans le cas où cette résilience se maintiendrait dans cet écosystème, cela traduirait un avantage considérable car les fonctions écologiques fournies par ces communautés resteraient présentes malgré les pressions de submersion plus fréquentes.

L'atout principal de cette expérience de simulation *in situ* est son modèle expérimental innovant permettant d'avoir une estimation plus proche de ce qui pourrait être observé en milieu naturel que les précédentes expériences en mésocosmes contrôlés, où seuls quelques facteurs liés à la submersion marine étaient testés (*e.g.*, température, salinité, concentration en nutriments dans la colonne d'eau). Kobayashi et al. (2009) ont mesuré en mésocosmes déployés sur site (zone humide au nord-ouest de l'Australie) les concentrations en nutriments et en carbone organique dissous dans l'eau en lien avec les abondances en bactério- et phytoplancton afin d'évaluer l'impact de l'inondation de ce milieu sur ces communautés. Waterkeyn et al. (2010) ont étudié l'effet de changements de salinité sur l'assemblage des communautés de microcrustacés dans des zones humides temporaires en Camargue (France). En plus du modèle expérimental, du fait de l'approche « Before-After-Control-Impact » (BACI), cette expérience permet également d'avoir un état contrôle de référence tout au long de l'expérience pour comparer l'évolution des communautés planctoniques. Cela n'est pas le cas lorsque des études de suivis sont réalisés à la suite d'événements météorologiques extrêmes, où le contrôle ne peut être qu'un état antécédent au même marais, donc dans une temporalité différente (Tortajada et al., 2011).

3. Plans de gestion des marais côtiers : inclusion du compartiment planctonique

A l'échelle du globe, de nombreux projets ont vu le jour ces dernières années pour étudier la question de dépoldérisation des marais côtiers comme solution pour restaurer leur biodiversité et fonctions écologiques (Adam, 2019 ; Musseau et al., 2021 ; Schmitt et

Chaumillon, 2023). A l'échelle nationale, on peut citer par exemple le projet PEPPS (Pertinence Environnementale de la restauration des Petits Prés et marais Salés) dont l'objectif est d'analyser « de façon transversale les potentialités environnementales liées à la restauration de petits marais salés poldérisés » ([Restauration et reconnexion des marais littoraux – Regards croisés sur une solution d'adaptation aux changements globaux. - Sciencesconf.org](#)). Ces études sont focalisées sur des marais anciennement poldérisés situés sur le littoral armoricain, qui ne le sont plus aujourd'hui. A l'échelle internationale, on peut citer le projet « Intégration du savoir local et scientifique dans la restauration d'écosystèmes côtiers à forte valeur écologique dans le golfe du Saint-Laurent » mené notamment par des chercheurs de l'UQAR (Université du Québec à Rimouski) qui a eu pour objectif de « mesurer l'efficacité des techniques de restauration mises en œuvre ainsi que les gains d'habitats anticipés, soit les gains en superficie, le fonctionnement biologique augmenté des portions aménagées ainsi que les services écosystémiques augmentés des sites aménagés » ([Un projet de restauration d'écosystèmes côtiers d'envergure aux Îles-de-la-Madeleine \(uqar.ca\)](#)). Les échanges entre scientifiques et gestionnaires sont un atout essentiel à la mise en place de meilleurs plans de gestion et restauration des marais côtiers pour préserver au mieux leur biodiversité, leurs fonctions écologiques et leurs services écosystémiques.

Un des principaux intérêts de mes travaux et résultats dans le cadre du projet PAMPAS est de fournir les informations relatives aux compartiments planctoniques aux gestionnaires des marais afin qu'ils puissent les prendre en compte lors de la mise en place de nouveaux plans de gestion et de restauration des marais côtiers. Dans le cadre plus spécifique du projet PAMPAS, la finalité est de fournir un outil informatisé interactif de sorte que les gestionnaires puissent évaluer l'impact de différentes opérations de gestion sur les composantes paysagère, culturelle et naturelle des marais.

Dans le cadre de ces travaux de thèse, les échanges avec les gestionnaires ont été effectués de différentes façons, notamment lors de discussions pendant les suivis et échantillonnages sur le terrain. Des échanges de mails étaient également faits pour maintenir la communication pendant ces trois années, et permettre notamment dans le cas du marais de Tasdon, d'adapter au mieux les échantillonnages post-travaux de restauration. Des réunions dédiées à chacun des marais étudiés avaient également lieu, et les gestionnaires de ces marais y étaient conviés. Enfin, les résultats principaux ont été présentés à l'ensemble des gestionnaires des sites étudiés lors d'un colloque de restitution du projet PAMPAS. Concernant les communautés planctoniques, comprises dans la composante naturelle des marais, les gestionnaires seront capables grâce aux

données fournies d'adapter au mieux la gestion de ces écosystèmes pour préserver les fonctions écologiques associées, dont la fonction nourricière, la fonction épuratrice et la captation de Carbone atmosphérique. En effet, peu d'informations étaient disponibles concernant la biodiversité « non visible », en particulier concernant leur rôle en tant qu'acteur de fonctions écologiques clés liées aux marais côtiers. Par exemple : lors de questionnement sur de la préservation des fonctions épuratrices et captation de Carbone atmosphérique dans les marais côtiers étudiés, les gestionnaires se concentraient sur les communautés végétales (*e.g.*, macrophytes, plantes halophiles) comme actrices de ces fonctions, sans prendre en compte les communautés phytoplanctoniques comme acteurs complémentaires. En outre, concernant la fonction nourricière, les gestionnaires prennent majoritairement des mesures de protection de la biodiversité visible (*e.g.*, ichtyofaune, oiseaux limicoles) sans forcément prendre en compte les communautés planctoniques comme base essentielle au réseau trophique aquatique. Si ces communautés ne sont pas préservées, les maillons trophiques supérieurs seront impactés car leur ressource alimentaire deviendra un facteur limitant. Par exemple, dans le cas du marais de Tasdon, une diminution de l'abondance des communautés planctoniques entraînerait une diminution de la ressource nutritive disponible pour les alevins ; ce manque de nourriture entraînerait une diminution des communautés piscicoles, et donc une diminution de ressources nutritive disponible pour de nombreux oiseaux limicoles, qui ne pourraient donc plus utiliser le marais comme habitat de refuge et nurserie. Les gestionnaires disposant à présent de toutes les informations relatives aux communautés planctoniques et leur rôle clé dans ces marais, ils seront en mesure d'inclure cette biodiversité « non visible » dans leurs études de gestion, de préservation et de restauration de ces écosystèmes dans leur ensemble.

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Conclusion générale

1. Importance des communautés planctoniques dans les marais côtiers

Les travaux réalisés au cours de cette thèse ont relevé l'importance du rôle des communautés planctoniques comme acteurs clés des fonctions écologiques des marais côtiers. Les études réalisées aux marais du Fier d'Ars et de Tasdon ont montré que plus la diversité des différents compartiments est grande, plus la probabilité d'avoir une grande diversité de réseaux trophiques planctoniques ayant leurs fonctions écologiques associées est également élevée. La comparaison entre un marais côtier salé et un marais côtier doux a de plus permis de montrer que les fonctions écologiques fournies par les communautés planctoniques sont intimement liées à leur fonction trophique. Pour illustrer ce point : il est admis par la littérature que concernant le mézozooplancton, les milieux d'eau salée sont majoritairement dominés par des Copépodes alors que les milieux d'eau douce sont surtout dominés par des Cladocères. Malgré cette différence d'assemblage des communautés mézozooplanctoniques, des réseaux trophiques planctoniques similaires ont été retrouvés à la fois dans le marais du Fier d'Ars et dans celui de Tasdon (*e.g.*, réseau multivore). Il est donc nécessaire de préserver la diversité spécifique des communautés planctoniques pour, par extension, préserver la diversité trophique de ces organismes, et donc leurs fonctions écologiques.

L'étude comparative des assemblages des communautés planctoniques du marais de Tasdon avant et après la restauration du marais a confirmé l'impact direct des modifications hydrologiques sur l'abondance, la diversité et la succession saisonnière du plancton, allant jusqu'à modifier la succession des réseaux trophiques planctoniques et la perte de la saisonnalité à l'heure actuelle. Cette étude a également permis de relever des avantages et inconvénients d'une modification de la gestion d'un marais. D'une part, les données de pCO₂ ont montré que la restauration a modifié la capacité de captation du carbone dans le marais de Tasdon, qui est maintenant devenu un faible puit de carbone atmosphérique plutôt qu'une source : cette restauration a donc permis, au moins sur le court terme, de favoriser la fonction de captation du carbone. D'autre part, l'apport d'eau de mer périodique sur une partie du marais induit un stress répété sur les communautés planctoniques, notamment les Cladocères qui forment davantage d'éphippies sur ces périodes en prévision de pouvoir se développer à nouveau quand les conditions environnementales leur seront plus favorable. Cette manœuvre hydraulique ayant lieu notamment pendant la période de recrutement des alevins dans les marais (*i.e.*, printemps, été), un déclin de l'abondance des communautés planctoniques peut défavoriser la fonction nourricerie. Par effet en cascade, si la fonction nourricerie n'est pas assurée efficacement par le marais, les maillons supérieurs du réseau trophique aquatique peuvent être

impactés. Pour illustrer avec l'exemple du marais de Tasdon, dont l'objectif du plan de restauration est de favoriser des zones refuges pour les oiseaux migrateurs limicoles, ces derniers pourraient à terme trouver de meilleurs habitats, avec davantage de ressources pour leur développement, comme refuge si la fonction nourricière est trop défavorisée par la nouvelle gestion hydraulique.

Globalement, beaucoup de paramètres sont à prendre en compte pour adapter au mieux les plans de gestions et de restauration des marais côtiers pour préserver la base du réseaux trophiques en plus des niveaux supérieurs. La difficulté est aussi de prendre en compte la résilience des communautés planctoniques et de leur assemblage face aux mesures de restauration mises en œuvre.

2. Résilience des communautés planctoniques face à l'aléa de submersion marine

L'impact de la submersion marine est complexe à évaluer comme il existe divers cas d'étude (submersion sur court ou long terme, submersion sur marais côtier salés ou doux). Néanmoins, l'expérience *in situ* réalisée à l'Houmeau couplés aux résultats de David et al. (2020) sur le suivi des communautés planctoniques après la tempête Xynthia montre une bonne résilience de ces organismes face à ce phénomène. Plus la submersion est sur un temps court, plus l'assemblage des communautés planctoniques revient rapidement à son état initial. Dans le contexte du changement climatique, cette résilience représente un avantage car si les communautés planctoniques se maintiennent dans les marais côtiers malgré des épisodes répétés de submersion marine, leurs fonctions écologiques restent présentes également. Si leur diversité est modifiée, mais que les fonctions trophiques planctoniques restent similaires, leurs fonctions écologiques ne seront pas impactées (cf. ci-dessus).

Néanmoins, il reste important de prendre en compte que les fonctions écologiques planctoniques risquent d'être plus fortement impactées si ce phénomène se produit au printemps ou en été, où les abondances planctoniques sont les plus importantes : une perturbation sur ces périodes pourrait fortement impacter la fonction nourricière si elle survient pendant la période de recrutement des alevins. Il est donc nécessaire de rester vigilant dans le futur pour adapter au mieux les plans de gestion des marais côtiers pour prévenir ces éventualités.

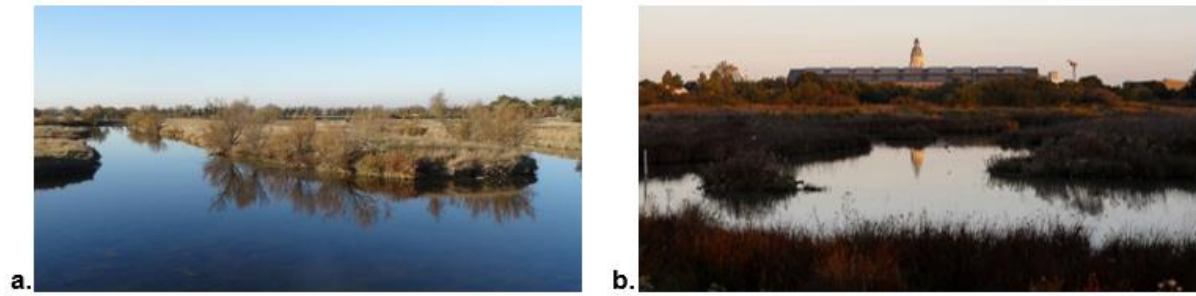
Perspectives

En définitive, force est de constater que l'importance des communautés planctoniques dans les marais côtiers est à ce jour peu prise en compte dans la mise en place des projets de gestion et de restauration pour préserver ces écosystèmes et leurs fonctions. Des suivis sur ces communautés planctoniques sur le long terme sont nécessaires, ainsi que des suivis dans des marais côtiers subissant des perturbations répétées, pour établir la résilience du plancton dans ce cas d'étude pour adapter les mesures de gestion et de restauration pour ces écosystèmes.

A ce jour, les mesures de gestion et restauration des marais côtiers ont surtout une volonté de préserver le paysage dans son ensemble, les services écosystémiques et les espèces « visibles » patrimoniales présentes, sans forcément évaluer sur le long terme qu'une dégradation des niveaux trophiques inférieurs « non visibles » impactera la conservation des milieux côtiers. Il est effectivement compliqué d'envisager une patrimonialisation des communautés planctoniques du fait de leur appréhension et représentation moins évidente pour les gestionnaires et riverains. Cependant, il serait intéressant de valoriser de façon indirecte mais pertinente le plancton en le présentant comme acteurs essentiels fournissant une partie importante des fonctions écologiques des marais côtiers, et en soulignant leur rôle indispensable comme base du réseau trophique aquatique soutenant les espèces patrimoniales de ces marais. Cette valorisation peut autant se faire dans le domaine de la recherche, à travers des présentations lors de congrès, que dans le domaine public par de la médiation scientifique sous forme d'ateliers ludiques et pédagogiques.

Annexes

Chapitre 1



Appendix 1. 1: Pictures of the a. Fier d'Ars marsh (FA), b. Tasdon marsh (TC) (overview of the ponds and surrounding vegetation).

Appendix 1. 2: Summary of the main characteristics describing both marshes.

	Fier d'Ars (saltwater marsh)		Tasdon (freshwater marsh)		
Station	FA (N 46° 14' 5.964"; W 1° 30' 20.707")	FB (N 46° 13' 26.4"; W 1° 27' 21.599")	TA (N 46° 8' 56.4"; W 1° 7' 26.4")	TB (N 46° 9' 3.6"; W 1° 8' 9.599")	TC (N 46° 8' 49.2"; W 1° 8' 13.2")
Surface	40 097 m ²	8 483 m ²	72 000 m ²	21 400 m ²	23 700 m ²
Maximum depth	0.6 m	5.5 m	1.35 m	0.8 m	1.0 m
Salinity	22.9-37.6		0.1-0.5		
Coastal vegetation	<i>Halimione</i> sp., <i>Salsola soda</i> , <i>Tamarix</i> sp.		<i>Arrhenatheretea elatioris</i>		
Distance from the sea	0.1 km	2.0 km	2.5 km	1.5 km	1.8 km
Annual drought	No	Yes	No	No	No
Water inlets	Yes	Yes	Yes	Yes	Yes
Source of water inlets	Sea	Sea	River	River	River
Minimum tidal range allowing connection	5.5 m	5.5 m	X	X	X
Water outlets	Yes	Yes	No	No	No
Introduction of non-native species	No	No	Yes (<i>Lepomis gibbosus</i> , <i>Micropterus salmoides</i>)	Yes (<i>Lepomis gibbosus</i> , <i>Micropterus salmoides</i>)	Yes (<i>Lepomis gibbosus</i> , <i>Micropterus salmoides</i>)
Dominant native species of fish	<i>Atherina</i> spp., <i>Anguilla anguilla</i> , <i>Chelon aurata</i> , <i>Dicentrarchus</i> spp., <i>Pomatoschistus</i> spp.,		<i>Carassius</i> spp., <i>Gambusia</i> spp., <i>Rutilus</i> , <i>Dicentrarchus</i>		

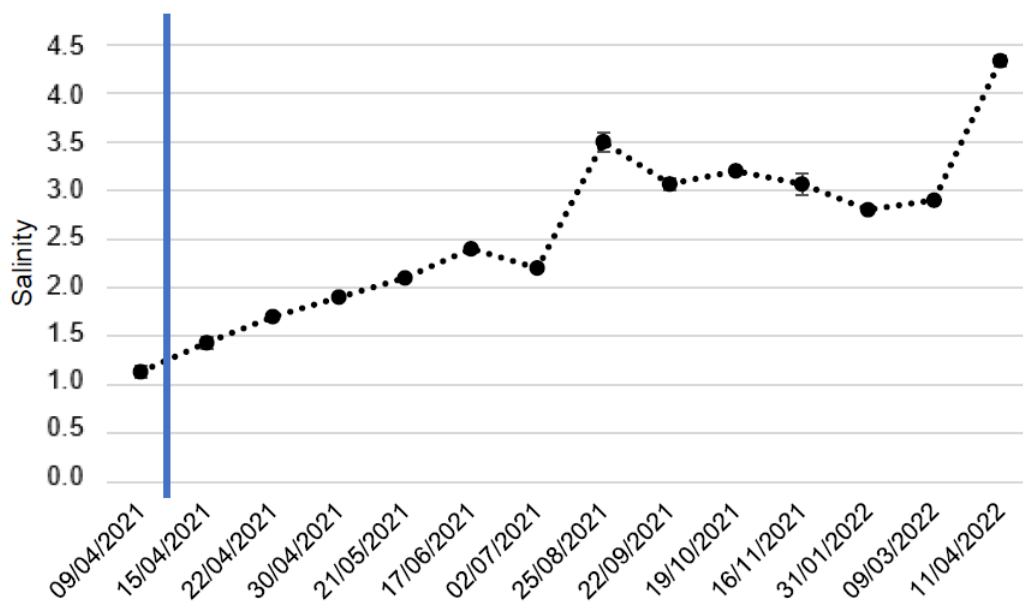
Chapitre 2

Appendix 2. 1: List of the phytoplanktonic and metazooplanktonic taxa identified and their associated abbreviations used in the analyses.

Phytoplanktonic species		Zooplanktonic species	
<i>Actinastrum</i> sp.	Act_sp	<i>Acanthocyclops trajani</i>	A_t
<i>Alexandrium minutum</i>	Alx_min	<i>Aiona affinis</i>	A_a
<i>Alexandrium tamarense</i>	Alx_tam	<i>Aiona rustica</i>	A_r
<i>Amphora</i> sp.	Amp_sp	<i>Aiona weinertii</i>	A_w
<i>Anabaena</i> sp.	Ana_sp	<i>Aionella excisa</i>	A_e
<i>Anabaenopsis</i> sp.	Anae_sp	<i>Asplanchna</i> sp.	A_sp
<i>Ankistrodesmus</i> sp.	Ank_sp	<i>Bdelloid</i>	Bd
<i>Aphanizomenon</i> sp.	Aphz_sp	<i>Bosmina longirostris</i>	B_l
<i>Aphanocapsa</i> sp.	Apha_sp	<i>Brachionus calyciflorus</i>	B_c
<i>Aphanothece</i> sp.	Aphh_sp	<i>Brachionus falcatus</i>	B_f
<i>Aulacoseira granulata</i>	Aul_gra	<i>Calanoid copepodites</i>	Ca_c
Bacillariophyceae	Baci	<i>Centodaphnia pulchella</i>	C_p
<i>Centric</i> spp.	Gen_spp	<i>Chydorus</i> sp.	Ch_sp
Chlorophyceae sp.	Chlo_sp	<i>Cyclopoid copepodites</i>	Cy_c
<i>Chodatella</i> sp.	Chod_sp	Cypris larvae	C_lrv
<i>Chroococcus</i> sp.	Chroc_sp	<i>Daphnia ambigua</i>	D_a
<i>Chroomonas</i> sp.	Chroo_sp	<i>Daphnia magna</i>	D_m
<i>Closterium</i> sp.	Clo_sp	<i>Disparalona rostrata</i>	D_r
<i>Coelastrum proboscideum</i>	Coel_pro	Ephippia	Eph
<i>Coelastrum</i> sp.	Coel_sp	<i>Euchlanis</i> sp.	E_sp
<i>Cosmarium</i> sp.	Cos_sp	<i>Eucyclops</i> sp.	Ecy_sp
<i>Crucigenia tetrapedia</i>	Cru_tet	<i>Eurycerus lamellatus</i>	E_l
<i>Cryptomonas curvata</i>	Cry_cur	<i>Euterpina acutifrons</i>	E_a
<i>Cylindrotheca closterium</i>	Cyl_cl	<i>Filinia</i> sp.	F_sp
<i>Cymatopleura</i> sp.	Cym_sp	Foraminifera	For
<i>Dictyosphaerium</i> sp.	Dict_sp	<i>Harpacticoida copepodites</i>	Ha_c
<i>Dinobryon</i> sp.	Din_sp	Ichthyoplankton	Ipk
Dinophyceae sp.	Dinp_sp	<i>Isocryptus</i> sp.	I_sp
<i>Entomonels</i> sp.	Ent_sp	<i>Keratella</i> sp.	K_sp
<i>Euglena</i> sp.	Eug_sp	<i>Keratella tropica</i>	K_t
Flagellate sp.	Flg_sp	<i>Lecane bulla</i>	L_b
<i>Gomphosphaeria</i> sp.	Gomp_sp	<i>Macrothrix hirsuticornis</i>	M_h
<i>Gyrodinium</i> sp.	Gyr_sp	<i>Moina micrura</i>	M_m
<i>Harlothia reticulata</i>	Har_ret	Nauplii	Npl
<i>Haslea</i> sp.	Has_sp	Ostracoda	Ost
<i>Kirchneriella</i> sp.	Kir_sp	<i>Pleuroxus denticulata</i>	Pl_d
<i>Lepocincilis acus</i>	Lep_ac	<i>Polyarthra major</i>	P_m
<i>Lepocincilis oxyuris</i>	Lep_ox	<i>Scapholeberis mucronata</i>	S_m
<i>Melosira</i> sp.	Mel_sp	<i>Sida crystallina</i>	S_c
<i>Mertensopedina</i> sp.	Mer_sp	<i>Simocephalus vetulus</i>	S_v
<i>Micractinium</i> sp.	Micra_sp	<i>Thermocyclops oithonoides</i>	T_o
<i>Microcystis</i> sp.	Mic_sp		
<i>Monactinus simplex</i>	Mona_sim		
<i>Monoraphidium</i> sp.	Mono_sp		
<i>Navicula</i> sp.	Nav_sp		
<i>Nitzschia lorenziana</i>	Nit_lor		
<i>Nitzschia</i> sp.	Nit_sp		
<i>Oocystis</i> sp.	Oo_sp		
Oscillatoria spp.	Osc_spp		
<i>Pediastrum subgranulatum</i>	Ped_sub		
<i>Pennate</i> sp.	Pen_sp		
<i>Phacotus</i> sp.	Pht_sp		
<i>Phacus acuminatus</i>	Pha_ac		
<i>Phacus circumflexus</i>	Pha_cir		
<i>Plagioseimis nannoplantica</i>	Pla_nan		
<i>Planktoiyngbya limnetica</i>	Plk_lim		
<i>Pseudanabaena</i> sp.	Peda_sp		
<i>Pseudopediastrum boryanum</i>	Pseu_bor		
<i>Rhabdogloea</i> sp.	Rha_sp		
<i>Rhodomonas</i> sp.	Rho_sp		
<i>Scenedesmus</i> sp.	Sce_sp		
<i>Staurastum</i> sp.	Stau_sp		
<i>Stauridium tetras</i>	Sta_tet		
<i>Strombomonas</i> sp.	Stro_sp		
<i>Synedra</i> sp.	Syn_sp		
<i>Tellingia</i> sp.	Tei_sp		
<i>Tetraedron caudatum</i>	Tetra_cau		
<i>Tetraedron minimum</i>	Tetra_min		
<i>Tetraedron trigonum</i>	Tetra_tri		
<i>Tetrastrum</i> sp.	Tetr_sp		
<i>Thalassionema nitzschioides</i>	Thal_nitz		
Tintinnida	Tint		
<i>Trachelomonas</i> sp.	Tra_sp		
<i>Willea rectangularis</i>	Wil_rec		

Appendix 2. 2: Conversion factors used to calculate the biomasses of the different planktonic compartments from their initial abundances determined.

Compartment	Conversion factor	References
Heterotrophic Prokaryotes	14 fgC/cell	Guntersen <i>et al.</i> (2002)
Picophytoplankton	836 fgC/cell	Verity <i>et al.</i> (1992)
Nanoflagellates	3140 fgC/cell	Pelegri <i>et al.</i> (1999)
Ciliates	2318 pgC/cell	Putt & Stoecker (1989)
Dinoflagellates	225 pg C/cell	Fournier <i>et al.</i> (2012)
Diatoms	225 pg C/cell	Fournier <i>et al.</i> (2012)
Metazoan microzooplankton	28 ng C/cell	Dumont <i>et al.</i> (1975)
Metazoan mesozooplankton	0,768 µg C/cell to 1,44 µg C/cell	Dumont <i>et al.</i> (1975)



Appendix 2. 3: Monthly evolution of the salinity in the Tasdon marsh in TC the year following the end of the restoration works. The blue line indicates the first inlet of sea water in the station TC.

Chapitre 3

Appendix 3. 1: Punctual measurements of concentrations of SPM, PIM, POM, DOC, NH₄, NO₃, NO₂, PO₄, Si measured in all six ponds for both treatments (control and submerged) in the l’Houmeau marsh.

CODE SAMPLE	SPM (mg/l)	PIM (mg/l)	POM (mg/l)	DOC (mg/l)	NH ₄ (μmol/l)	NO ₃ (μmol/l)	NO ₂ (μmol/l)	PO ₄ (μmol/l)	Si (μmol/l)
CR1 T0	7.17	5.23	1.94	1.2	2.44	83.00	0.67	0.71	29.15
CR2 T0	15.67	13.53	2.13	1.3	2.99	61.70	0.85	0.74	26.43
CR3 T0	4.45	3.46	0.98	1.2	1.52	64.31	0.57	1.02	28.68
IR1 T0	21.21	18.37	2.84	1.2	1.60	82.60	0.91	1.03	39.50
IR2 T0	6.27	4.87	1.40	1.2	1.61	57.76	0.48	0.93	34.50
IR3 T0	5.86	4.67	1.19	1.4	2.00	70.02	0.68	1.01	29.49
CR1 T1	26.61	21.24	5.37	1.5	1.73	55.54	0.61	0.94	18.32
CR2 T1	45.03	37.10	7.93	1.2	0.35	71.46	0.92	0.56	16.13
CR3 T1	36.33	29.09	7.24	1.9	1.75	52.16	0.52	1.20	17.56
IR1 T1	65.12	51.38	10.74	1.3	0.22	90.22	0.97	0.69	17.42
IR2 T1	42.39	35.10	7.29	1.7	2.45	59.03	0.48	0.86	12.01
IR3 T1	33.46	26.71	6.75	1.2	2.93	36.32	0.73	0.90	18.82
CR1 T2	30.45	24.43	6.02	2	2.29	31.06	0.76	0.86	23.17
CR2 T2	64.50	52.46	12.04	1.7	0.45	21.72	0.79	0.02	22.89
CR3 T2	31.99	25.94	6.05	2	0.98	11.23	0.22	1.12	20.74
IR1 T2	68.70	56.60	12.10	1.6	0.25	39.53	1.05	0.59	26.93
IR2 T2	36.49	29.56	6.93	1.7	2.33	21.59	0.32	0.55	23.72
IR3 T2	25.71	20.26	5.45	1.8	1.80	11.30	0.40	0.64	22.94
CR1 T3	28.18	21.76	6.42	2.1	0.25	12.21	0.31	0.35	10.52
CR2 T3	65.30	49.94	15.36	1.9	0.58	2.49	0.03	0.07	21.99
CR3 T3	32.25	25.88	6.38	2	0.32	4.73	0.09	0.80	21.51
IR1 T3	69.22	55.26	13.96	1.8	0.48	36.18	0.52	0.15	14.16
IR2 T3	31.66	26.20	5.46	1.9	1.06	5.60	0.15	0.43	20.57
IR3 T3	24.37	18.79	5.58	1.9	0.89	2.32	0.15	0.67	17.33
CR1 T4	26.34	20.12	6.22	2.4	0.32	0.57	0.11	0.14	23.70
CR2 T4	82.40	64.23	18.18	1.8	0.23	1.86	0.03	0.16	24.26
CR3 T4	34.65	26.73	7.93	2.2	0.28	0.36	0.05	0.88	25.39
IR1 T4	72.48	54.96	17.52	2.1	0.22	3.07	0.04	0.21	37.27
IR2 T4	44.04	36.48	7.56	2.1	0.26	5.00	0.10	0.48	20.32
IR3 T4	29.28	22.04	7.24	2.2	0.42	3.96	0.08	0.46	25.39
CR1 T5	38.24	29.36	8.88	2.8	0.26	0.39	0.08	0.21	20.75
CR2 T5	101.40	77.83	23.57	2.3	0.29	0.30	0.03	0.13	18.54
CR3 T5	49.61	37.86	11.76	2.6	0.24	0.24	0.08	1.24	18.86
IR1 T5	28.64	20.98	7.66	2.2	2.80	7.27	0.24	0.57	24.02
IR2 T5	15.54	11.06	4.48	2.4	0.55	6.29	0.09	0.86	8.89
IR3 T5	25.70	19.61	6.09	2.6	0.38	4.36	0.07	1.02	22.66
CR1 T6	26.63	19.00	7.63	3	0.13	5.77	0.09	0.55	15.82
CR2 T6	49.40	38.90	10.50	2	0.22	4.10	0.03	0.20	14.00
CR3 T6	30.51	22.30	8.21	2.2	0.26	2.24	0.08	1.55	21.97
IR1 T6	66.02	52.00	14.02	2.3	0.23	3.24	0.06	0.83	31.06
IR2 T6	31.68	24.20	7.48	2.3	0.22	4.32	0.11	1.06	17.14
IR3 T6	25.45	19.21	6.24	2.3	0.24	0.89	0.09	0.78	26.06
CR1 T7	31.58	24.55	7.03	3.2	0.58	1.51	0.04	0.20	36.14
CR2 T7	63.07	41.90	21.17	4.9	0.34	5.74	0.13	0.31	79.59
CR3 T7	26.16	20.71	5.45	2.8	1.37	3.35	0.13	0.84	83.98
IR1 T7	95.27	76.10	19.17	2.8	0.43	15.42	0.17	0.37	95.92
IR2 T7	32.53	26.88	5.65	2.4	2.48	2.07	0.15	0.86	64.69
IR3 T7	12.06	8.44	3.61	2.1	0.62	8.51	0.11	0.64	77.56
CR1 T8	29.99	23.19	6.80	2.8	0.96	0.03	0.03	0.35	47.88
CR2 T8	96.03	76.13	19.90	3.4	0.22	1.76	0.04	0.41	86.34
CR3 T8	31.85	25.18	6.68	2.6	0.53	0.11	0.05	0.97	102.03
IR1 T8	83.87	66.63	17.23	2.6	0.26	3.38	0.04	0.53	105.98
IR2 T8	43.08	35.10	7.98	2.3	1.22	2.65	0.09	0.91	72.86
IR3 T8	45.24	36.64	8.60	2.6	0.28	2.79	0.09	1.05	98.68
CR1 T9	22.86	18.04	4.81	3	0.60	15.41	0.06	0.41	65.81
CR2 T9	68.35	55.70	12.65	3.7	0.98	23.16	0.15	0.51	102.29
CR3 T9	15.01	13.01	2.00	2.8	4.36	10.88	0.32	1.44	118.00
IR1 T9	73.43	59.88	13.55	2.9	1.09	8.25	0.30	1.06	123.65
IR2 T9	61.65	50.88	10.77	2.6	0.57	17.61	0.15	0.92	98.16
IR3 T9	32.06	26.06	6.00	3.1	2.13	22.70	0.15	1.14	123.98

Structure et fonctionnement planctonique des marais des Pertuis-Charentais : effet de l'aléa submersion sur leurs fonctions écologiques

Résumé

Les marais côtiers font parties des écosystèmes les plus productifs de la planète. En plus de fournir de nombreux services écosystémiques, les marais côtiers abritent une vaste biodiversité, en plus de servir de refuge pour des espèces migratrices. Or, ces milieux tendent à disparaître à cause de pressions naturelles et anthropiques. Récemment, davantage de personnes prennent conscience de l'importance des marais côtiers, et des plans de gestion et restauration de ces écosystèmes voient le jour pour préserver leur biodiversité et les fonctions écologiques qu'ils fournissent. Ces travaux de thèse se focalisent spécifiquement sur la détermination du fonctionnement des communautés planctoniques dans les marais côtiers des Pertuis-Charentais selon leur gestion, et l'impact de la submersion marine sur ces communautés. L'intérêt de cette thèse est d'étudier la biodiversité « non visible » mais essentielle, actrice de nombreuses fonctions écologiques. Pour se faire, différents suivis saisonniers ont été effectués sur des marais salés et doux pour déterminer les réseaux trophiques planctoniques et leur fonctions écologiques associées, en lien avec la gestion de ces marais. De plus, une étude des communautés planctoniques a été effectuée sur un marais côtier ayant été restauré pour évaluer l'impact de cette restauration sur le plancton. Enfin, une expérience de simulation *in situ* de submersion marine a été réalisée pour évaluer l'impact potentiel de cet aléa sur ces organismes. L'ensemble de ces travaux ont souligné l'importance de prendre en compte la préservation des communautés planctoniques et leur fonctions écologiques, qui jouent un rôle essentiel dans les marais côtiers.

Mots-clés : communautés planctoniques ; marais côtiers ; identité patrimoniale ; réseau trophique ; fonction écologique ; submersion marine

Structure and functioning of plankton in the marshes of the Pertuis-Charentais: the effect of marine submersion on their ecological functions

Abstract

Coastal marshes are among the most productive ecosystems on the planet. In addition to providing numerous ecosystem services, coastal marshes shelter a wide biodiversity and serve as a refuge for migratory species. However, these environments tend to disappear due to natural and anthropogenic pressures. Recently, more people are becoming aware of the importance of coastal marshes and plans to manage and restore these ecosystems are emerging to preserve their biodiversity and the ecological functions they provide. This thesis focuses specifically on determining the functioning of planktonic communities in the coastal marshes of the Pertuis-Charentais according to their management, and the impact of marine submersion on these communities. The relevance of this thesis is to study the "invisible" but essential biodiversity that plays a key role in many ecological functions. To accomplish this, two seasonal surveys were conducted on salt and freshwater marshes to determine planktonic food webs and their associated ecological functions, in relation to marsh management. In addition, a plankton community study was conducted on a restored coastal marsh to assess the impact of restoration on plankton. Finally, an *in situ* simulation of marine submersion was conducted to assess the potential impact of this hazard on these organisms. All this work underlined the importance of considering the preservation of plankton communities and their ecological functions, which play an essential role in coastal marshes.

Keywords: planktonic communities; coastal marshes; patrimonial identity; food web; ecological function; marine submersion