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Rapport de stage de **Lucila XAUS**

RELATIONSHIP BETWEEN WATER CARBON AND PLANKTONIC FOOD WEBS IN “BLUE CARBON” ECOSYSTEM

Internship welcoming organizations: LIENSs, CNRS and LER-PC, Ifremer

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« *Fais de ta vie un rêve, et d'un rêve, une réalité* », Antoine de Saint-Exupéry

Synthèse

Au cours des dernières années, les études portant sur la dynamique du dioxyde de carbone (CO₂) dans l'atmosphère dans les écosystèmes terrestres et aquatiques se sont multipliées. En effet, les émissions de CO₂ atmosphérique se sont intensifiées du fait des actions anthropiques, telles que l'utilisation intensive des énergies fossiles, la déforestation ou encore l'agriculture. Une évaluation précise de ces émissions anthropiques de CO₂ ainsi que leur redistribution entre l'atmosphère, l'océan et la biosphère terrestre dans un climat changeant est donc essentielle afin de mieux comprendre les cycles régionaux et globaux de carbone, et d'inciter le développement de politiques climatiques et prévoir les changements climatiques futurs.

La pression partielle de CO₂ (pCO₂) est relativement constante dans l'atmosphère, alors qu'elle peut varier de plus de 4 ordres de grandeur dans l'espace et dans le temps au niveau des eaux de surface. Les flux de CO₂ reflétant les processus physico-chimiques et biologiques mis en jeu, peuvent être calculés comme la différence entre la pCO₂ de l'eau de surface et celle de l'atmosphère. Ces variations peuvent être contrôlées par différents processus, comme les échanges horizontaux de CO₂ entre les différentes masses d'eau (eau douce / eau de mer), les processus physico-chimiques (température, vents, mélange des eaux de surface) et biologiques associés (dissolution/précipitation du CaCO₃, production primaire et respiration). Dans ce contexte, les prairies marines, et d'autres systèmes végétalisés côtiers comme les marais salés et les mangroves ou encore les herbiers de phanérogames marines, ont été reconnus pour leur importance dans la captation et la séquestration du "carbone bleu", avec une moyenne de plus de $200 \pm 24 \text{ g.C.m}^{-2}.\text{an}^{-1}$. En particulier, la Charente-Maritime présente près de 100 000 ha de marais, soit près de 15 % de la superficie de ce département d'où l'importance de les prendre en compte face aux problématiques du carbone et du changement climatique. En fonction de leur localisation, chaque marais peut présenter une structure/typologie différente, où ils peuvent être connectés à des eaux terrestres en amont et océaniques en aval, via un système d'écluses plus ou moins important, comme le marais d'eau douce de Tasdon étudié ici. En outre, les marais peuvent être gérés par l'homme pour l'agriculture, la conchyliculture, etc., comme le marais salé de L'Houmeau, autre marais étudié au cours de ce stage.

Les réseaux trophiques planctoniques sont définis comme des interactions entre les organismes présents dans un écosystème donné. Ils ont été largement décrits dans les zones marines et côtières et, plus récemment, dans les marais. Cinq groupes principaux ont été décrits pour les marais : "herbivore", "multivore", "réseau microbien", "boucle microbienne" et "hiver biologique", avec quelques nuances pour chacun d'entre eux. L'étude des réseaux trophiques planctoniques s'est avérée très utile pour comprendre le fonctionnement des écosystèmes. Bien que les variations de CO₂ et les réseaux trophiques aquatiques aient été étudiés séparément et de façon hétérogène suivant le type de systèmes côtiers considérés, peu d'études

ont été menées de concert afin de faire le lien carbone (CO₂) versus réseau trophique dans divers marais notamment. Par conséquent, cette relation reste inconnue. L'objectif de cette étude est (1) d'étudier si les variations de CO₂ de l'eau peuvent être expliquées par les réseaux trophiques planctoniques, (2) de déterminer si la relation possible entre les réseaux trophiques planctoniques et les échanges de CO₂ dans l'eau reste la même dans deux écosystèmes "Blue Carbon" différents. Afin de répondre à ces objectifs, le marais salé de L'Houmeau et le marais d'eau douce de Tasdon renaturisé récemment, ainsi que leurs facteurs environnementaux, biogéochimiques et biologiques ont été étudiés.

Le marais salé de l'Houmeau est un ancien bassin d'élevage d'huîtres situé au nord de La Rochelle. En 1988, le marais et ses bassins sont devenus un site expérimental, actuellement détenu par le LIENS-CNRS. Le marais doux de Tasdon (123 hectares) est situé dans l'agglomération de La Rochelle et a récemment fait l'objet d'un processus de renaturation (de 2019 à 2021), qui a consisté en autre à réouvrir la connexion entre l'océan et le marais. Il est important de souligner que ce marais périurbain est situé à l'intérieur d'une zone naturelle d'intérêt écologique, faunistique et floristique (ZNIEFF de type I) et qu'il est influencé par différents apports d'eau provenant à la fois de l'océan Atlantique (Parc naturel marin de l'estuaire de la Gironde et de la mer des Pertuis) et des apports fluviaux (rivière de la Moulinette). Les prélèvements d'eau et les différentes mesures associées au marais de l'Houmeau ont eu lieu mensuellement entre mars et août 2021. En ce qui concerne Tasdon, des échantillons saisonniers ont été prélevés en 2019 et en 2021/2022 sur trois stations différentes (T2, T6 et T7). Des mesures des paramètres abiotiques (température, salinité, turbidité), biogéochimiques (pCO₂ de l'eau, flux de CO₂, O₂%) ainsi que biotiques (biomasse de chlorophylle a (Chla), biomasse de mesozooplankton (Meso) et des procaryotes hétérotrophes (HTTP)) ont été réalisées pour les deux marais. Un regroupement hiérarchique agglomératif (HAC) a été réalisé afin d'identifier les types de réseaux trophiques existants à L'Houmeau et Tasdon. Ensuite des corrélations entre les paramètres biotiques, biogéochimiques et abiotiques ont été réalisées à l'aide d'analyses statistiques.

Les zones humides restaurées, par exemple les marais, les deltas ou les tourbières, peuvent être transformées de sources de CO₂ atmosphérique en puits de CO₂, ce qui peut entraîner une diminution des gaz à effet de serre et donc une atténuation du réchauffement climatique. Au contraire, les perturbations anthropiques peuvent transformer un marais d'eau douce, fort puits de CO₂, en une source de CO₂. Au cours de notre étude, le marais doux renaturé de Tasdon a montré un comportement faiblement source voire puits de CO₂ après la renaturation ($-3.70 \pm 2.37 \text{ mmol.m}^{-2}.\text{h}^{-1}$), alors qu'il était source de CO₂ avant renaturation. Le marais salé de L'Houmeau est toujours resté une faible/moyenne source de CO₂ (< 900 ppmv). Durant cette étude, les effets température ont eu une influence sur les variations de pCO₂ de l'eau même si les effets non-température et notamment biologiques ont été prédominants à Tasdon et à L'Houmeau. Ces résultats

coïncident avec des études réalisées précédemment sur d'autres systèmes côtiers. Le marais salé de L'Houmeau a présenté une biomasse de Chla relativement faible pour un marais ($>8 \mu\text{g.L}^{-1}$) principalement dominée par des fractions de taille nano et pico. De plus, les abondances de Meso et HTTP ont suivi la même tendance que la Chla (toutes maximales en juin), ce qui suggère une claire relation prédateur – proie sur ce site. En parallèle, la valeur maximale de pCO_2 et minimale de $\text{O}_2\%$ ont été enregistrées aussi en juin. Dans le marais de Tasdon aux stations T2 et T6 (après la renaturation), les biomasses de Chla ont montré une forte augmentation après renaturation, tandis que T7 présentait une tendance inverse. Cependant, une diminution des abondances Meso et Micro a été constatée à presque toutes les saisons et sur tous les stations au cours de l'année 2021. Cette dernière pourrait expliquer aussi l'augmentation de $\text{O}_2\%$ et la diminution des valeurs de pCO_2 , conduisant aux flux de CO_2 négatifs (puits) mesurés.

L'étude simultanée des réseaux trophiques de deux typologies de marais différentes a permis de montrer certaines similitudes et différences entre les sites étudiés et de faire clairement le lien entre typologie de réseaux trophiques et carbone. Par exemple, la renaturation à Tasdon a entraîné une baisse des valeurs de pCO_2 de l'eau et un comportement légèrement source voire puits de CO_2 , comparables aux valeurs de pCO_2 mesurées à L'Houmeau. Bien que les deux marais aient des typologies très différentes (valeurs de salinité contrastées, concentration de nutriments, gestion du site), cinq typologies de réseaux trophiques ont été trouvées en commun, trois étant plutôt stables dans le temps (quelques semaines de présence): 'hiver biologique', 'réseau microbien', 'multivore' et deux transitoires : 'multivore faible' et 'herbivore faible'. En outre, dans les deux marais, un lien entre une pCO_2 élevée et les réseaux trophiques type 'réseau microbien' et 'multivore' a été trouvée. D'autre part, le réseau trophique type 'multivore faible' a été associé à des valeurs de pCO_2 faibles (L'Houmeau), moyennes ou élevées (Tasdon), tandis que le réseau trophique de type 'herbivore faible' a quant à lui été associé soit aux pCO_2 les plus faibles (Tasdon), soit à des pCO_2 moyennes (L'Houmeau). Malgré les différences des deux marais étudiés, un lien général entre la typologie de réseau trophique et la dynamique des pCO_2 a été obtenue. Il est important de souligner que la saisonnalité semble jouer un rôle important à la fois dans les mesures de pCO_2 , dans les typologies de réseaux trophiques et donc dans les relations entre les deux, ce qui implique que dans l'analyse des données, la période d'échantillonnage est fondamentale. Après la renaturation récente du marais de Tasdon, les réseaux trophiques n'ayant pas encore retrouvé a priori un état d'équilibre saisonnier, une meilleure compréhension de cet environnement reste à ce stade limitée mais nécessiterait sans aucun doute d'être poursuivie via d'autres suivis *in situ* à poursuivre sur ce marais. Cela pourrait conforter le fait que certains types de réseaux trophiques planctoniques puissent expliquer les variations de pCO_2 observées. Dans tous les cas, cette étude via une approche originale et innovante a permis d'établir pour la première fois une relation entre la typologie de réseau trophique et le pCO_2 dans des marais différents et justifie donc d'être poursuivie.

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1. Introduction

This master's internship was carried out under the joint supervision of two organizations: the Littoral ENvironnement et Sociétés (LIENSs) laboratory attached to La Rochelle University and the CNRS (La Rochelle), and the Laboratory Environnement et Ressources des Pertuis Charentais (LER-PC) of IFREMER, La Tremblade Station.

LIENSs reaches for the mixt of environmental and human science, as well as chemistry and biotechnology. It is mainly focused on the functioning of the coastal system in a global changing context cause by human disruptions. This is why it is of great importance to maintain the interdisciplinary between every teams. There are six research teams inside this institution, each of which leads one or more projects on an integrative approach to sustainable development issues. In the year 2021, there were up to 168 people working at LIENSs. In particular, the BIOFEEL team in which I did my internship, the structure and functioning of coastal ecosystems is studied, mainly through a trophic ecology approach. Inside this team, Christine Dupuy is a teacher-researcher who focuses on microbial and trophic ecology and their structure in a coastal environment as well as in Blue Carbon ecosystems.

Ifremer is a French institute fully committed to the protection and restauration of the oceans, by the hand of a sustainable development of marine resources. Moreover, Ifremer is involved in national, European and international scientific programs and initiatives. La Tremblade station carries out studies in the fields of shellfish farming, aquaculture and coastal environment monitoring. There are three entities on this site: the Pertuis Charentais Environment and Resources Laboratory (LER-PC), the Marine Invertebrate Health Adaptation Unit (ASIM unit) and La Tremblade Marine Mollusc Platform (PMMLT). Currently, there are 55 people working there. Pierre Polsenaere is a researcher at the LER-PC, who's studies focus on of carbon processes and fluxes in coastal systems.

The frame of this internship lies on La Rochelle Territoire Zéro Carbone (LRTZC) project, which began in 2019. This project aims to reduce carbon emissions by 30% by 2030 and achieves carbon neutrality by 2040. A better understanding and quantification of the processes associated with blue carbon systems among all the ecosystems of the CDA (Agglomération de La Rochelle) is essential to implement effective measures to mitigate CO₂ emissions. It is important to highlight that the study takes part in a "Blue Carbon" ecosystem, as it is held at different marsh typologies (freshwater and salt water). "Blue Carbon" indicates the capacity of specific environments to sequester/store carbon in their plants and or sediments in costal and marine ecosystems, such as tidal marshes, seagrasses and mangroves. This master's research aims to contribute to the study of carbon capture and sequestration, and the association between carbon processes/fluxes and planktonic trophic chains in a freshwater and saltwater marshes.

2. Subject contextualization

2.1. Theoretical framework

During the last few years, an increase in the number of studies focusing on atmospheric carbon dioxide (CO₂) dynamics has been seen. It is a fact that CO₂ atmospheric emissions are rapidly growing due to anthropogenic impact, such as intensive use of fossil energies, deforestation and or agriculture (Huston and Marland, 2003). These emissions are 47 % higher than those during the Industrial Age, representing an increase of atmospheric carbon dioxide from near 280 parts per million (ppm) in 1970 to 417 ppm in 2022 (NOAA annual report, 2023). Moreover, this phenomenon is far from coming to an end, since from 2021 to 2022 a rise of more than 2 ppm has been seen (NOAA annual report, 2023) and is causing an environmental disequilibrium between atmospheric and oceanic CO₂, leading to an increment on greenhouse gases and a temperature increase.

Accurate assessment of anthropogenic CO₂ emissions and their redistribution among the atmosphere, ocean, and terrestrial biosphere in a changing climate is critical to better understand the global carbon cycle, to support the development of climate policies, and project future climate changes (Friedlingstein et al., 2021). Coastal oceanic domains have a main role in connecting terrestrial and ocean systems, which has a great impact in vertical and horizontal CO₂ exchanges (figure 1). This is why it is crucial to study carbon fluxes inside and among coastal subsystems (e.g. marine, estuarine, oceanic nearshore and offshore), and their alteration by climate and anthropogenic changes (Bauer et al., 2013).

Even if location changes, atmospheric CO₂ partial pressure (pCO₂) remains relatively constant (Takahashi et al., 2002), whereas at surface waters it can vary by more than 4 orders of magnitude spatially and temporally (Takashi et al., 2002; Sobek et al., 2005). CO₂ fluxes can be calculated by the difference between surface water and atmospheric pCO₂, so the water-air pCO₂ gradient can greatly varies, being controlled by water mass (freshwater / seawater) pCO₂ variations and associated processes. In turn, water pCO₂ is influenced by several physical (i.e. temperature, winds, surface water mixing) and biological processes (i.e. CaCO₃ dissolution/precipitation, primary production and respiration) (figure 1) (Moreau et al., 2013). Moreover, CO₂ fluxes are also controlled by the gas transfer coefficient (*k*). This coefficient is strongly related to the turbulence at the water-air interface induced by wind and heat fluxes for instance (Cole and Caraco, 1998). Nonetheless, Dai et al., (2009) found that, despite CO₂ oceanic flux are generally controlled by temperature effects, other coastal systems such as marshes seem to rather be influenced by non-temperature effects, highlighting a strong biological control on water pCO₂ along with horizontal advection and benthos-pelagos couplings in these shallow land-sea interface ecosystems.

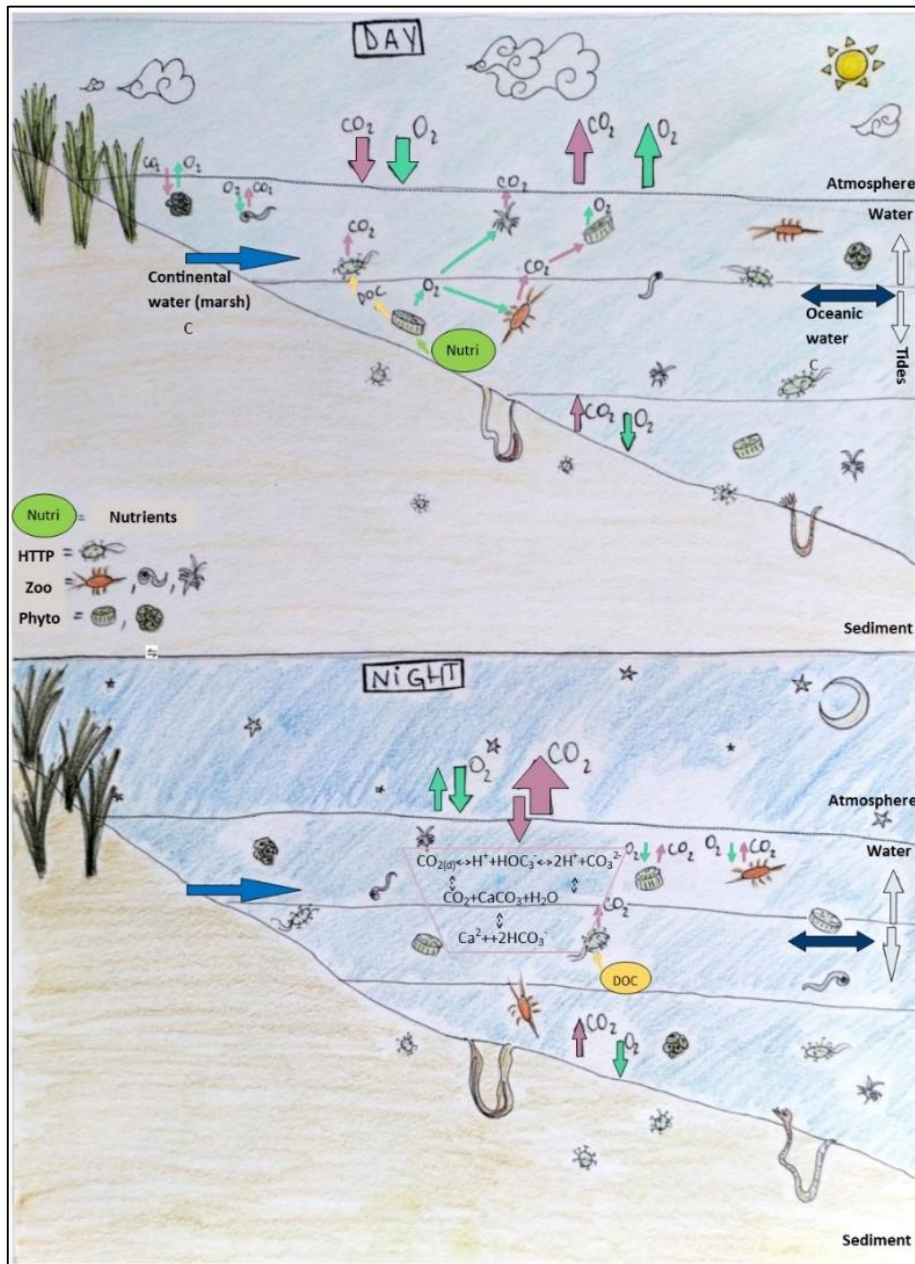


Figure 1. Planktonic community CO_2 and O_2 exchanges during daytime and nighttime in the water column at a coastal environment. DOC: dissolved organic carbon, Nutrients: NO_3 , NO_2 , PO_4 , NH_4 , SI , HTTP: heterotrophic prokaryotes, Zoo: micro and mesozooplankton, Phyto: pico, nano and microphytoplankton. The equation shows the CO_2 solubility and dissolution/calcification processes involving bicarbonate ions (HCO_3^-), carbonate ions (CO_3^{2-}) and calcium carbonate (CaCO_3) by the biological carbon pump. Illustration from L. Xaus.

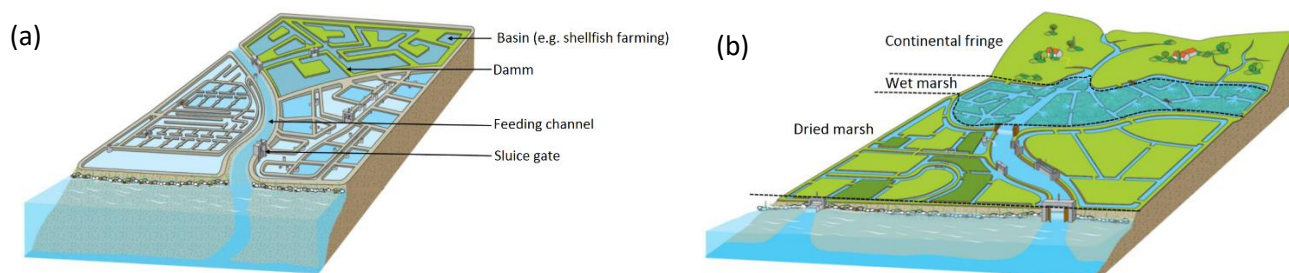


Figure 2. Illustrative figure of an anthropogenic modified salt (a) and fresh marsh (b). FMA (Forum des Marais Atlantique) figure adaptation. (Moncelon, 2022)

Within this context, seagrass meadows, and other coastal vegetated systems like salt marshes and mangroves, have been recognized for their importance in “blue carbon” sequestration and storage (Duarte et al., 2005; Mcleod et al., 2011; Greiner et al., 2013), with an average of over $200 \pm 24 \text{ g.C.m}^{-2}.\text{yr}^{-1}$ (Wedding et al., 2021). In particular, the Charente-Maritime region presents nearly 100,000 ha of marshes, which is almost 15% of this department superficies (Moncelon, 2022). Depending on their location, each marsh can present a different structure, where they can be connected to inland rivers, have some kind of dam or be linked to the sea, like the studied Tasdon freshwater marsh (figure 2.b). Additionally, marshes can be managed by human beings for agriculture, shellfish farming, etc., e.g. L’Houmeau saltwater marsh also studied during this internship (figure 2.a, i.e. shell farming). In addition, diurnal and tidal cycles have been proven to influence carbon budgets and dynamics in coastal systems and subtropical bays (Dai et al., 2009; Yates et al., 2007), as well as in equatorial mangrove waters (Maher et al. 2013; Bouillon et al., 2007; Borges et al., 2003) and salt marsh-estuary coastal ecosystems (Wang et al., 2018). All of these possibilities lead to different and specific environments associated to a great variety of living organisms, nutrients and carbon cycling, processes and exchanges (figure 1). Therefore, it is essential to accurately understand marsh ecological functions for a better understanding of CO_2 fluxes regulating factors and how they affect carbon budgets in these dynamic and heterogeneous systems.

Food webs are defined as feeding (or trophic) interactions between species inside a particular environment (Dunne, 2005) and have been greatly described in marine and coastal areas (Legendre and Rassoulzadegan, 1995; Dupuy, 1999; Marquis et al., 2007) and more recently in marshes (Tortajada, 2011; Masclaux et al., 2014, Bergeon et al., 2023). Five main food web types s have been described for marshes: ‘herbivore’, ‘multivorous’, ‘microbial food web’, ‘microbial loop’ and ‘biological winter’, with some nuances inside each of them (Tortajada, 2011). The study of planktonic food webs (basically constituted by prokaryotes, phytoplankton and zooplankton) has been proven to be very useful in the understanding of ecosystem functioning (Vincent et al. 2002; Beaugrand, 2005; Masclaux et al., 2014). As an example,

planktonic food webs play a main role in water-air and horizontal carbon exchanges, due to photosynthesis (using CO₂ and light to create O₂) and respiration processes (taking O₂ and liberating CO₂), both during daytime and night time (figure 1). In addition, these communities seem to have a purifying function in coastal marshes, owing to the retention of suspended matter, nutrients and pollutants in the water column, which helps preventing eutrophication (Azim et al., 2005; Verhoeven et al., 2006; Nyman, 2011). Likewise, phytoplankton (mainly picophytoplankton) has been proven to consume both inorganic and organic source of nitrogen (Bradley et al., 2010). Legendre and Rivkin (2005) mentioned that, in the upper ocean, food web structure has a great influence in energy and chemical elements flow inside ecosystems, which, subsequently, can also be modified by direct (physical and chemical regimes) or indirect (human impact) constraints (figure 3).

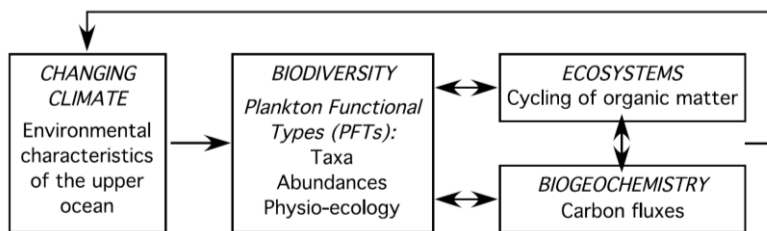


Figure 3. Illustrative scheme of interactions between an ecosystem, its biodiversity, biochemical associated exchanges and how it affects the global ecosystem. Legendre and Rivkin (2005).

Primary production, can increase or decrease depending on the phytoplankton size (picophytoplankton (0.2 to 2 μm), nanophytoplankton (2 to 20 μm) and microphytoplankton (> 20 μm) (Sieburth et al., 1978)), phytoplankton and autotrophic prokaryotes biomass, photosynthetic activity as well as many environmental factors, like e.g. temperature, light availability or nutrients concentration. Shiomoto (1997) found that, at the Okhotsk Sea small-sized phytoplankton (nano and pico) could contribute up to 70% of primary production. The respiration process will also vary if there are environmental and heterotrophic organisms' abundances changes (prokaryotes, meso- and micro- zooplankton, heterotrophic protozoan, macrofauna), as well as phytoplankton and autotrophic prokaryotes respiration process (figure 2). Del Giorgio and Williams (2005) suggested that, on global basis, mesozooplankton consumes between 12 and 35% of primary production each day, whereas microzooplankton grazes between 60 and 75%. Consequently, the effect of both micro and mesozooplankton, in different regions of the Ocean, have been proven to consume approximately 3/4 of total primary production (Schmoker et al., 2013). In addition, heterotrophic prokaryotes' respiration leans toward a greater value than primary production in aquatic

ecosystems (Del Giorgio et al., 1997), which reinforce the need to know as much as possible food web typology to fully understand the ecosystem functioning itself.

Although, both pCO₂ cycle and aquatic food webs have been widely but separately studied over the coastal zone, few research has been made to link them (Legendre and Rivkin, 2005; Niquil et al., 2006; Moreau et al., 2013), especially in diverse marsh typologies (Masclaux et al., 2014; Adamczyk and Shurin, 2015). Therefore, the relationship between planktonic food webs and water CO₂ changes in marshes remains unknown. The objectives of this study are to (1) study if pCO₂ and atmospheric CO₂ flux variations can be explained by planktonic food webs, (2) determine if the possible relationship between planktonic food webs and water CO₂ exchanges remains the same in two different “Blue Carbon” ecosystems. To address these objectives, L’Houmeau saltwater marsh and Tasdon renatured freshwater marsh and their environmental, biogeochemical and biological factors were studied. These data allowed to achieved the first known relationships between food web typology and pCO₂ in two different marshes.

2.2. Materials and Methods

2.2.1. Studied marsh sites

L’Houmeau saltwater marsh is a formerly system basin used as an oyster farming at the North side of La Rochelle. In 1988, the marsh and its basins became an experimental site, firstly used by Ifremer and currently held by LIENSs-CNRS. Nowadays, this site lies both inside a Natura 2000 site connected with a Marine Natural Park (figure 4.a). The sampled basin (10 m wide, 1.5 m high top) gets naturally filled up with tide coefficients > than 60, with a maximal volume of 270 m³. On the other hand, there is a mechanical valve system, which manages the salty water effluent from the sea and inversely. For this study, water volume fluctuated between 90 and 144 m³, which would indicate that the basin was only field up to 0.50 or 0.80 m high (figure 4.b and c). Both biotic and abiotic data used for this site was collected by Raphael Moncelon for this PhD Thesis (Moncelon, 2022).

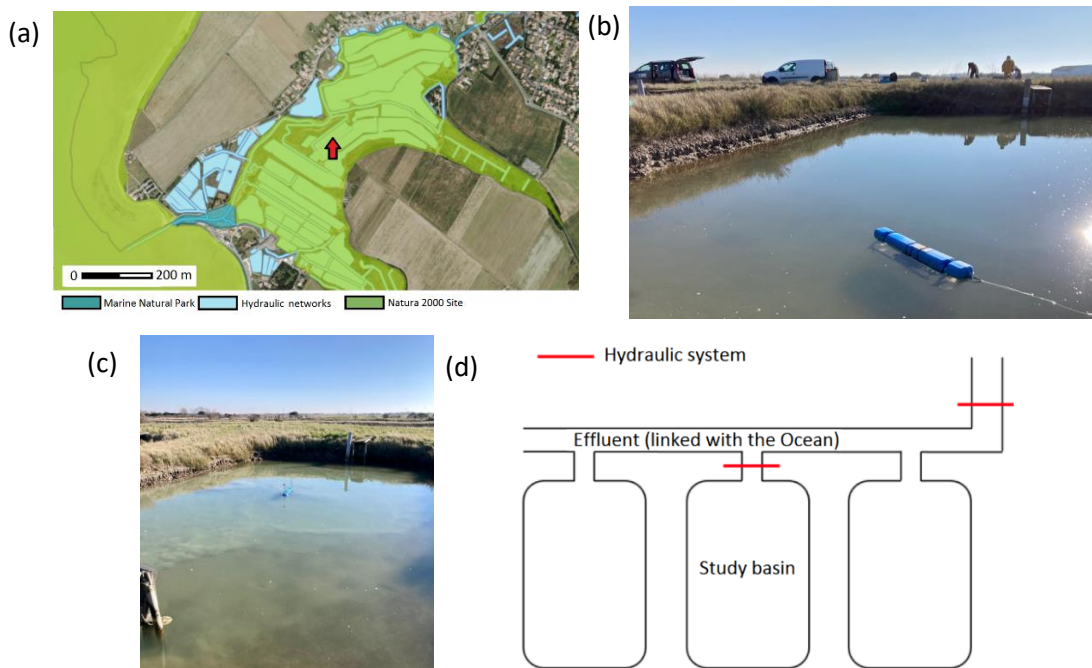


Figure 4. L'Houmeau marsh experimental site. (a) The red arrow in the satellite image (geoportal) shows the location of the studied basin ($46^{\circ}12'17.4''N$ $1^{\circ}11'41.3''W$). The light blue lines represent hydraulic network and the water path between marsh and sea waters. In dark blue the small fraction of the Marine Natural Park, and in green the Natura 2000 site. Basins are shown in (b) and (c) with autonomous deployed water probes. (d) Represents the hydraulic system. (Moncelon, 2022; photo: Polseneare Pierre)

Tasdon freshwater marsh (123 hectares) is located in La Rochelle urban area and has recently been involved in a renaturation process (from 2019 until 2021), which consisted in re-opening the connection between the ocean and the marsh (figure 5.a). It is important to highlight that this peri-urban marsh is located inside a Natural Areas of Ecological, Faunistic and Floristic Interest (ZNIEFF type I) and is influenced by different water inputs from both the Atlantic Ocean (Marin Natural Park) and river discharges. Before and after the restauration, Tasdon marsh mutated from a high CO_2 source to a moderate source if note a CO_2 sink depending on sampled seasons and stations (Bergeon et al., Mayen et al., in prep.). In addition, by 2021, this marsh had regained its ecological, regulatory and protective functions, thanks to major restoration work covering almost 83 hectares (La Rochelle town, pers. Comm.). Biotic and abiotic parameters were gathered by Lauriane Bergeon and Jeremy Mayen during their PhD and associated research projects PAMPAS and LRTZC (Bergeon et al., Mayen et al., in prep).

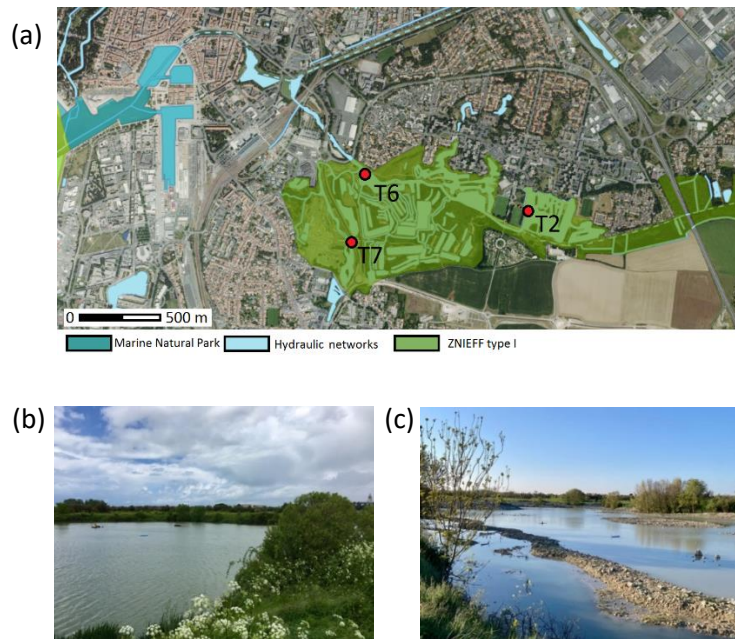


Figure 5. Satellite image from geoportal (a). The light blue lines represent hydraulic network and the water path between marsh and seawaters. In dark blue a small fraction of the Marine Natural Park is shown, and in green a ZNIEFF type I. Station T2, T6 and T7 (46°8'56.4" N, 1°7'26.4" W; 46° 9'3.6" N, 1°8'9.6" W; 46° 8'49.2" N, 1°8'13.2" W respectively) are marked by red points. Images from stations T2 before renaturation (b) and after renaturation (c) (photo: Polsenaere Pierre).

2.2.2. Abiotic parameter samplings

Measurement samplings at L’Houmeau marsh have taken place monthly between March and August 2021 (table 1). Over 90% of water was changed once a month by the hand of the mechanical valve system, with an adjustment period of 2-3 days before starting the samplings (figure 4.d). The remaining 10% above the sediment helped limiting disturbance of the water-sediment interface. At Tasdon, seasonal samples were done for both 2019 and 2021/2022 at three different stations (T2, T6 and T7). In 2019 only spring and autumn samples were held, whereas in the year 2021 all seasons were collected (table 1).

For both L’Houmeau and Tasdon marshes, temperature (in °C), salinity/conductivity, turbidity (NTU), dissolved oxygen concentration (DO in $\mu\text{mol l}^{-1}$) and oxygen saturation percentage (DO-sat. in %) in subsurface waters (at 0.50 m below the surface) were measured continuously (one measurement every 15 minutes) with a YSI sensor with a wide measurement range (0-10.000 $\mu\text{S.cm}^{-1}$) (table 1). Besides, discrete samples of water temperature, salinity, pH and DO were taken with a VWR multimeter. An autonomous pCO₂ underwater probe (C-SenseTM pCO₂ sensor, PME/Turner Designs, 0-2000 ppm range,

precision 3% of the range; figure 6) and a miniPAR logger (PME) were used to measure water pCO₂ and PAR respectively, continuously (per minute) during 24h (table 1). CO₂ flux estimations were done using the methodology described by Polsenaere et al. (2013). For more details on the CO₂ flux estimation and C-Sense probe calibration see annex 8.1.



Figure 6. Floating bati equipped with the C-Sense probe (Photo: Polsenaere Pierre).

Aminot and K  rouel (2004) methodology was applied to determine nutrient concentrations (nitrate (NO₃), nitrite (NO₂), ammonium (NH₄), phosphate (PO₄) and silicate (Si)) on filtered water (0.7 µm GF/F glass fiber membrane, Whatman) using a SEAL AA3 autoanalyzer with: 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) detection limit. At l’Houmeau, dissolved organic carbon (DOC, mg.L⁻¹) was analyzed, while particulate inorganic and organic material (PIM and POM) were also taken by weighing filters after calcination at Tasdon (table 1).

Table 1. Samples and measurement methods for L’Houmeau and Tasdon campaigns. Sampling periods are mentioned at the bottom of the table.

	Temperature (°C)	Salinity	Turbidity (NTU)	O ₂ %	Wind gust (m ⁻¹ .s ⁻¹)	pCO ₂ (ppmv)	CO ₂ flux (mmol.m ⁻² .h ⁻¹)
L’Houmeau	YSI sensor (continuous) + VWR multimeter (discrete)				Infoclimat.fr	C-Sense probe, 24h, measured every minute	Estimation (Annex)
Tasdon	YSI sensor (continuous)				Infoclimat.fr	C-Sense probe, 24h, 3 days, measured every minute	Estimation (Annex)
	Nutrients (µmol.L ⁻¹)		DOC (mg.L ⁻¹)	PIM (mg.L ⁻¹)	POM (mg.L ⁻¹)	PP (mgC.m ⁻³ .h ⁻¹)	
	Triplicated x 15 L		Triplicated x 2 L	Triplicated x 5 L		Triplicated x 2 L	
L’Houmeau	SEAL AA3 autoanalyzer		QUALYSE laboratory	-		Nielson’s (1951) radiation protocol	
Tasdon	SEAL AA3 autoanalyzer		-	Weighing filters after calcination		-	
	Chla (µg.L ⁻¹)		Meso (ind.m ⁻³)	Micro (ind.m ⁻³)	Proto (ind.L ⁻¹)	HTTP (ind.mL ⁻¹)	
	Triplicated x 15 L		Triplicated x 6 L	Triplicated x 6 L		Triplicated x 1.5 mL	
L’Houmeau	Filtres: 20 µm, later 3 µm and 0.7 µm		200 µm filter	-	-	Flow cytometry analysis	
Tasdon	Filters: 20 µm, later 3 µm and 0.7 µm		200 µm filter	63 µm filter	Flowcam analysis	Flow cytometry analysis	
	Chla	Meso	Micro	Proto		HTTP	
	Carbon biomass (µgC.L ⁻¹)						
L’Houmeau	50 (µg.L ⁻¹) ^a	1.44 (ind.L ⁻¹) ^b	-	-		*14 (fgC.cell ⁻¹) ^e	
Tasdon	50 (µg.L ⁻¹) ^a	0.768 to 1.44 (ind.L ⁻¹) ^b	0.028 (ind.L ⁻¹) ^b	2318 (cil) (pgC.cell ⁻¹) ^c , 225 (din) (pgC.cell ⁻¹) ^d		*14 (fgC.cell ⁻¹) ^e	

Conversion factors used. ^a(Tilzer and Dubinsky, 1987); ^b(Dumont et al., 1975); Ciliates (cil): ^c(Putt and Stoecker, 1989); Dinoflagelates (din): ^d(Fournier et al., 2012); ^e(Guntersen et al., 2002).

Abiotic and water CO₂ measurement dates - Tasdon: spring: 23 to 25/04/2019, autumn: 25 to 27/11/2019, spring: 13 to 15/04/2021, summer: 16 to 18/08/2021, autumn: 13 to 15/12/2021, winter: 01 to 03/03/2022; L’Houmeau: 17/03/2021, 14/04/2021, 18/05/2021, 14/06/2021, 15/07/2021, 09/08/2021.

Nutrients, DOC, PIM, POM and biotic sampling dates - Tasdon: spring: 25/04/2019, autumn: 22/11/2019; spring: 15/04/2021, summer: 25/08/2021, autumn: 16/11/2021, winter: 09/03/2022; L’Houmeau: 18/03/2021, 14/05/2021, 19/05/2021, 13/06/2021, 15/07/2021, 09/08/2021

2.2.3. Biological parameters sampling

Biological parameters samplings at L’Houmeau marsh were taken between March and August 2021, while at Tasdon they were taken seasonally during 2019 and 2021/22 (table 1). Each biotic parameter was sampled in triplicates. At L’Houmeau saltwater marsh, surface water samples were taken in the morning, as soon as the sun rose, and returned to the laboratory at the end of the morning. At both L’Houmeau and Tasdon, 15 L volumes of water were sampled to measure chlorophyll-*a* biomass by fraction (first filtration on a 20 μm filtered (micro), followed by a 3 μm (nano) one and finishing with a 0.7 μm filter (pico)) (table 1). During each campaign, a 200 μm mesh size net (WP2 net for plankton) was deployed to sample metazoan mesozooplankton (Meso) and measure its abundance (ind.m^{-3}). Metazoan microzooplankton (Micro) abundance was calculated at Tasdon filtering 6 L of water with a 63 μm mesh size net (table 1). Furthermore, heterotrophic prokaryote abundance (HTTP) was measured by flow cytometry of a 1.5 mL water sample and heterotrophic protozoan (Proto) by flowcam. Primary production (PP) by size class (pico, nano and micro, in $\text{mgC.m}^{-3}.\text{h}^{-1}$) was only measured at L’Houmeau using Nielsen’s (1951) radioactivity protocol (table 1). For further information about identifying and measurement methodology, see Moncelon (2022) and Bergeon et al. (2023).

2.2.4. Statistical analysis

Statistical analysis was performed using R software (version 4.2.3.). As data did not respect a normal distribution (Shapiro-Wilk, $p\text{-value} < 0.05$), non-parametric test had to be held (packages: rstatix (Kassambara, 2019), ggbreak (Xu et al., 2021)). Chla biomass and PP by size class, HTTP, Meso abundance (plus Micro and Proto in Tasdon), nutrients and DOC (L’Houmeau) or PIM-POM (Tasdon) differences were tested with one way or two ways Kruskal-Wallis (for non-parametric analysis), followed by a Dunn’s post hoc test (package: dunn.test (Dinno and Dinno, 2017)) when necessary (if Kruskal-Wallis test presented a $p\text{-value} < 0.05$). The same method was applied to search for the differences between day / night CO_2 flux, $p\text{CO}_2$, $\text{O}_2\%$ and wind speeds within each month.

A hierarchical agglomerative clustering (HAC) was used to identify the food web type (packages: FactoMineR (Lê et al., 2008), factoextra (Kassambara and Mundt, 2020), cluster (Maechler, 2018), ade4 (Thioulouse et al., 1997), agricolae (De Mendiburu, 2020)). For this analysis, the Euclidean distance was used to measure the distance among groups, followed by to the Ward method (D1 or D2) as described in Masclaux et al. (2014). Each of the biological parameters was transformed to carbon biomasses ($\mu\text{g C.L}^{-1}$) (from HTTP, Chla by size class (micro, nano, pico) and metazoans (Micro and Meso), table 1). Later on, at L’Houmeau, a PP/Chla biomass for each size class ratio was calculated to see the photosynthetic efficiency and the predation pressure of Chla by fraction.

In order to summarize and understand the dimensionality between planktonic food web with environmental factors water CO₂ variables, a Principal Component Analysis (PCA) (package: vegan (Dixon, 2003)) were performed (only for L'Houmeau due to a lack of data at Tasdon per station). As the continuous multiparameter sensor was not able to measure O₂% during the month of March, PCA analysis were made with O₂% discrete measures (dissolved oxygen from VWR multimeter). A Kendall test was achieved between each parameter to see if these relationships were significant.

3. Results

3.1. L'Houmeau salt water marsh

3.1.1. Monthly variations of environmental parameters

Salinity and temperature values increased from 26.38 ± 0.09 and 11.51 ± 0.47 °C respectively in March to a salinity of 34.28 ± 0.06 in July and a temperature of 25.02 ± 0.31 °C in June. Turbidity's values did not present a seasonal pattern, with the highest and lowest values recorded during August and March (34.44 ± 72.77 NTU, 9.38 ± 2.61 NTU, respectively). DOC presented weak values at L'Houmeau, increasing from the beginning of the sampling period (0.54 ± 0.02 mg.L⁻¹, March) until the end (3.63 ± 0.07 mg.L⁻¹, August) (table 4.A, annex 8.2.).

No clear trend was observed for NO₃, NO₂, NH₄, PO₄ and Si (table 4.A, annex 8.2.). Both NO₃ and NH₄ reached their maximum values in April (22.09 ± 1.41 µmol.L⁻¹ and 5.30 ± 1.86 µmol.L⁻¹ respectively) and their lowest values in June (0.00 µmol.L⁻¹ and 0.09 ± 0.06 µmol.L⁻¹ respectively). NO₂ also presented a minimum value in June (0.20 ± 0.08 µmol.L⁻¹), but its highest value in July (2.26 ± 1.41 µmol.L⁻¹). PO₄ concentrations increased continually along the whole study period, from 0.13 ± 0.01 µmol.L⁻¹ in March to 1.42 ± 0.02 µmol.L⁻¹ in August. Lastly, Si varied from 33.67 ± 0.44 µmol.L⁻¹ in March to 45.48 ± 0.39 µmol.L⁻¹ in June (table 4.A, annex 8.2.).

3.1.2. Water pCO₂, water-air CO₂ flux, water O₂ and wind speed variations

At L'Houmeau saltwater marsh, pCO₂ values remained slightly oversaturated in comparison with the atmospheric equilibrium (417 ppm) during the whole study period (between 541 (night) and 842 (day) ppmv). At the same time, CO₂ flux were always positive and a source for the atmosphere. A seasonal and inversed-correlated trend was found between pCO₂ and O₂%, with the highest pCO₂ and lowest O₂ % values measured in May (843.15 ± 8.11 ppmv, $68.74 \pm 1.68\%$ respectively) (figure 7.a,b). On the other hand, CO₂ fluxes and wind gust reached their peak values in April (7.32 ± 2.93 mmol.m⁻².h⁻¹, 11.40 ± 0.47 m.s⁻¹

respectively) and their minimum value in August ($0.13 \pm 0.02 \text{ mmol.m}^{-2}.\text{h}^{-1}$, $3.63 \pm 1.01 \text{ m.s}^{-1}$ respectively) (figure 7.c,d). Both pCO_2 , $\text{O}_2\%$, CO_2 flux and wind gust (only July and August) showed significant differences when comparing day versus night values (Kruskal-Wallis, $p\text{-value} < 0.05$), except for $\text{O}_2\%$ in July (Kruskal-Wallis, $p\text{-value} < 0.05$). Dunn's post hoc test showed that pCO_2 values from April had a positive correlation with the rest of the months ($p\text{-value} < 0.05$). The same pattern was found for CO_2 flux and wind gust but not for $\text{O}_2\%$. This last parameter showed an inverse trend compared to the three other parameters.

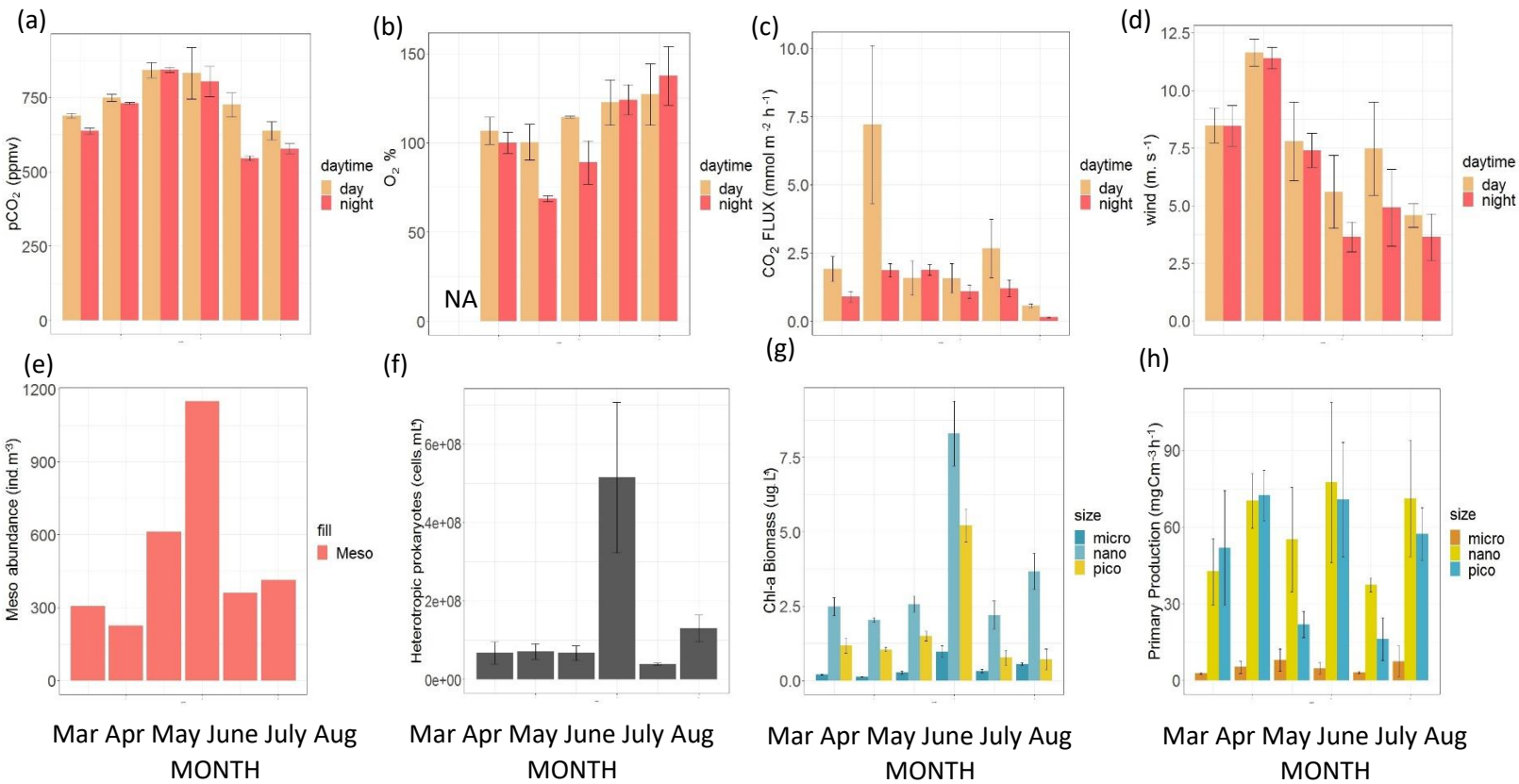


Figure 7. Monthly continuous measures and biological samplings at L'Houmeau (between March and August 2021) of (a) water CO_2 partial pressure (ppmv), (b) $\text{O}_2\%$ saturation, (c) estimated water-air CO_2 flux ($\text{mmol.m}^{-2}.\text{h}^{-1}$), (d) wind speed (m.s^{-1}), (e) Meso abundance (individus.m^{-3}), (f) HTPP abundance, (g) Chl-a biomass (mean \pm sd) by size class (micro: microphytoplankton ($>20 \mu\text{m}$), nano: nanophytoplankton ($3\text{-}20 \mu\text{m}$) and pico: picophytoplankton ($< 3 \mu\text{m}$)) and (h) Chl-a PP by fraction ($\text{mgC.m}^{-3}.\text{h}^{-1}$) (micro, nano, pico) (mean \pm sd). NA for $\text{O}_2\%$ measures during March because of a sensor issue.

3.1.3. Biological parameters variation and associated food web analysis at L’Houmeau salt marsh

During the month of June, Chla biomass, Meso and HTTP abundances were maximal (Chla: 10.37 $\mu\text{g.L}^{-1}$, Meso: 1149.30 ind.m^{-3} , HTTP: 7.48×10^5 cells.mL^{-1}) (figure 7.e,f,g). In opposite, the lowest Chla biomass, Meso abundance were found during April (Chla = 0.12 $\mu\text{g.L}^{-1}$, Meso = 225.35 ind.m^{-3}) (figure 7.e,g), and HTTP both in July (3.92×10^4 cells.mL^{-1}) (figure 7.f). These three biological parameters presented significant differences on a monthly scale (Kruskal-Wallis, p-value < 0.05). Particularly, Chla nano and pico fractions were always positively correlated but did not present any significant difference, yet the Chla micro had an inversed correlation with nano and pico (Dunn’s post hoc test, p-value < 0.05).

PP results did not present the same trend as biotical parameters, but they matched with their maximum values in June (figure 7.d). For the whole study period, the smaller forms of phytoplankton were the most productive (e.g. nano value in April: 77.45 ± 31.25 $\text{mgC.m}^{-3}.\text{h}^{-1}$), while micro PP remained the lowest producer among all forms from March until August (figure 7.d). No significant differences were found between months and sizes class PPs (Kruskal-Wallis, p-value > 0.05) besides from a negative difference between Chla micro and nano values in March and April (Dunn’s post hoc test, p-value < 0.05).

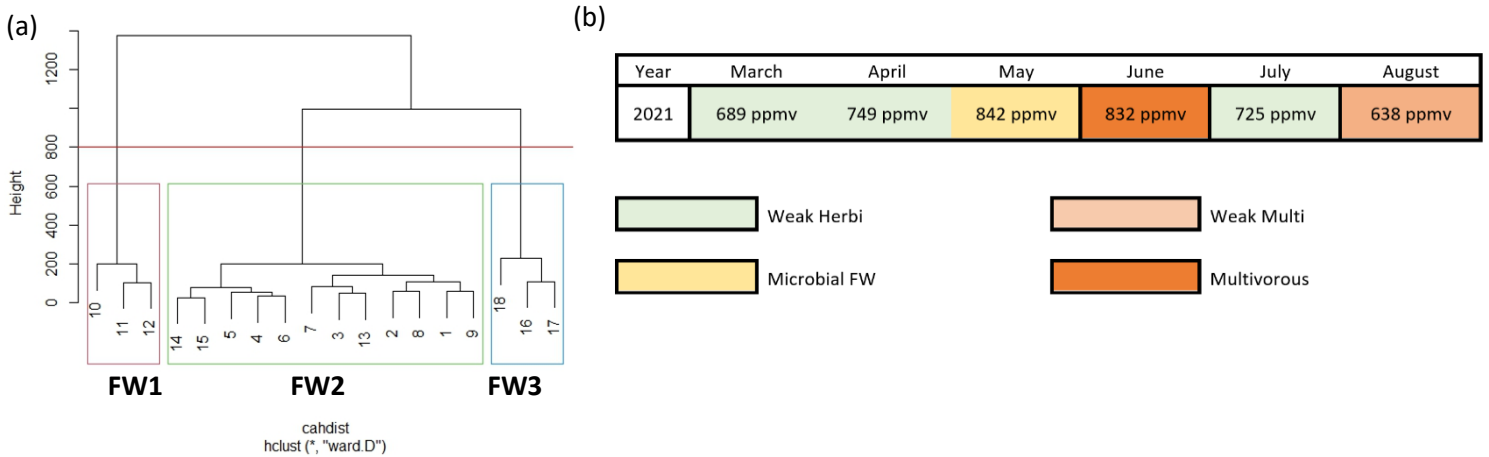


Figure 8. (a) Clustering Dendrogram for the HAC as applied to the biological matrix. There are three different food webs (FW1, FW2, FW3) defined by the cutting method “Ward.D1” (red line). Each number represents a replicate (1 to 3: March (FW2), 4 to 6: April (FW2), 7 to 9: May (FW2), 10 to 12: June (FW1), 13 to 15: July (FW2), 16 to 18: August (FW3)). (b) food web nuances by month with their respective pCO₂ mean value (ppmv).

To prove the photosynthetic efficiency of Chla fraction, a PP vs biomass ratio (P/B) was achieved (table 2). All three sizes had their greatest P/B ratio values during June (micro: 27.47, nano: 12.65, pico: 11.16) (table 2). Even though nano and pico presented a large PP contribution along the whole studied period (figure 7.h), micro presented the highest P/B ratio most of the time (9 measures out of 18). To find out which food web was producing more efficiently, the P/B ratio was calculated for each one separately. Despite the fact that FW3 had the highest PP values (figure 9), FW1 was the most presented the largest P/B ratio, showing a strong productive efficiency (FW3: 2.18 vs FW1: 17.40, table 2).

Table 2. PP/Biomass ratio for all the three phytoplankton sizes. Num: each number represents a replicate (1 to 3: March (FW2), 4 to 6: April (FW2), 7 to 9: May (FW2), 10 to 12: June (FW1), 13 to 15: July (FW2), 16 to 18: August (FW3)). Each color represents a food web (FW1: red, FW2: green, FW3: yellow). Efficient production > 0 (in bold), not efficiently < 0. At right the P/B ratio for each food web types is shown.

Num	Month	Food Web	P/B micro	P/B nano	P/B pico	P/B micro	P/B nano	P/B pico
1	Mar	FW2	0.92	1.90	0.46	3.17	2.07	1.36
2	Mar		10.36	1.43	1.69			
3	Mar		1.85	1.91	0.50			
4	Apr		0.67	2.14	3.41			
5	Apr		0.51	1.08	2.17			
6	Apr		0.00	3.47	2.02			
7	May		0.88	0.76	1.05			
8	May		4.19	2.00	2.43			
9	May		11.07	5.15	0.62			
10	June	FW1	17.12	12.65	11.16	17.49	11.17	6.60
11	June		27.47	12.20	0.0			
12	June		7.60	8.66	8.64			
13	July		0.64	1.35	0.84			
14	July		0.00	2.27	0.44			
15	July		6.96	1.42	0.70			
16	Aug	FW3	1.80	0.83	0.00	2.18	0.60	0.23
17	Aug		3.58	0.56	0.50			
18	Aug		1.16	0.40	0.18			



Figure 9. *Box plot* displaying the mean per food web type for Chla by size class, Meso, HTTP and PP by fraction used for the HAC analysis. *Box plot* labelled with the same letters are not significantly different (ANOVA followed by Fisher's LSD). All biotic variables have the same unity ($\mu\text{gC}\cdot\text{L}^{-1}$) but scales were different. In addition, *Box plot* with pCO_2 , CO_2 flux and O_2 % mean per food web were added.

At L'Hourmeau salt marsh, the results from the HAC analysis allowed us to identify three different planktonic food web types, named FW1, FW2 and FW3 (figure 8.a). June's food web (FW1) was characterized as a 'multivorous' food web, thus it presented the highest carbon biomasses for all three fractions of Chla, Meso, HTTP and DOC, as well as low nutrients values (NO_3 , NO_2 , PO_4 and NH_4) (figure

9). Inside FW2, a temporal food web succession with three different food webs were described (Dupuy personal communication). First a ‘weak herbivore’ formed in March and April, due to important nutrient concentrations, a low Meso biomass and relatively high microphytoplankton production (figure 8.b, 9). In May, a ‘microbial food web’ was found, since DOC was starting to accumulate thanks to the Chla PP at the same time that a weak Meso appearance. July was also described as ‘weak herbivorous’ (figure 9.b). Lastly, FW3 was target as a ‘weak multivorous’ (August), because it had very high Chla production for all three sizes, but lower biomasses “planktonically” speaking, especially Meso and HTTP, as well as great nutrients concentrations.

3.1.4. Temporal variations of biogeochemical parameters along food web typologies

Analyzing figure 8.b, an association between high pCO₂ value (832 ppmv) and the ‘multivorous’ food web type can be found. Likewise, the ‘very weak multivorous’ seems to be related to the weakest pCO₂ values found (638 ppmv), but no association appeared with FW2 because of the great (FW, pCO₂) variability inside this food web type. However, as certain food web nuances were found inside FW2, so association can be done with each food web type separately. For instance, the ‘microbial food web’ was present when pCO₂ values were at their maximum (842 ppmv), while the ‘weak herbivorous’ food web type were mainly associated with lower pCO₂ values (figure 8.b).

Results from the principal component analysis are shown in figure 10. The first two principal components (PC1 and PC2) explained 66.85 % of the variability of data. This plotting allowed to create a monthly and food web discrimination graphic against every parameter used (biotic and abiotic). A seasonal gradient can be distinguished along the first component, with the summer season being placed at left (maximal temperatures) and winter at right. HTTP, Meso, Chla, CO₂ flux, NO₃ and wind were the principal components of PC1, whereas PC2 was composed mainly by PO₄ and turbidity. A high level of Chla, Meso and HTTP seemed to be associated with increasing pCO₂ and PP. Likewise, all biotical factors are related to FW1, which represent the month of June (figure 8.b and 10). At the same time, this seasonal gradient also highlighted a decrease in O₂ % saturation and in CO₂ flux at that month.

Kendall correlation tests results did not show a significant correlation between pCO₂ and biotic parameters (p-value > 0.05). Unlike this result, significant negative correlation between the three biotic parameters and CO₂ flux were found (p-value < 0.05). Chla was also positively correlated to Meso abundance and PP, but negatively with O₂% and nutrients (p-value < 0.05). A negative correlation between Meso and O₂%, NO₃ and NO₂ were found (p-value < 0.05), yet a positive one appeared for Meso and HTTP (p-value < 0.05). The only additional significant negative correlation of HTTP was with NO₃ (p-value <

0.05). As expected, CO₂ flux was positively related with wind gust (p-value < 0.05). pCO₂ and CO₂ flux did not show a significant correlation (p-value > 0.05). Lastly, pCO₂ was negative related to turbidity and positively with DOC (p-value < 0.05).

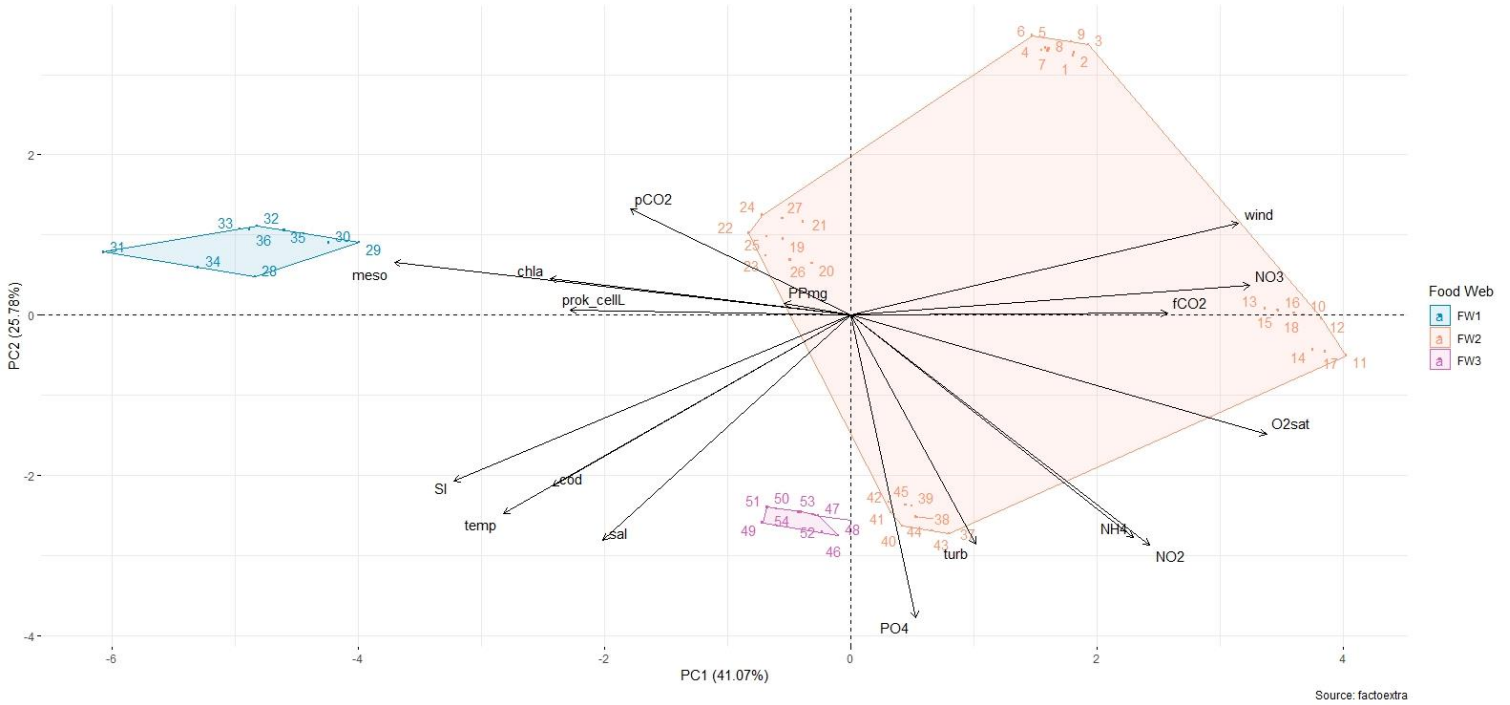


Figure 10. Principal Component Analysis of abiotic (DOC, Si, temperature, salinity, PO₄, NO₂, turbidity, NH₄, O₂% saturation, NO₃, flux CO₂, wind gust and pCO₂) and biotic parameters (PP, Chla biomass, Meso and HTTP) at l’Houmeau site between March 2021 and August 2021. Food web types are represented by different colors and months by group of numbers (1 to 9: March, 10 to 18: April, 19 to 27: May, 28 to 36: June, 37 to 45: July, 46 to 54: August).

3.2. Tasdon freshwater marsh

3.2.1. Seasonal environmental parameter variations

Environmental parameters as well as nutrients values for the seasonal monitoring in Tasdon during the year 2019 and 2021 are presented in table 5.A. Both salinity and temperature presented a seasonal pattern, with its maximum value during summer 2021 (7.96 ± 0.20 (T6), 23.42 ± 2.00 °C (T7), respectively), whereas salinity had its lowest value during spring 2019 (0.31 ± 0.02 (T2)) and temperature during autumn 2021 (6.87 ± 0.77 °C (T2)). A similar pattern was found for both turbidity, PIM and POM, with maximum

values during summer 2021 at T2 (178.22 ± 5.33 NTU, 183.03 ± 9.23 mg.L⁻¹, 23.93 ± 0.29 mg.L⁻¹, respectively) and minimum values during spring 2019 (turbidity: 20.61 ± 1.94 NTU (T6)) or at T2 during autumn 2019 (PIM: 9.79 ± 2.02 mg.L⁻¹, POM: 2.06 ± 0.32 mg.L⁻¹).

Nutrients did not share a similar pattern along the sampling period at Tasdon freshwater marsh (table 5.A, annex 8.3.). NO₃ presented a large decrease from 2019 (1265.87 ± 99.43 μmol.L⁻¹) to 2021 (342.67 ± 3.55 μmol.L⁻¹) with its lowest NO₃ value being 12.87 ± 3.53 μmol.L⁻¹ during the autumn of 2021. On the other hand, NO₂ increased after renaturation, and it presented both its highest and lowest concentrations in autumn 2021 but at different stations (9.45 ± 1.19 μmol.L⁻¹ (T7), 0.43 ± 0.03 μmol.L⁻¹ (T2)). PO₄ concentrations' remained between 0.00 and 0.90 μmol.L⁻¹, except for winter 2021, site T7 (4.18 ± 4.00 μmol.L⁻¹). On the contrary, Si showed its lowest value during winter 2021 at site T7 (14.95 ± 5.53 μmol.L⁻¹) and the maximum in summer, station T2 (429.05 ± 19.33 μmol.L⁻¹). Lastly, NH₄ rose between before and after renaturation at T2 (2019: 3.37 ± 0.37 μmol.L⁻¹ vs 2021: 22.32 ± 1.33 μmol.L⁻¹).

3.4.2. Water pCO₂, water-air CO₂ flux, water O₂ and wind speed variation

At Tasdon freshwater marsh, great fluctuation in pCO₂, CO₂ flux, O₂% and wind gust were found between seasons and stations (figure 11.a,b,c,d). A decrease in pCO₂ and CO₂ flux was found between 2019 and 2021. In particular, water pCO₂ at Tasdon varied largely in all three stations, but the main difference was found at T6, which shifted from pCO₂ over saturated (3463 ± 54 ppmv) to under saturated waters (142 ± 27 ppmv) (figure 11.a). The greatest CO₂ flux difference was found at station T2, with its highest value during autumn 2019 (167.76 ± 27.04 mmol.m⁻².h⁻¹) and the lowest at T7 in summer 2021 (-3.70 ± 2.37 mmol.m⁻².h⁻¹) (figure 11.b). Wind gust followed a similar pattern to pCO₂, except at T7 (figure 11.c). On the other hand, in summer 2021, O₂% seemed to have lower values in T2 than the other two stations (41.82 ± 4.04 %) (figure 11.d). Every site was significantly different from the other, plus T6 and T7 always presented inversed correlation (Dunn's post hoc test, p-value < 0.05). All four parameters had significant differences between day/night periods (Kruskal-Wallis, p-value < 0.05), except for CO₂ flux during spring, summer and winter 2021 at T2 and every seasons of T7; pCO₂ values in winter at station T6; winter values for wind gust at the three stations and 2019 spring O₂% day/night measures at T2 and T7 (Kruskal-Wallis, p-value > 0.05).

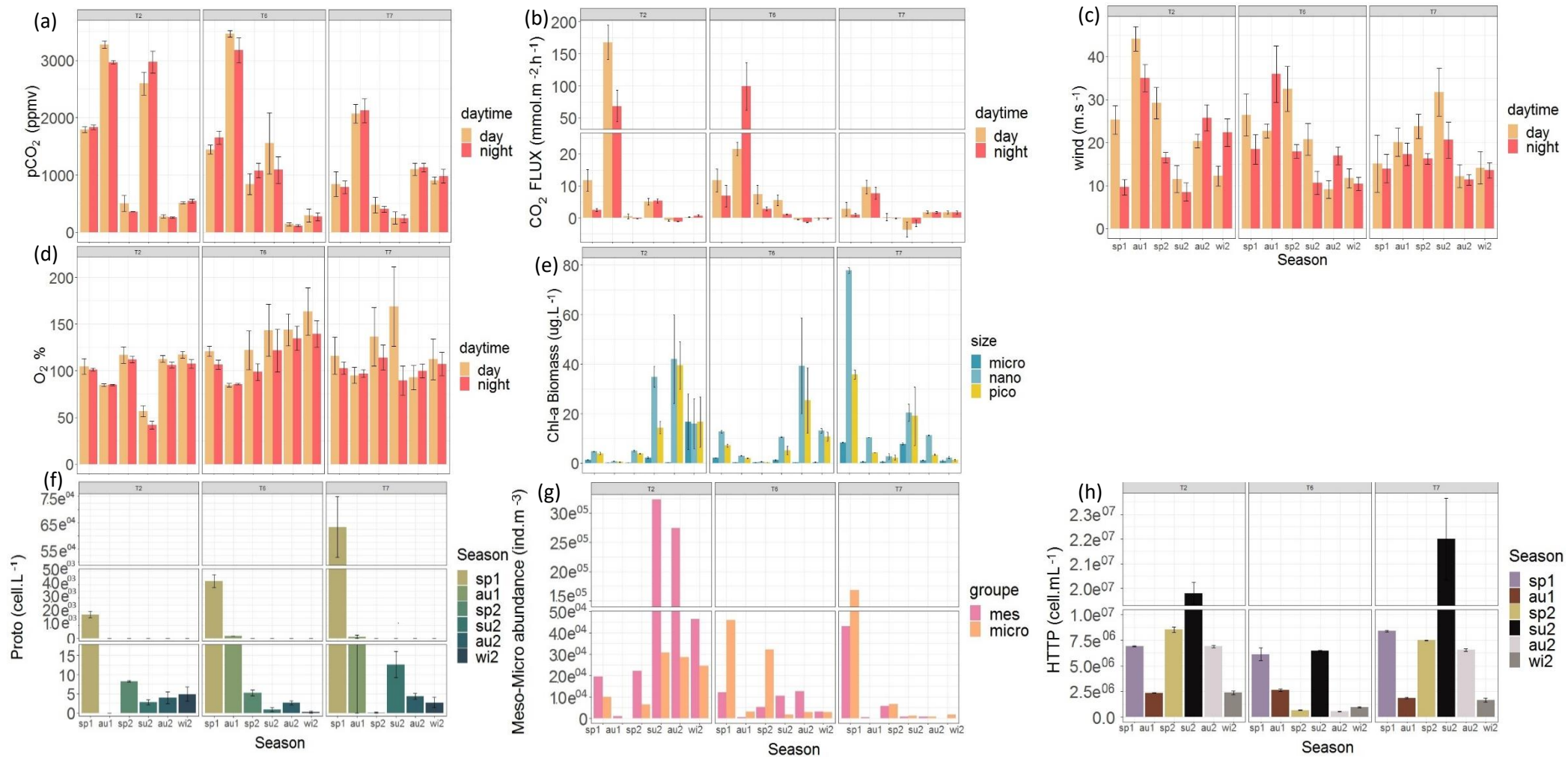


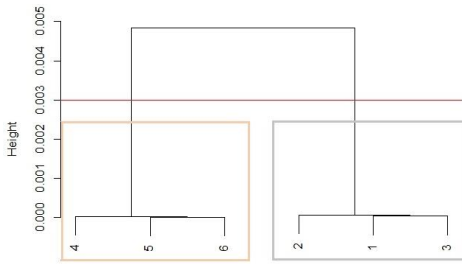
Figure 11. (a) Water CO₂ partial pressure (ppmv), (b) estimated water-air CO₂ flux (mmol.m⁻².h⁻¹), (c) wind speed (m.s⁻¹), (d) O₂ % saturation, (e) Chl-a biomass by size class (micro: microphytoplankton (>20 μm), nano: nanophytoplankton (3-20 μm) and pico: picophytoplankton (< 3 μm)), (f) protozoa heterotrophic (cells.L⁻¹), (g) Micro and Meso abundance (individus.m⁻³) and (h) HTPP abundance (cells.mL⁻¹) (mean ± sd) at Tasdon seasonal sampling (spring and autumn 2019: sp1, au1, spring, summer, autumn and winter 2021: sp2, su2, au2, wi2).

3.4.3. Biological parameter variations and associated food web analysis at Tasdon freshwater marsh

Biotic parameters' seasonal distribution at Tasdon presented a great variation between stations (figure 11). For instance, during spring 2019 and 2021 at station T2, Chla, Meso, Micro had low biomass/abundances, while the rest of the season of 2021 showed a higher biomass of Chla, mostly nano and pico. At T6, their tendencies matched greatly those at T2, whereas T7 had its abundance/biomass peak during spring 2019, followed by a decrease of biomass at every season and size class (figure 11.e.g). During spring 2019 at all three stations, Proto abundance peaked, with a great decrease after renaturation (figure 11.f). Lastly HTTP always had its greatest abundance during summer and the lowest during winter, excluding autumn 2021 at T6, where HTTP minimal value was found (figure 11.h). Significant negative differences were observed between Chla micro and nano at every station and season (Dunn's post hoc test, p -value < 0.05), except for T2 in winter and for T7 in spring, summer and winter 2021 (Dunn's post hoc test, p -value > 0.05). Meso, Micro, HTTP and Proto abundances had significant differences between stations and seasons (Dunn's post hoc test, p -value > 0.05).

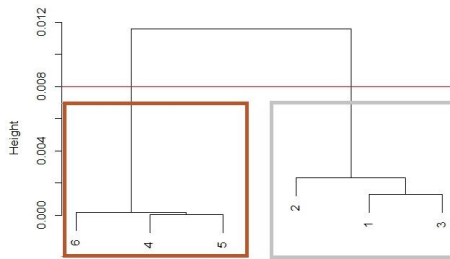
Since a large variability was found between each station, the Hierarchical Agglomeration Clustering analysis was held separately for sites T2, T6 and T7. Despite the fact that this method used found two different food webs per station (T2, T6 and T7), certain nuances were found inside some food webs (figure 12). In spring before renaturation, all three stations presented a 'multivorous' (or 'weak multivorous') food web (FW1.b), meanwhile in autumn only 'biological winter' food web (FW3.b) were seen. After renaturation, station T2 was separated in two different 'multivorous' food webs: FW1.b (from spring: 'weak multivorous' to summer and autumn: 'multivorous'), with fluctuant biomasses of all biological variables, but with important nutrients values and FW2.b (winter: 'multivorous (with low nutrients)') who had higher biological biomasses but lower nutrient concentrations (figure 15A, annex 8.4.). On the other hand, station T6 was built by FW3.b (spring 2021), a 'biological winter' created by only predators' biomasses and some nutrients and FW4.b. Two typologies were found inside FW4.b: a 'weak multivorous' food web in summer (high values of more Chla, low presence of predators, HTTP and fluctuating nutrients concentration) and 'weak herbivorous' food web during autumn and winter (figure 15A, annex 8.4.). Lastly, T7 was divided in FW5.b (spring and winter 2021), conformed by a 'weak multivorous' food web and a 'biological winter', and a clear 'microbial food web' (summer and autumn 2021) (figure 15A, annex 8.4.).

T2 2019



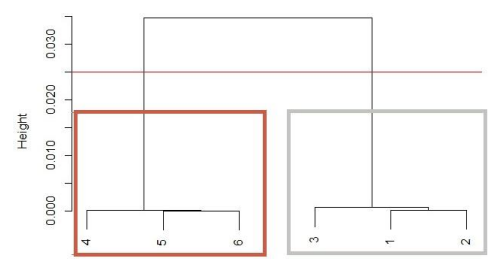
HAC_LH_T2.ch
hclust("ward.D2")

T6 2019



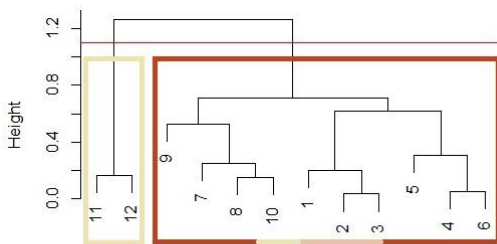
HAC_LH_T6.ch
hclust("ward.D2")

T7 2019



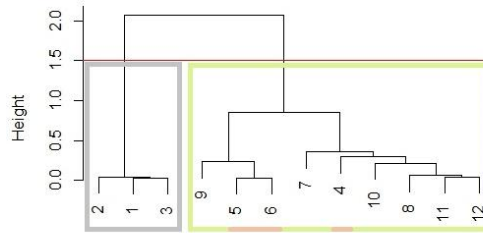
HAC_LH_T7.ch
hclust("ward.D2")

T2 2021



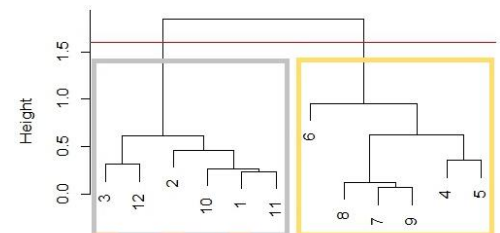
HAC_LH_2.ch
hclust("ward.D2")

T6 2021



HAC_LH_2.ch
hclust("ward.D2")

T7 2021



HAC_LH_2.ch
hclust("ward.D2")

Year	Sites	Spring	Summer	Autumn	Winter
2019	T2	1793 ppmv		3274 ppmv	
2019	T6	1444 ppmv		3464 ppmv	
2019	T7	841 ppmv		2068 ppmv	
2021	T2	407 ppmv	3020 ppmv	298 ppmv	606 ppmv
2021	T6	971 ppmv	1402 ppmv	127 ppmv	299 ppmv
2021	T7	446 ppmv	304 ppmv	1136 ppmv	959 ppmv



Bio Wint



Multi (- Nutri)



Weak Herbi



Weak Multi

Figure 12. Up: Clustering Dendrogram for the HAC as applied to the biological matrix at Tasdon stations (T2, T6, T7) in 2019 and 2021. There are two different food webs per station defined by the cutting method “Ward.D2” (red line). Each number represent a replica (in 2019: 1 to 3: spring, 4 to 6: autumn; in 2021: 1 to 3: spring, 4 to 6 summer, 7 to 9: autumn, 10 to 12: winter). Down: food web nuances by month with their respective pCO₂ (ppmv) mean value.

At this freshwater marsh, before renaturation (2019), the highest pCO₂ values were always associated with ‘biological winter’ food web type (figure 12). During the year 2021, at T2 station, the highest pCO₂ value (3020 ppmv) coincided with a ‘multivorous’ food web, while at T6 the largest measure of pCO₂ was associated to a ‘weak multivorous’ food web (1402 ppmv), followed by a ‘biological winter’ (971 ppmv) (figure 12). Lastly, both the highest and lowest pCO₂ peaks at T7 were associated with the ‘microbial food web’, and the second largest pCO₂ value occurred with a ‘biological winter’ food web (figure 12).

The Kendall correlation test for biotic and abiotic parameters showed that, during the year 2019, at three sites (T2, T6, T7), Chla, Meso, Micro, HTTP and Proto had a positive relationship with each other, as well as O₂% (Kruskal-Wallis, p-value < 0.05). On the other hand, biotic parameters were negatively correlated with pCO₂, CO₂ flux values at the three stations (Kruskal-Wallis, p-value < 0.05). Again, at stations T2, T6 and T7, both CO₂ flux and pCO₂ were positively associated with one another, while they had a negative correlation with temperature and O₂% (Kruskal-Wallis, p-value < 0.05). Contrary to 2019, correlations after renaturation did not present a similar pattern within stations, except for Chla’s with CO₂ flux, which was negative for all three stations (Kruskal-Wallis, p-value < 0.05) and a positive correlation between pCO₂ and CO₂ flux (Kruskal-Wallis, p-value < 0.05).

4. Discussion

4.1. Marsh typology as carbon sinks around the globe

‘Blue Carbon’ ecosystems are not only important from an ecological point of view, but also for economy and society by acting as regulatory systems. This aptitude lies on their capacity to limit flooding risks, improve water quality, favor biodiversity and store large amounts of carbon in their soils and biomass (Duarte et al., 2005, 2013; Monnoyer-Smith, L., 2019). Both salt and freshwater marshes can behave as carbon sinks (Guo et al., 2010; Schäfer et al., 2014; Kostyrka 2021) or carbon sources (Kayranli et al., 2009) depending on spatial (typology, water, sediment compartments) and temporal (diurnal, tidal, seasonal etc.) scales. Furthermore, Artigas et al. (2015), Miller and Fuji (2011) and Tuittila et al. (1999) remarked that restored wetlands, e.g. marshes, deltas or peatlands, can changed from a CO₂ source to sink behavior (in Artigas et al. (2015) CO₂ flux during mid-July: -48.42 mmol.m⁻².h⁻¹) leading to a decrease of greenhouse gases and so on global warming as well. On the contrary, Jimenez et al. (2012) saw that anthropogenic disruption (driven-hydrologic changes) made a freshwater marsh shifting from a strong CO₂ sink changes into a CO₂ small source. In this study for instance, Tasdon renatured freshwater marsh presented, after renaturation, lower CO₂ source values with even some CO₂ sink behavior according to stations and seasons (like at station T7 with input of salt water during the summer of 2021: -3.70 ± 2.37 mmol.m⁻².h⁻¹), whereas L’Houmeau salt water marsh remained a CO₂ source during the whole study period.

4.2. Environmental and water CO₂ relationships with biotic factors and food web typologies at L'Houmeau salt marsh

As mentioned before, from March until August of 2021, L'Houmeau salt marsh remained a weak carbon source, presenting oversaturated pCO₂ waters (between 600 and 900 ppmv). Both temperature (TpCO₂) and non-temperature (NtpCO₂) effects influenced water pCO₂ values in coastal systems such as L'Houmeau marsh, though NtpCO₂ seemed to have a greater impact on measured pCO₂ (data not shown). Non temperature effects on pCO₂ can be linked to environmental factors like salinity, DO (i.e. advection processes, etc.) or biological factors, (i.e. photosynthesis and microbial respiration processes) that took place at L'Houmeau marsh as well. Mayen et al. (submitted) showed that horizontal (upstream and downstream) advection processes can have a great influence on pCO₂ dynamics in nearby salt marshes of the Fier d'Ars (Ile de Ré). Biotic parameters were also important in pCO₂ control at L'Houmeau marsh as endorsed by O₂% values inversely related to pCO₂ values from March to August 2021 implying a rather low phytoplankton production and a greater respiration according to our measurements.

L'Houmeau saltwater marsh presented a relatively low Chla biomass (> 8 µg.L⁻¹) for a marsh mainly dominated by nano and pico size fractions. These results coincide with previous data which showed that saltwater marshes tend to present lower Chla biomasses than freshwater ones (Tortajada et al., 2011). There are many factors that may influence Chla biomass, like temperature, salinity, luminosity as well as nutrient concentrations. For instance, saltwater marshes are mainly filled up with oceanic waters, which usually have limited nutrient concentrations (Arrigo, 2005). Similarly, it also could be linked to the monthly water renewal at L'Houmeau salt marsh, this washing up process along Chla consumption decreasing nutrient concentration in turn. Furthermore, other organisms could compete for nutrients in salt marshes, like microphytobenthos (Sand-Jensen and Borum, 1991) and each planktonic Chla size fractions for instance.

With regards to grazing pressure, in this study, both Chla, Meso and HTPP “bloomed” during June 2021, while nutrient concentration was at its lowest point, which suggest a clear prey-predator chain. Unfortunately, as there was missing data on other predators as Micrometazoan organisms and Protozoan abundances, no clear further perception on this trophic web could be given. Anyhow, the relationship between PP and Chla size classes could indicate that all three Chla fractions were consumed and not accumulated in biomass. This result coincides with the study of Dupuy et al. (2011) in the same marsh, who saw that HTPP growth was correlated with planktonic bloom.

Although no significant correlations between pCO₂ and biological factors were found, relationships between the food webs and water pCO₂ were clearly established during our study. Three different food web typologies, with some nuances inside them were found at L'Houmeau saltwater marsh between March and

August 2021: a ‘multivorous’ in June (FW1) with high pCO₂ values, a ‘weak multivorous’ with lower pCO₂ values during August (FW3), a ‘weak herbivorous’ in March, April and July (FW2) and a ‘microbial food web’ in May (FW2) both associated to variable pCO₂ values. These food webs have been previously described by Legendre and Rassoulzadegan (1996), Tortajada et al. (2011) and Masclaux et al. (2014) without any pCO₂ values as done here in the present study. Then, we cannot compare to the bibliography. However, Legendre and Rassoulzadegan (1996) explained that some planktonic food webs are more stable in time, as multivorous and microbial food web found more stable than others (i.e. herbivorous food web). Here at L’Houmeau marsh, the two stable food webs (‘multivorous’ and ‘microbial food web’) were associated with high pCO₂ values. This could either be explained by the great Meso and HTPP abundance and the weak PP (‘multivorous’) or the increase concentration of DOC in May (‘microbial food web’). Prairie et al. (2002) and Lapierre et al. (2013) have shown that DOC increments could directly affect pCO₂ values. On the other hand, the transitory food webs (‘weak herbivorous’ and ‘weak multivorous’) were associated with mid or lower pCO₂ values. These finding could implied that pCO₂ have a tendency to accumulate when there is a more stable food web and not a transition one.

4.3. Relationships between environmental parameters / water pCO₂ and biotic factors / food web typologies at Tasdon freshwater marsh

As others restored wetlands, Tasdon freshwater marsh changed its CO₂ values from strong carbon source to weak carbon source and sink during some periods. A similar result was found by Schäfer et al. (2014), where the studied restored urban tidal marsh (previously CO₂ source) happened to act as a CO₂ source during winter but a CO₂ sink in the summer. Many factors could influence this CO₂ decrease, such as environmental factors or biotic ones. It has been seen (Mayen, 2020, Bergeon et al., Mayen et al. in prep.) that NpCO₂ have a great influence at Tasdon marsh as well, and sometimes even more important than temperature effects (TpCO₂) (figure 13). The NpCO₂ could be linked to the replanted vegetation (63.000 aquatic plants), the nutrient concentrations, the salinity changes (at T7) or the increase of Chla phytoplankton biomass.

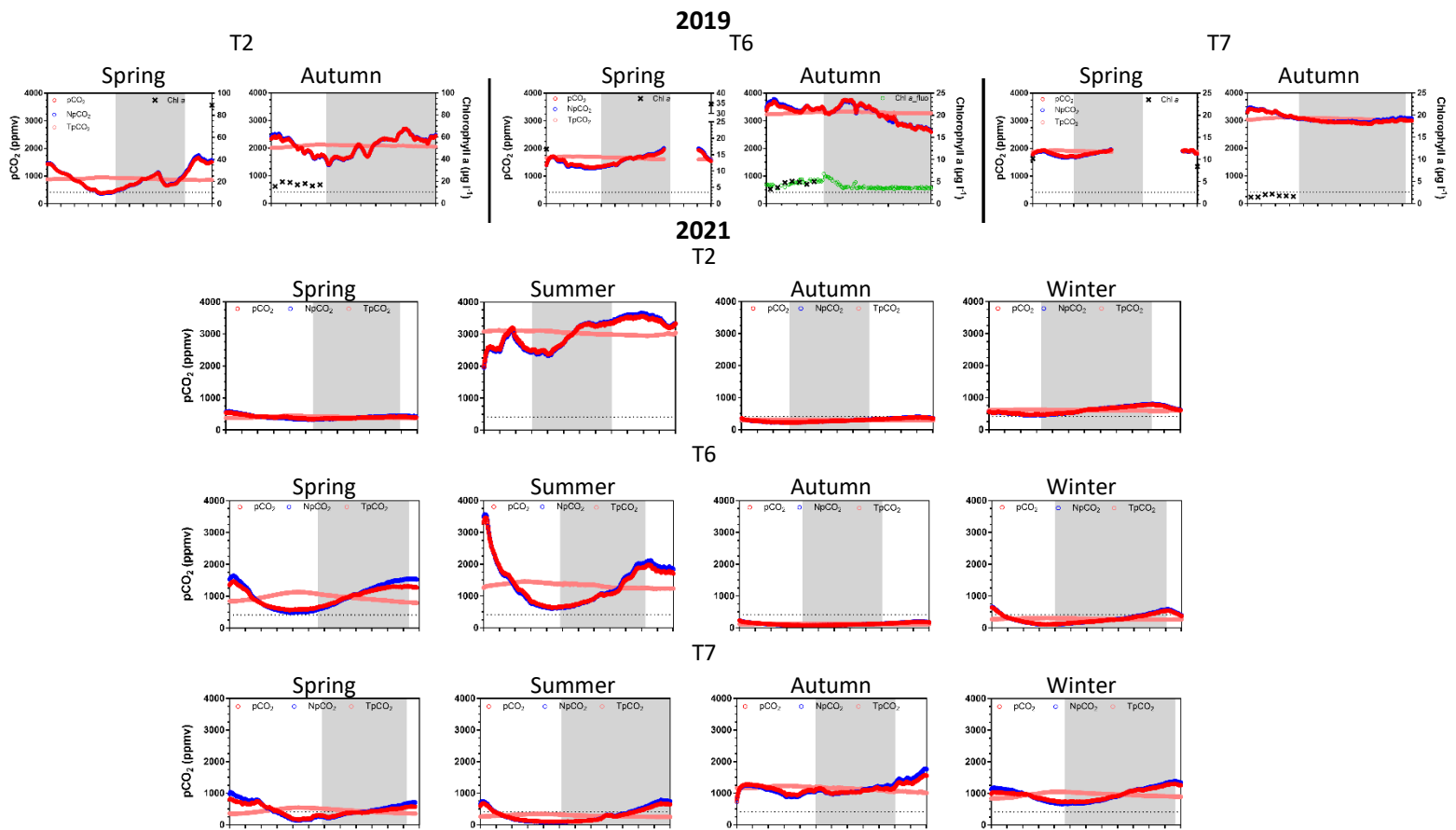


Figure 13. Water pCO₂ (red), NpCO₂ (blue) and TpCO₂ (pink) curves at Tasdon during the day (white) and night (grey) per station (T2, T6 and T7) before (2019) and after (2021) renaturation per season. Figure modify from Bergeon et al. (in prep).

When comparing all three stations, a globally similar pattern between T2 and T6 biotic and abiotic parameters was seen. For instance, after renaturation, both T2 and T6 showed a great Chla increase biomass, while T7 had an inverse trend. Likewise, stations T2 and T6 (autumn) presented an increase of both Meso and Micro, while at T7, abundances of Meso and Micro decreased. On the other hand, after renaturation, both T2 and T6 nutrient concentrations decreased greatly. This nutrient decrease could be associated to the freshwater marsh reducing nutrients capacity (Verhoeven et al. 2006) or to the Chla biomass' rose and, potentially, a higher PP. Schindler et al. (1997), Cole et al. (2000) and Pacheco et al. (2013) saw that a high nutrient source could help incrementing autotrophic production, followed by a better CO₂ sequestration and uptake. Contrarily to Adamczyk and Shuring (2015) results obtained in a San Diego freshwater reservoir, a negative relationship between both pCO₂ and CO₂ flux and biotical factor was found in our study, indicating a possible regulation of carbon dynamics by biological factors. Another difference between T7 and the other two stations, was that it's the only one receiving direct salt water from the Ocean. This is an

essential factor, because it has modified T7 salinity (max S values below 10) and it may be one of the causes of lower Chla biomass. A remarkable result was that, for all three stations, nano and pico Chla fraction sizes presented higher biomasses than micro, coinciding with L'Houmeau saltwater marsh, even when T7 was the only one connected to the Sea.

At Tasdon marsh before renaturation, a clear food web seasonality was found. Indeed, all three stations presented a sort of 'multivorous' / 'weak multivorous' food web during spring 2019 (as for L'Houmeau marsh), and during autumn 2019 only a 'biological winter' food web. All of the 'biological winters' were characterized by high nutrient concentrations and very weak biotic biomasses. The 'biological winter' food webs were always associated with the highest pCO₂ values. Nonetheless, T7 presented slightly higher biological biomass, which could explain its pCO₂ decrease (over 1000 ppmv) compared to the other two stations. On the other hand, no clear seasonality was seen in food web types during the year 2021 after this recent renaturation not allowing an equilibrium state of the marsh in turn. After Tasdon renaturation, the 'biological winter' food web found during spring at T6 and winter T7 were associated to high pCO₂ (971 and 959 ppmv respectively), whereas the 'weak herbivorous' seen from autumn to winter at T6 to the weakest pCO₂ values (127 and 299 ppmv). At T2, both the greatest and weakest pCO₂ values were attributed to the 'multivorous' food web. A possible explanation for this great difference would be that, during the summer 2021 (3020 ppmv), Chla nano and pico biomasses were lower than during autumn, plus HTTP and Meso biomasses were higher than autumn (298 ppmv). A similar justification could be given for the 'microbial food web' food webs found at T7, because very high Chla biomasses were found during summer 2021. No clear relation could be done between the 'weak multivorous' food webs and pCO₂ values.

4.4. Salt versus freshwater marsh food web typology comparison

The simultaneous study of two different marsh food web typologies at the same time allowed finding certain similitudes and differences between those sites from a carbon versus food web relationship point of view. Despite having different typologies, both L'Houmeau and Tasdon (before renaturation) were CO₂ sources, whereas Tasdon became a weaker source and sometimes sink of carbon after renaturation. Even though both marshes had different typologies (contrasting salinity values, nutrient concentration, water regulation/management), five food web typologies and associated pCO₂ values were clearly highlighted through our original approach. Three stable ones: 'biological winter', 'microbial food web', 'multivorous' food webs with high pCO₂ values at both sites and two transitory ones: 'weak multivorous' and 'weak herbivorous' with lower and more variable pCO₂ values. Four of these food webs (excepting 'weak herbivorous') were previously described in previous researches (Legendre et Rassoulzadegan, 1995;

Tortajada et al., 2011; Masclaux et al., 2014) though never in relationship with CO₂ dynamics and values as done here. However, two food webs were not seen in our study: ‘herbivorous’ and ‘microbial loop’ food webs and ‘biological winter’ food web was not found at L’Houmeau.

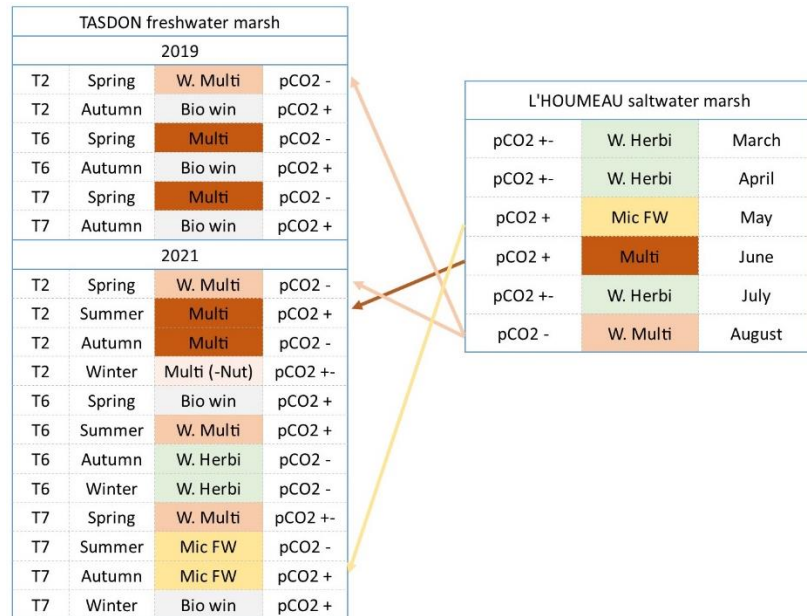


Figure 14. Food webs versus pCO₂ values respective relationships (arrow) at studied marshes (Tasdon and L’Houmeau).

Despite the fact that L’Houmeau and Tasdon environments are different, a general food web- pCO₂ relation could be drawn along specificities for both sites too. Nonetheless, it would not seem to be possible to characterize a single food web with a particular pCO₂ value. It is important to highlight that seasonality would seem to play an important role in both pCO₂ measures and food web typologies, implying that, in order to see a link between these factors, the sampling period remains highly important. Unfortunately, after renaturation at Tasdon, food webs did not go back to a ‘seasonal’ equilibrium state, preventing, maybe, a better or a clearer understanding of this environment. For instance, while L’Houmeau ‘microbial food web’ occurred in May, it was found during summer and autumn at Tasdon (figure 14).

4.5. Perspectives and advices for a more accreted understanding of the planktonic food web – water CO₂ relation

Even if a direct relation between a specific food web with a precise pCO₂ value was not found, important links were found. As this is the first registered study to have search for the link between plankton food webs and water carbon (CO₂), some adjustments could be made for improving this research:

- It would be important to carry out monthly samplings rather than seasonal ones if possible. Those samples should also be taken strictly simultaneously for biotic and abiotic parameters at each site.
- The following parameters for the food web construction need to be measured: Chlorophyll a biomass by size class, Mesozooplankton, metazoan microzooplankton, heterotrophic prokaryotes, heterotrophic protozoa abundances and biomasses Dissolved Organic Carbon, nutrient concentrations, Primary Production.
- pCO₂ measurements need to be acquired in parallel.
- The focus of this study was on the relationship between planktonic food webs and water carbon (CO₂). If the relation was not clearly found, potentially, the addition of benthic organisms (as macrofauna), macroalgae and other vegetation studies could be of great help to explain the water carbon (CO₂).

Furthermore, several perspectives related to this study are planned. For instance, there will be an upcoming follow up on Tasdon freshwater marsh as well as at Brouage marsh (Charente-Maritime) by the hand of MaVi program (INRAE and Région Nouvelle-Aquitaine).

5. Integration into working life

First of all, the results of this study will be presented at the “colloque de restitution du projet Pampas” in November 2023. Likewise, the possibility of writing a scientific is being considered due to the originality and innovative aspect of such approach.

On the other hand, I will be starting a PhD Thesis by the hand of my master’s internship director Christine Dupuy, as well as Cédric Gaucherel (INRAE, Montpellier) in December 2023. The PhD title is “Un modèle intégré du littoral et des marais de La Rochelle: comment atteindre la neutralité carbone sur le territoire ?”, and it will focus in the construction of ‘socio-ecosystems’. This is a very fulfilling perspective, because I will be able to mix both the recent acquired knowledges of this internship as well as all the information learned along the GLM master classes.

5.1. Chronogram of your work and/or missions

During these last six months, a wide range of activities were held, either to help other project (cytometry analysis or field work) (table 3). Being able to work both for my internship as well as for different projects (mostly LRTZC), helped me gather new and very valuable experience, both personally and humanly. Likewise, as my “data interpretation” time was achieved at the office, I was able to spend time with my co-workers and to see the functioning of each institution (both LIENSs and Ifremer).

Table 3. Weekly schedule of activities throughout the whole internship. Different activities are highlighted with different colors.

Week 1 - 3	Data interpretation and familiarization		
Week 4	Cytometry analysis	Data analysis	
Week 5	Data analysis and interpretation		
Week 6	Data analysis and interpretation	Field work (LRTZC)	Data analysis and interpretation
Week 7 - 8	Data analysis and interpretation		
Week 9	Data interpretation and stage report writing		
Week 10 - 12	Data analysis and interpretation		
Week 13 -14	Data interpretation and stage report writing		
Week 15	Data interpretation and stage report writing	Field work (LRTZC)	
Week 16 - 17	Data interpretation and stage report writing		
Week 18	Data interpretation and stage report writing (end of results and M&M)	Field work (LRTZC)	
Week 19 - 20	Data interpretation and stage report writing (end of results and M&M)		
Week 21 to 25	Report writing		

5.2. Personal remarks on the work of the company

Both LIENS and Ifremer were great places to work. Not only friendly but also open environments, which let me feel very comfortable.

5.3. Difficulties

Communicate in French, write in English and think in Spanish was sometimes hard. Also, as I am a “strict” with myself, I was (still am) scared of not being able to achieve this research goals. Likewise, the data used for this internship was sampled/measured previously by different people, it took me some time to integrate correctly all the data. Lastly, as it was a long time since I finished my first master, I was scared of not remembering how to used specific tools, such as R software correctly.

5.4. Internship, personal, academic and professional report

I was able to lean and enjoy this experience largely. Both Pierre and Christine were very helpful as well as the other researchers and students which whom I have spent time. I would happily recommend this place to any future student, either for a master’s internship or any other job possibility.

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7. Glossary

Biological acronyms

Chla:	Chlorophyll-a
Meso:	Metazoan mesozooplankton
Micro:	Metazoan microzooplankton
HTTP:	Heterotrophic prokaryotes
Proto:	Heterotrophic protozoan (ciliates, dinoflagellates)
DOC:	Dissolved organic carbon
PIM:	Particulate inorganic matter
POM:	Particulate organic matter

Geochemical abbreviations

NO ₃ :	Nitrate
NO ₂ :	Nitrite
PO ₄ :	Phosphate
Si:	Silica
NH ₄ :	Ammonium
CO ₂ :	Carbon dioxide

pCO ₂ :	Partial pressure of carbon dioxide
O ₂ %:	Oxygen precentral saturation

Unities

°C:	Celsius degree
g, mg, µg:	Gram, milligram, microgram
d, h, min, s:	day, hour, minute, second
km, m, cm,	Kilometer, meter, centimeter,
mm, µm:	millimetrer, micrometer
L, mL, µL:	Litre, millilitre, microliter
mol, mmol,	Molar, millimolar, micromolar
µmol, :	
NTU:	Nephelometric Turbidity Unit

8. Annexes

8.1. C-Sense probe calibration and CO₂ flux estimation equations

C-Sense probe values of pCO₂ are influenced by the total dissolved gas pressure (TDGP) in the water column, reason why calibration needs to be applied for outliers pCO₂ values. Later on, this correction was also employed considering both TDGP and atmospheric pressure (1009 hPa) and the measured pCO₂ by the C-Sense probe (gross values), as per equation $(pCO_{2meas.} \times 1009) / TDGP$ (Turner Designs). Over all 24-hour cycles performed at the seasonal and spatial scales, the corrected pCO₂ with TDGP were $2.37 \pm 0.95\%$ lower than the raw pCO₂ values (Bergeon et al., 2023). According to Polsenaere et al. (2013), CO₂ flux at the water-air interface were estimated using the following equation:

$$(1) FCO_2 = CO_2 solubility \times k \times [pCO_2(water) - pCO_2(atm.)]$$

With FCO_2 the CO₂ fluxes at the water-atmosphere interface (mmol.m².h⁻¹); $CO_2 solubility$ the CO₂ solubility coefficient in water (mol.Kg⁻¹.atm⁻¹); k the CO₂ gas exchange coefficient (cm.h⁻¹); $pCO_2(water)$ the corrected pCO₂ in water (ppmv) and $pCO_2(atm.)$ the atmospheric pCO₂ (414 ppmv in February 2020, NOAA). By looking equation (1), a great influence of the gradient between water and atmosphere of CO₂ can be found upon CO₂ fluxes. The CO₂ solubility coefficient depends on water temperature and salinity and was calculated according to Weiss (1974):

$$(2) CO_2 solubility = \exp(\alpha + \beta + \gamma)$$

$$(3) \alpha = -60.2409 + 93.4717 \times 100T$$

$$(4) \beta = 23.3585 \times \ln(T100)$$

$$(5) \gamma = S \times (0.023517 - 0.023656 \times T100 + 0.0047036 \times (T100)^2)$$

Where T and S are temperature (K) and salinity in water.

As air-water FCO_2 use directly turbulence movement at the air-water exchange interface (Polsenaere et al. 2013), gas transfer velocity (k) has a large influence on it. k (or k_{600}) was calculated according to Raymond and Cole (2001) matching to closed freshwater systems (equation (6)). This gas transfer coefficients (normalized to a Schmidt number of 600 (k_{600})) and found with the RC01 parametrization were then converted to the gas transfer velocity of CO₂ according to Jähne et al. (1987) as per the equation (7):

$$(6) k_{600} = 1.91 \times \exp[0.35 \times U10]$$

$$(7) k = k_{600} / (600/Sc)^{-0.5}$$

where k is the gas transfer velocity of CO_2 at the in situ temperature and salinity (cm h^{-1}) according to the parametrizations of RC01, U_{10} is the wind speed normalized to 10 m (m s^{-1}) using the relationship of Amorocho and DeVries (1980) and Sc is the Schmidt number which describes both the water viscosity and the molecular diffusion of the subsurface layer (Bade 2009). Wind speed data were retrieved from the “Infoclimat” station on La Rochelle (<https://www.infoclimat.fr/>) measured at a height of 10 m (6 km from sampled stations at Tasdon marsh).

8.2. Seasonal variation of environmental parameters, L’Houmeau

Table 4.A. Measured monthly values between March and August 2021 at L’Houmeau salt marsh (mean \pm standard deviation (sd)). Unities: Salinity, Temperature ($^{\circ}\text{C}$), Turbidity (NTU), DOC (mg.L^{-1}) and nutrients (Nitrate (NO_3), Nitrite (NO_2), Orthophosphates (PO_4), Slice (Si), Ammonium (NH_4) ($\mu\text{mol.L}^{-1}$)).

	Salinity	sd	Temperature	sd	Turbidity	sd	DOC	sd		
March	26.38	± 0.09	11.51	± 0.47	10.32	± 8.01	0.54	± 0.02		
Apr	30.75	± 0.01	12.43	± 0.34	28.79	± 5.86	1.83	± 0.09		
May	31.85	± 0.24	15.50	± 0.15	9.38	± 2.61	2.50	± 0.10		
June	33.61	± 0.04	25.02	± 0.31	15.61	± 10.52	2.37	± 0.03		
July	34.28	± 0.06	24.26	± 1.15	19.81	± 8.01	2.13	± 0.03		
Aug	31.91	± 0.07	22.25	± 1.07	34.44	± 72.77	3.63	± 0.07		

	NO₃	sd	NO₂	sd	PO₄	sd	Si	sd	NH₄	sd
March	12.76	± 0.41	0.33	± 0.01	0.13	± 0.01	33.67	± 0.44	1.17	± 0.04
Apr	22.09	± 1.41	0.85	± 0.06	0.72	± 0.08	34.44	± 0.17	5.30	± 1.86
May	2.85	± 0.11	0.36	± 0.05	0.51	± 0.05	37.76	± 0.08	2.73	± 0.34
June	0.00	± 0.00	0.20	± 0.08	0.34	± 0.01	45.48	± 0.39	0.09	± 0.06
July	10.39	± 4.86	2.26	± 1.41	1.34	± 0.12	41.78	± 1.03	4.38	± 0.23
Aug	2.15	± 0.04	0.70	± 0.02	1.42	± 0.02	42.57	± 0.26	3.11	± 0.13

8.3. Seasonal variation of environmental parameters, Tasdon

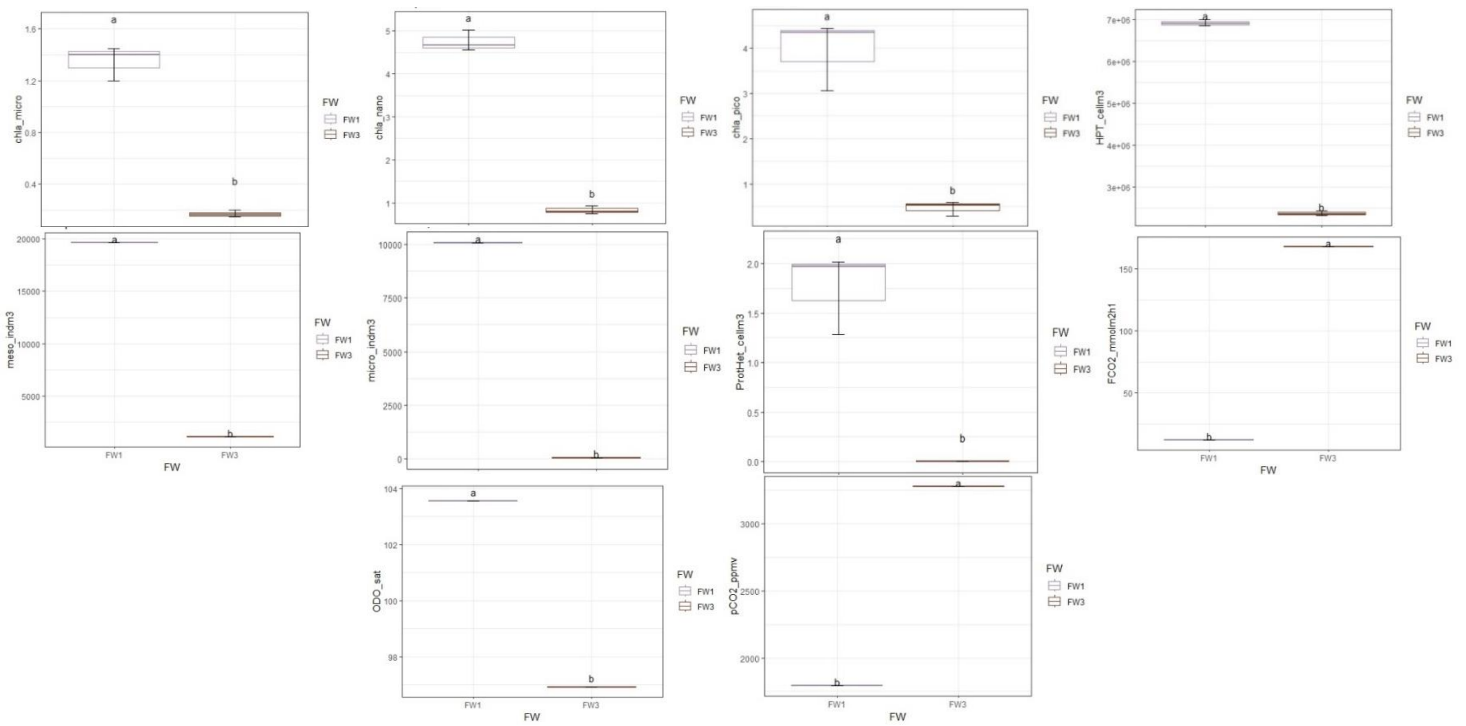
Table 5.A. Continuous values taken at L’Houmeau between March and August 2021 (mean \pm standard deviation (sd)). Unities: Salinity, Temperature ($^{\circ}\text{C}$), Turbidity (NTU), Particulate Inorganic Material (PIM, mg.L^{-1}), Particulate Organic Material (POM, mg.L^{-1}) and nutrients (Nitrate (NO_3), Nitrogen Dioxide (NO_2), Orthophosphates (PO_4), Slice (SI), Ammonium (NH_4) ($\mu\text{mol.L}^{-1}$)).

Year	Season	Site	Sal	sd	Temp	sd	Turb	sd	PIM	sd	POM	sd
2019	Spring	T2	0.31	± 0.02	16.16	± 1.38	25.88	± 7.10	35.43	± 5.81	5.51	± 0.40
	Autumn	T2	0.35	± 0.00	13.01	± 0.19	22.98	± 1.06	13.62	± 0.73	1.79	± 0.04
	Spring	T6	0.36	± 0.01	17.07	± 0.25	20.61	± 1.94	25.60	± 0.76	5.83	± 0.24
	Autumn	T6	0.44	± 0.01	12.27	± 0.21	29.58	± 1.57	26.89	± 1.77	3.03	± 0.20
	Spring	T7	0.64	± 0.00	17.53	± 0.64	51.68	± 6.07	96.73	± 3.15	16.29	± 0.75
	Autumn	T7	0.39	± 0.00	11.24	± 0.48	43.50	± 5.84	39.51	± 3.56	3.81	± 0.34
2021	Spring	T2	0.41	± 0.00	13.08	± 1.28	35.21	± 2.44	31.35	± 2.17	4.68	± 0.13
	Summer	T2	7.68	± 0.04	20.40	± 0.05	178.22	± 5.33	183.03	± 9.23	23.93	± 0.29
	Autumn	T2	0.35	± 0.00	7.36	± 0.19	72.22	± 1.40	63.02	± 1.61	14.20	± 0.30
	Winter	T2	0.34	± 0.00	12.85	± 0.20	45.47	± 3.13	29.03	± 0.64	5.79	± 0.31
	Spring	T6	0.37	± 0.01	13.23	± 2.44	80.50	± 7.19	9.79	± 2.02	2.06	± 0.32
	Summer	T6	7.96	± 0.20	21.50	± 0.75	59.84	± 8.55	57.80	± 7.93	5.91	± 0.47
	Autumn	T6	1.20	± 0.00	6.87	± 0.77	28.49	± 1.94	49.84	± 11.67	11.33	± 2.72
	Winter	T6	0.51	± 0.00	13.80	± 0.85	45.69	± 9.77	14.59	± 4.75	2.75	± 0.39
	Spring	T7	1.90	± 0.11	14.91	± 3.76	15.42	± 5.62	65.23	± 25.17	9.22	± 1.92
	Summer	T7	3.05	± 0.03	23.42	± 2.00	88.82	± 24.62	30.30	± 2.54	14.62	± 7.26
	Autumn	T7	2.31	± 0.00	9.90	± 0.54	35.23	± 10.79	40.56	± 5.17	7.67	± 0.60
	Winter	T7	2.85	± 0.00	13.60	± 1.98	46.54	± 10.80	55.04	± 1.52	5.27	± 0.20
Year	Season	Site	NO_3	sd	NO_2	sd	PO_4	sd	Si	sd	NH_4	sd
2019	Spring	T2	952.25	± 70.56	4.8	± 0.05	0.00	± 0.00	73.96	± 0.72	3.37	± 0.37
	Autumn	T2	851.39	± 4.68	2.57	± 0.05	0.26	± 0.01	124.05	± 0.44	5.41	± 0.22
	Spring	T6	1265.86	± 99.43	4	± 0.03	0.00	± 0.00	83.02	± 0.03	4.46	± 0.06
	Autumn	T6	823.62	± 2.95	3.51	± 0.03	0.08	± 0.01	124.86	± 0.60	7.59	± 0.15
	Spring	T7	14.16	± 11.89	0.77	± 0.08	0.21	± 0.03	85.7	± 0.55	2.19	± 0.05
	Autumn	T7	426.31	± 78.40	2.91	± 0.11	0.28	± 0.04	89.43	± 5.73	8.42	± 0.24
2021	Spring	T2	18.76	± 3.25	1.76	± 0.19	0.33	± 0.05	50.61	± 0.42	22.32	± 1.33
	Summer	T2	0.00	± 0.00	1.33	± 0.47	0.88	± 0.10	429.05	± 19.33	17.09	± 0.91

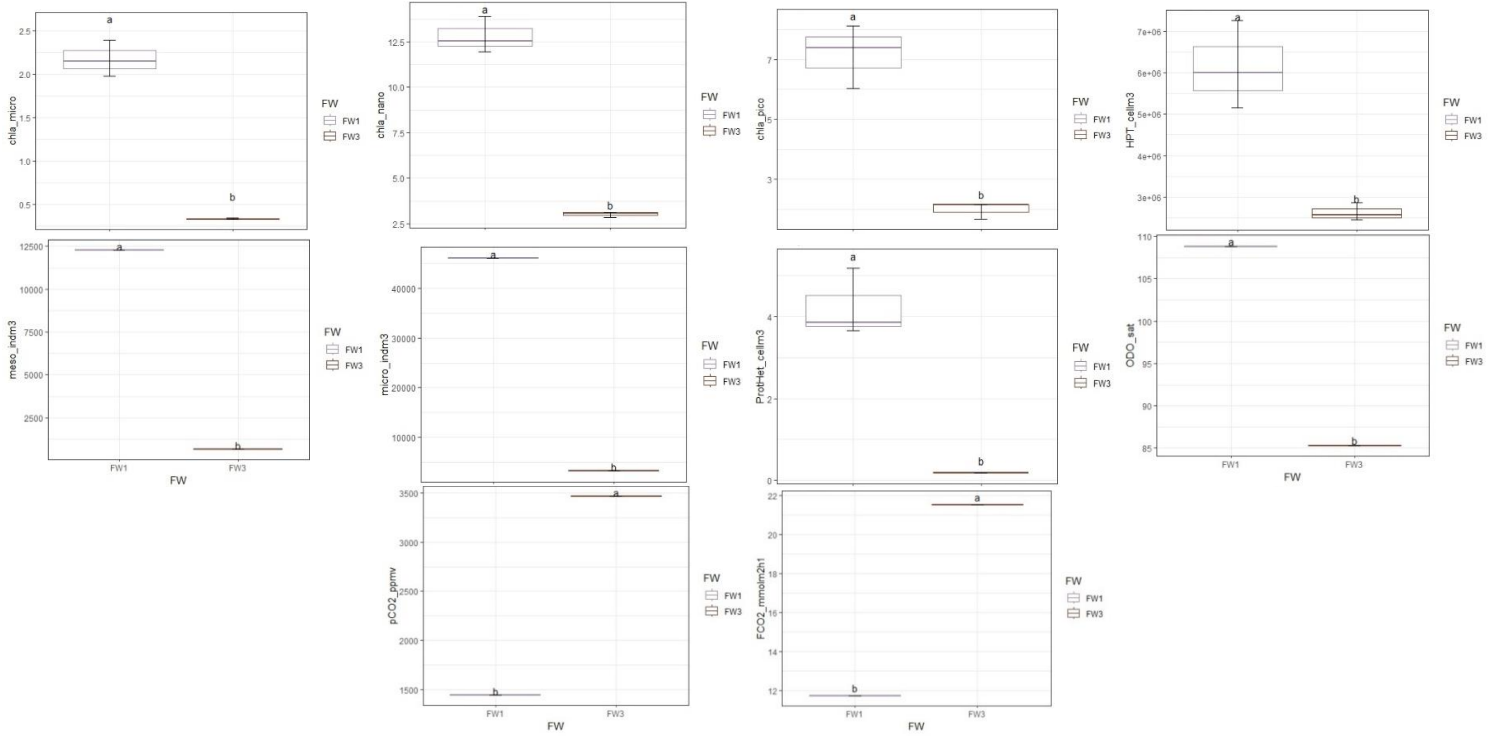
Autumn	T2	12.87	± 3.53	0.43	± 0.03	0.27	± 0.02	194.19	± 0.58	1.12	± 0.12
Winter	T2	35.65	± 1.25	1.53	± 0.09	0.18	± 0.04	26.25	± 4.64	1.09	± 0.23
Spring	T6	342.67	± 3.55	3.37	± 0.01	0.04	± 0.02	75.07	± 0.96	1.65	± 1.10
Summer	T6	417.56	± 29.69	5.98	± 0.47	0.06	± 0.01	114.75	± 2.20	8.37	± 0.22
Autumn	T6	503.52	± 10.55	6.83	± 0.14	0.02	± 0.01	105.61	± 11.96	6.96	± 0.38
Winter	T6	288.4	± 1.10	2.6	± 0.05	0.04	± 0.01	23.59	± 0.62	0.38	± 0.03
Spring	T7	293.95	± 8.42	3.78	± 0.22	0.07	± 0.01	22.69	± 1.18	2.22	± 0.10
Summer	T7	64.41	± 5.10	7.87	± 0.29	0.12	± 0.00	62.59	± 2.66	5.32	± 0.40
Autumn	T7	222.96	± 18.90	9.45	± 1.19	0.08	± 0.01	68.73	± 0.72	12.53	± 1.32
Winter	T7	227.02	± 20.42	2.82	± 0.15	4.18	± 4.00	14.95	± 5.53	16.25	± 8.08

8.4. Tasdon food web analysis

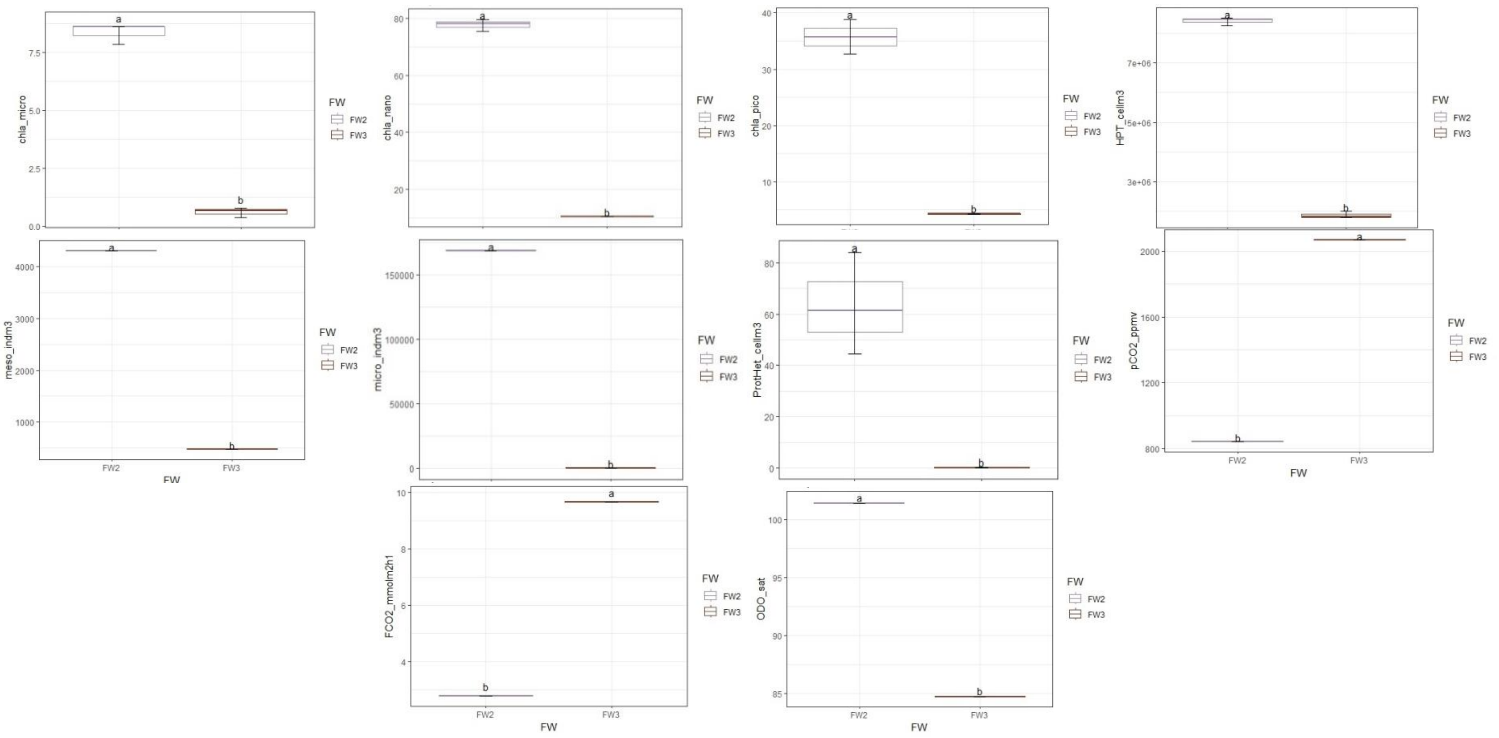
2019, T2



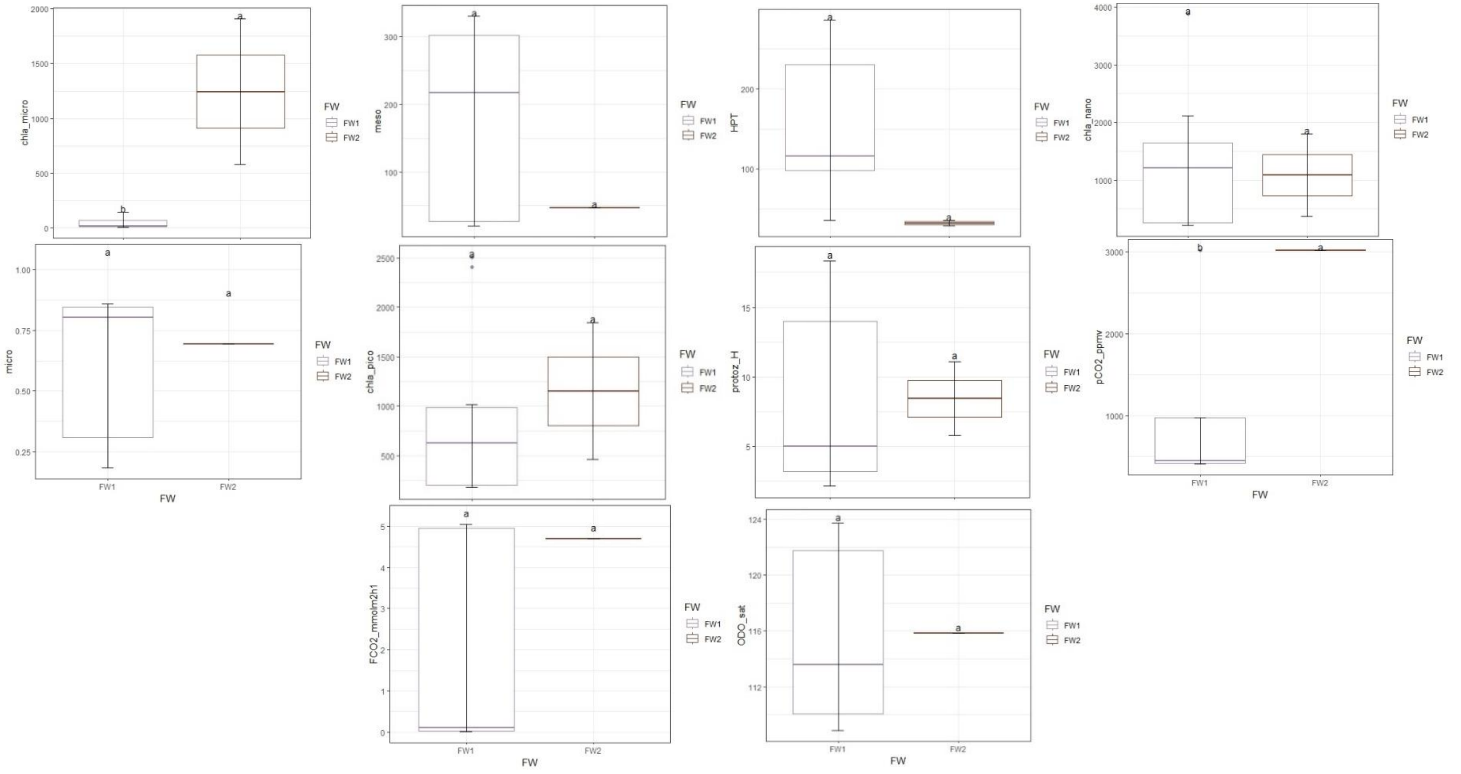
T6



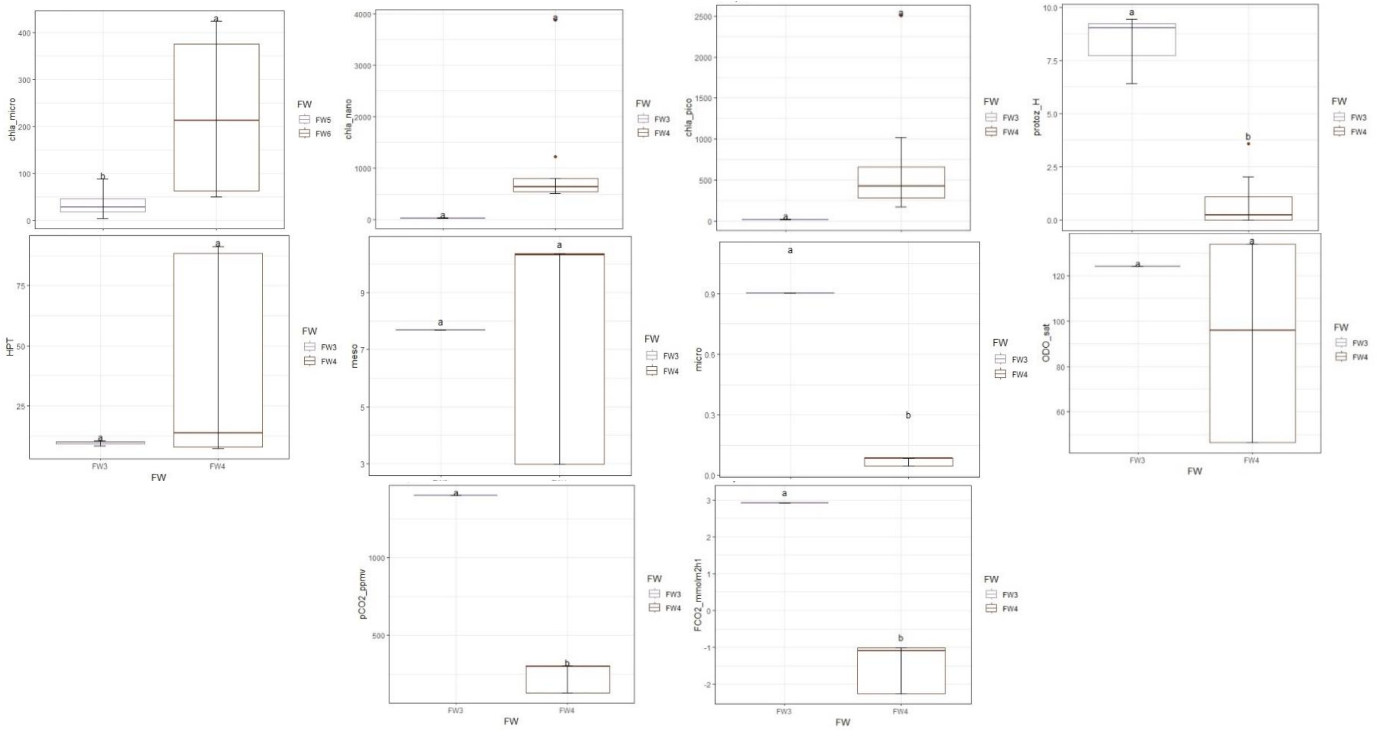
T7



2021, T2



T6



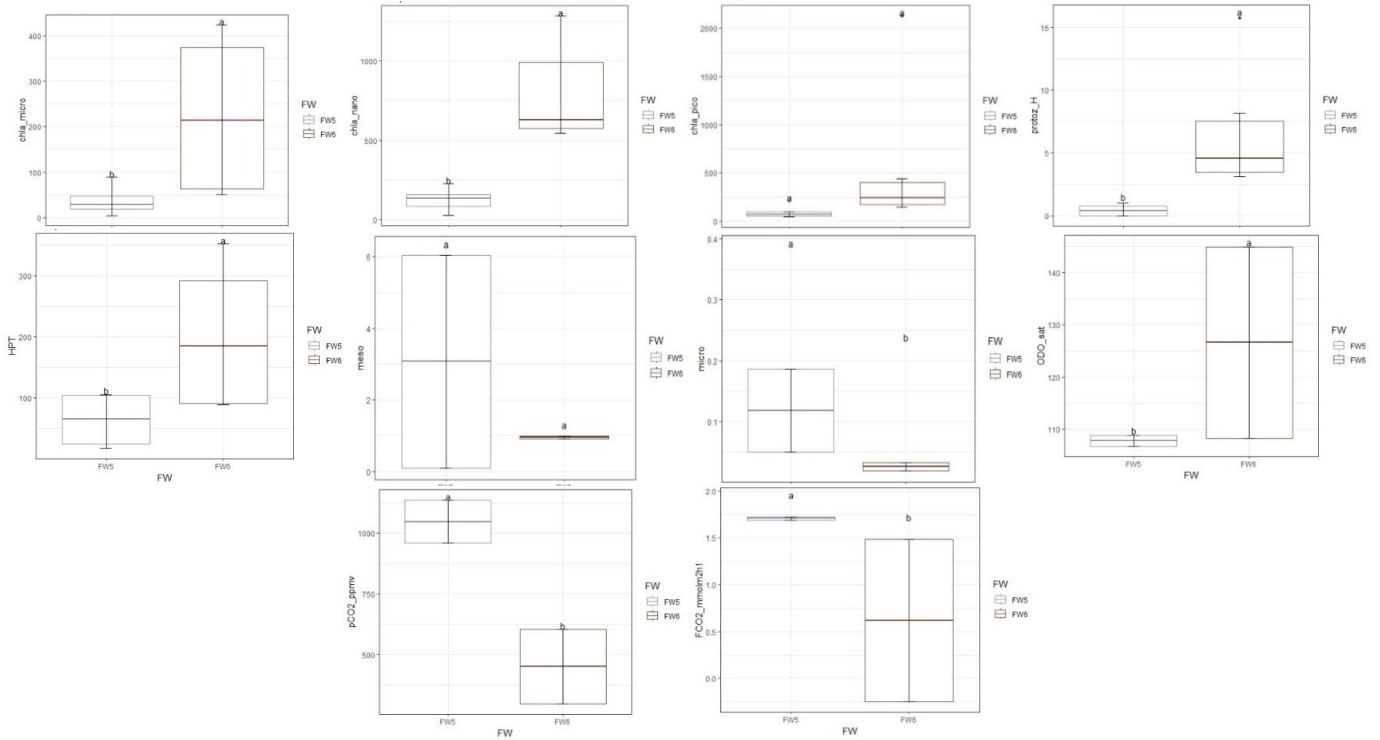


Figure 15.A. *Box plot* displaying the mean per food web type for Chla by size class, Meso, Micro, HTTP and Proto by fraction used for the HAC analysis during Tasdon sampling at each site. *Box plot* labelled with the same letters are not significantly different (ANOVA followed by Fisher's LSD). All biotic variables have the same unity ($\mu\text{gC}\cdot\text{L}^{-1}$) but scales were different. In addition, *Box plot* with pCO₂, CO₂ flux and O₂ % mean per food web were added.

Abstract:

Although, both $p\text{CO}_2$ cycle and aquatic food webs have been widely but separately studied over the coastal zone, few research has been made to link them, especially in diverse marsh typologies. Therefore, this relationship remains unknown. The objectives of this study are to (1) study if $p\text{CO}_2$ and atmospheric CO_2 flux variations can be explained by planktonic food webs, (2) determine if this relationship between planktonic food webs and water CO_2 exchanges remains the same in two different "Blue Carbon" ecosystems. To address these objectives, L'Houmeau saltwater marsh and Tasdon renatured freshwater marsh and their environmental, biogeochemical and biological factors were studied. Certain similarities and differences between those sites from a carbon versus food web relationship point of view were found. Despite having different typologies, both L'Houmeau and Tasdon (before renaturation) were CO_2 sources, whereas Tasdon became a weaker source and sometimes sink of carbon after renaturation. Furthermore, five food web typologies and associated $p\text{CO}_2$ values were clearly highlighted through our original approach. Three stable ones: 'biological winter', 'microbial food web', 'multivorous' food webs with high $p\text{CO}_2$ values at both sites and two transitory ones: 'weak multivorous' and 'weak herbivorous' with lower and more variable $p\text{CO}_2$ values. It is important to highlight that seasonality would seem to play an important role in both $p\text{CO}_2$ measures and food web typologies, implying that, in order to see a link between these factors, the sampling period remains highly important. Unfortunately, after renaturation at Tasdon, food webs did not go back to a 'seasonal' equilibrium state, preventing, maybe, a better or a clearer understanding of this environment. These data allowed to achieved the first known relationships between food web typology and $p\text{CO}_2$ in two different marshes.

Key words: "Blue carbon", marsh, food web, $p\text{CO}_2$, CO_2 flux

Résumé :

Bien que les variations de CO_2 et les réseaux trophiques aquatiques aient été étudiés séparément, peu d'études ont été menées à faire le lien carbone versus réseau trophique dans divers marais. Par conséquent, cette relation reste inconnue. L'objectif de cette étude est (1) d'étudier si les variations de CO_2 de l'eau peuvent être expliquées par les réseaux trophiques planctoniques, (2) déterminer si ça relation reste la même dans deux écosystèmes "Carbone Blue" différents. Le marais salé de L'Houmeau et le marais doux de Tasdon renaturalisé récemment, ainsi que leurs facteurs environnementaux, biogéochimiques et biologiques ont été étudiés. Certaines similitudes et différences entre ces sites du point de vue de la relation entre le carbone et le réseau trophique ont été constatées. Malgré ces différences, un lien général entre la typologie de réseau trophique et la dynamique des $p\text{CO}_2$ a été obtenue. Notre approche originale a permis de mettre en évidence cinq typologies de réseaux trophique et les valeurs de $p\text{CO}_2$ associées. Trois typologies stables : "hiver biologique", "réseau microbien", "multivores" avec des valeurs de $p\text{CO}_2$ élevées sur les deux sites et deux typologies transitoires : "multivores faibles" et "herbivores faibles" avec des valeurs de $p\text{CO}_2$ plus faibles et plus variables. Il est important de souligner que la saisonnalité semble jouer un rôle important à la fois dans les mesures de $p\text{CO}_2$ et dans les typologies de réseaux alimentaires, ce qui implique que, la période d'échantillonnage reste très importante. Malheureusement, après la renaturation à Tasdon, les réseaux trophiques ne sont pas revenus à un état d'équilibre "saisonnier", ce qui a peut-être empêché une meilleure compréhension de cet environnement. Ces données ont permis d'établir les premières relations connues entre la typologie des réseaux alimentaires et la $p\text{CO}_2$ dans deux marais différents.

Mots-Cles : "Carbone Blue", marais, réseaux trophique, $p\text{CO}_2$, CO_2 flux