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**Trajectoires d'évolution des communautés phytoplanctoniques
et des lagunes côtières du littoral corse et applications**

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*Alla nonna Anna
che ha “scoperto” la Corsica,
A mamma Laura e papà Roberto
che l’hanno fatta scoprire a me.*

PRÉFACE

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Les suivis *in situ*, les expérimentations et une partie des analyses de ce doctorat ont été réalisés au sein du laboratoire de la plateforme STELLA MARE de l'Università di Corsica, alors qu'une autre partie des analyses a été réalisée par des instituts externes : l'Institut Méditerranéen d'Océanologie (MIO) et l'Institut de la Mer de Villefranche (IMEV).



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ABSTRACT

Coastal lagoons are of high ecological, economic and social importance. Nevertheless, they are particularly vulnerable to anthropogenic pressure and climate change, especially in the Mediterranean region. Lagoons' conservation is hence fundamental for the protection of littoral systems and the well-being of human populations. This thesis aims to provide support for public policies for the restoration and conservation of coastal lagoons, but also to look for potential resources' valorisation. The works aim to deepen knowledge on the evolution trajectories of phytoplankton communities and coastal lagoons of the Corsican coast, (i) by questioning the evolutions of seasonal variations linked to abiotic factors, but also the impact of salinity variations, particularly in the context of climate change, on large and/or small lagoons, and (ii) by testing different integrated approaches taking into account the human impact, from the watershed to the sea.

Phytoplankton communities of six Corsican lagoons (Diana, Urbino, Biguglia, Arasu, Santa Giulia, Balistra) are studied in this framework. Analysis of long term historical datasets available, *in situ* monitoring and experimental essays performed allowed the identification of marked seasonal dynamics of phytoplankton communities and central elements for coastal lagoons' management. The trend towards the dominance of dinoflagellates, the emergence of stress-tolerant (e.g. extreme salinities), sometimes potentially toxic, the increase in phytoplankton blooms as well as changes in the seasonal cycles have been highlighted in large and small sized lagoons. These phenomena are mainly linked to anthropogenic impacts (pollution, urban wastewater, water use, tourism...), hydrogeological alterations caused by human interventions, and climate change.

The study of other biotic and abiotic compartments of the ecosystem, like biological invasion, fish production or hydrogeological functioning, has confirmed the need to apply an ecosystem-based approach, from the watershed to the sea, in order to understand the overall functioning of the system. The consideration of Humans in the study of ecological trajectories has also been highlighted, emphasizing that lagoons should be considered as social-ecological systems. This holistic vision is fundamental to consider an optimal integrated management of the complexity of the system.

Moreover, this thesis provides a new perspective on small surfaced lagoons at the scale of the Mediterranean coast, which are very reactive to change and can thus be considered as sentinels of climate change.

At the same time, the study of a diatom strain from the Diana lagoon has demonstrated promising ecophysiological and chemical characteristics for potential biotechnological applications in the aquaculture domain, due to its lagoon origin.

The overall results on the past and future evolution trajectories have highlighted the complexity and vulnerability of coastal lagoons (and those of small surface areas in particular) in the face of growing threats and some questions about their future. This work provides hence some supporting elements for the lagoon management and the valorisation of resources linked to these environments, by proposing an integrated and interdisciplinary management for the sustainable conservation of these ecosystems and of the services provided, particularly in the climate change context.

KEYWORDS: Mediterranean coastal lagoons · phytoplankton · ecosystem-based approach · sustainable management · microalgae valorisation

RÉSUMÉ

Les lagunes côtières présentent une forte importance écologique, économique et sociale. Toutefois, elles sont particulièrement vulnérables face aux pressions anthropiques et aux changements climatiques, notamment en région méditerranéenne. La conservation des lagunes est donc fondamentale pour la protection des systèmes littoraux et le bien-être des populations humaines. Cette thèse vise à apporter un soutien aux politiques publiques pour la restauration et la conservation des lagunes côtières, mais également à rechercher de potentielles valorisations des ressources. Les travaux ambitionnent d'approfondir les connaissances sur les trajectoires d'évolution des communautés phytoplanctoniques et des lagunes côtières du littoral corse, (i) en questionnant l'évolution des variations saisonnières face aux paramètres abiotiques, mais également l'impact des variations de salinité, notamment dans le cadre du changement climatique, sur de grandes et/ou de petites lagunes et (ii) en testant différentes approches intégrées avec la prise en compte de l'impact de l'homme, du bassin versant jusqu'à la mer.

Les communautés phytoplanctoniques de six lagunes du littoral corse (Diana, Urbino, Biguglia, Arasu, Santa Giulia, Balistra) sont étudiées dans ce cadre. Les analyses sur le long terme grâce aux données historiques disponibles, les suivis *in situ* et les expérimentations réalisées ont permis d'identifier des dynamiques saisonnières marquées des communautés phytoplanctoniques et des éléments centraux pour la gestion des milieux lagunaires. La tendance vers une dominance des dinoflagellés, l'émergence d'espèces tolérant le stress (e.g. salinités extrêmes), parfois potentiellement toxiques, l'augmentation des *blooms* phytoplanctoniques ainsi que des modifications des cycles saisonniers ont été mis en évidence sur des lagunes de grandes et de petites tailles. Ces phénomènes sont liés principalement à des impacts d'origine anthropique (pollution, rejets urbains, usage de l'eau, tourisme...), des altérations hydrologiques engendrées par des interventions humaines, et le changement climatique.

L'étude d'autres compartiments biotiques et abiotiques de l'écosystème, comme l'invasion biologique, la production halieutique ou le fonctionnement hydrogéologique, a confirmé la nécessité d'appliquer une approche écosystémique, du bassin versant jusqu'à la mer, pour comprendre le fonctionnement global du système. La prise en compte de l'Homme dans l'étude des trajectoires écologiques a été aussi mise en évidence, soulignant que les lagunes doivent être considérées comme des socio-écosystèmes. Cette vision holistique est fondamentale pour envisager une gestion optimale intégrée de la complexité du système.

Cette thèse apporte de plus un regard nouveau sur les lagunes de petites surfaces à l'échelle du littoral méditerranéen qui sont très réactives aux changements et qui peuvent être considérées comme des sentinelles de l'évolution climatique.

Parallèlement, l'étude d'une souche de diatomée issue de l'étang de Diana a démontré des caractéristiques écophysiologicals et chimiques prometteuse pour de potentielles applications biotechnologiques dans le domaine de l'aquaculture, en raison de son origine lagunaire.

L'ensemble de ces résultats sur les trajectoires d'évolution passées et futures a permis de marquer la complexité et la vulnérabilité des lagunes côtières (et celles de petites surfaces en particulier) face aux menaces croissantes et des interrogations sur leur avenir. Ce travail fournit donc des éléments d'appui pour la gestion des lagunes et de valorisation des ressources liées à ces milieux, en proposant une gestion intégrée et interdisciplinaire pour une conservation durable de ces écosystèmes et des services fournis, notamment dans le cadre du changement climatique.

MOTS CLÉS : Lagunes côtières méditerranéennes · phytoplancton · approche écosystémique · gestion durable · valorisation des microalgues

RIASSUNTU

Lagune custiere, anu una importanza ecològica, economica et suciale tamanta. È puru sò vulnirabile davanti à e prissionne antrupulugiche è a u cambiamentu climaticu, soprattutto in mediterraniu. Hé perchè chi a cunservazione di e lagune hé impurtantissima pè a prutezzione di i systemi litturali et u benestà di a pupulazione umana. Sta tesa voglie sustene à e pulitiche pubbliche per u ristoru è a cunservazione di e lagune custiere, mà dinò cercà a valorisazione di e risorse. Stu travagliu voglie approfondisce a sapienza nantu a strada di l'evuluzione di e cumunità fitoplanctoniche è di u litturale corsu, (i) mettendu in discussione l'evuluzione di i cambiamenti stagionali di fronte à i parametri abiotici, ma dinò l'impattu di un cambamentu di salinità, spicialmente in u cuntestu di cambiamentu climaticu, nant'à e grande lagune è/o e lagune chjuche è (ii) testendu diverse approcci integrati, cù l'impattu di l'omu, da u bacinu à u mare.

In stu cuntestu, e cumunità fitoplanctoniche di sei lagune di u litturale (Diana, Urbino, Biguglia, Arasu, Santa Giulia, Balistra) sò state studiate. L'analisi à longu andà sò state fate in grazia di riferenzi storici dispunibili, di u siguidatu *in situ* e à l'esperimentazione. Anu permessu l'identificazione di una dinamica di staggione marcata pè cumunità fitoplanctoniche è dinò elementi cintrali pè a gestione di l'ambienti lagunari. Una dominanza di i dinoflagelati, l'emergenza di spezie tolleranti à u stress (per esempiu, salinità estrema), di tantu in tantu tossiche, l'augmentazione di i *blooms* fitoplanctonani è i cambiamenti di cicli staghjunali sò stati messi in risaltu indè e lagune grande è chjuca. Sti fenòmeni sò principarmenti liati à un impatti antropicu (pulluzione, scarti urbani, usu di l'acqua, turisimu, etc.), alterazioni idrologiche causate da l'intervenzione umana, è u cambiamentu climaticu.

Studià l'altri compartimenti biotichi è abiotichi di l'ecosistema, cum'è l'invasione biologica, a pruduzione di pesci o u funziunamentu idrogeologicu, hà cunfirmatu a necessità di applicà un approcciu ecosystematicu, da u bacinu à u mare, pè capisce u funziunamentu glubale di u sistema. A cunsiderazione di l'omu in stu studiu di e strade ecologiche hè statu ancu evidenziatu, sottuliniandu ch'è e lagune deve esse cunsiderate cum'è socio-ecosistema. Questa visione olistica hè fundamentele per cunsiderà una gestione integrata ottima di a cumplexità di u sistema.

Sta tesa porta dinò una nova prospettiva nant'à e lagune di picculi spazii à scala di a costa mediterranea assai reattivi à i cambiamenti è ch'è ponu esse cunsiderati cum'è sintineddi di u cambiamentu climaticu.

À u listessu tempu, u studiu di una ceppa di diatomi da u stagnu di Diana hà mustratu caratteristiche ecophysiolugiche è chimiche ch'è ponu esse utilizzata pè un appiicazione biotechnologiche in aquacultura, di petu à so orìgine lagunaria.

Tutti sti risultati sopra à e strade di l'evuluzione, tempi fà è di l'avene, anu permessu di sottulinia a cumplexità è a vulnerabilità di e lagune custiere (è chelle di i picculi spazii in particolare) di fronte à e minacce di più in più importante è à e dumande sobre à e so avvene. Stu travagliu furnisce dunque elementi di supportu à a gestione di e lagune è à u sviluppu di e risorse ligate à sti ambienti, prupunendu una gestione integrata è interdisciplinaria per a cunservazione a longu andà di sti ecosistemi è di i servizii dispunibile, in particolare in u cuntestu di u cambiamentu climaticu.

PAROLE CHIAVE: Lagune custiere in mediterraniu · cumunità fitoplanctoniche · approcciu ecosystematicu · gestione sustenibile · valorisazione di microalghe

RIASSUNTO

Le lagune costiere presentano una forte importanza ecologica, economica e sociale. Tuttavia, esse sono particolarmente vulnerabili alle pressioni antropiche e ai cambiamenti climatici, in particolare nella regione mediterranea. La conservazione delle lagune è dunque fondamentale per la protezione dei sistemi litorali e il benessere delle popolazioni umane. Questa tesi ambisce ad apportare un sostegno alle politiche pubbliche per il restauro e la conservazione delle lagune costiere, ma anche a ricercare potenziali valorizzazioni di risorse. I lavori realizzati mirano ad approfondire le conoscenze sulle traiettorie d'evoluzione delle comunità fitoplanctoniche e delle lagune costiere del litorale corso, (i) investigando l'evoluzione delle variazioni stagionali a fronte dei parametri abiotici, ma anche l'impatto delle variazioni di salinità, in particolare nel contesto del cambiamento climatico, su grandi e/o piccole lagune e (ii) testando differenti approcci integrati che tengano conto dell'impatto dell'Uomo, dal bacino idrografico fino al mare.

In questo contesto sono studiate le comunità fitoplanctoniche di sei lagune del litorale corso (Diana, Urbino, Biguglia, Arasu, Santa Giulia, Balistra). Le analisi sul lungo termine, grazie ai dati storici disponibili, i monitoraggi *in situ* e le sperimentazioni effettuati hanno permesso di identificare marcate dinamiche stagionali delle comunità fitoplanctoniche e alcuni elementi centrali per la gestione degli ambienti lagunari. La tendenza verso una dominanza di dinoflagellati, l'emergenza di specie tolleranti lo stress (es. salinità estreme), talvolta potenzialmente tossiche, l'aumento dei *bloom* fitoplanctonici nonché alcune modificazioni dei cicli stagionali sono stati messi in evidenza in lagune di grande e piccola estensione. Questi fenomeni sono principalmente legati agli impatti di origine antropica (inquinamento, acque reflue urbane, utilizzo delle risorse idriche, turismo...), ad alterazioni idrologiche causate da interventi umani e al cambiamento climatico.

Lo studio di altri compartimenti biotici e abiotici dell'ecosistema, come l'invasione biologica, la produzione alieutica o il funzionamento idrogeologico, ha confermato la necessità di applicare un approccio ecosistemico, dal bacino idrografico fino al mare, per comprendere il funzionamento globale del sistema. Inoltre, la considerazione dell'Uomo nello studio delle traiettorie ecologiche è stata messa in evidenza, sottolineando che le lagune devono essere considerate come dei sistemi socio-ecologici. Questa visione olistica è fondamentale per considerare una gestione integrata ottimale della complessità del sistema.

Questa tesi apporta inoltre una nuova prospettiva sulle lagune di piccola estensione alla scala del litorale mediterraneo, che sono molto reattive ai cambiamenti e che possono quindi essere considerate come sentinelle dell'evoluzione climatica.

Parallelamente, lo studio di un ceppo di diatomea proveniente dalla laguna di Diana ha dimostrato delle caratteristiche ecofisiologiche e chimiche promettenti per delle potenziali applicazioni biotecnologiche nel campo dell'acquacoltura, per via della sua origine lagunare.

L'insieme di questi risultati sulle traiettorie di evoluzione passate e future ha permesso di marcare la complessità e la vulnerabilità delle lagune costiere (e quelle di piccola estensione in particolare) a fronte delle minacce crescenti e alcuni interrogativi riguardo al loro avvenire. Questo lavoro fornisce quindi degli elementi di supporto per la gestione delle lagune e la valorizzazione delle risorse legate a questi ambienti, proponendo una gestione integrata e interdisciplinare per la conservazione sostenibile di questi ecosistemi e dei servizi forniti, soprattutto nel contesto del cambiamento climatico.

PAROLE CHIAVE : Lagune costiere mediterranee · fitoplancton · approccio ecosistemico · gestione sostenibile · valorizzazione delle microalghe

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Introduction générale



INTRODUCTION GÉNÉRALE

1. LE PHYTOPLANCTON : MODÈLE D'ÉTUDE

1.1 Définition et rôle

Le plancton est généralement défini comme l'ensemble des organismes vivants qui sont adaptés à passer leur vie, ou une part de leur vie, en suspension apparente dans la colonne d'eau, des eaux marines jusqu'aux lacs, rivières et tous les autres systèmes aquatiques (Reynolds, 2006). Le phytoplancton, dont le nom vient du grec « *phyton* », « plante », et « *planktos* », « errer », est défini comme le compartiment planctonique constitué des organismes photosynthétiques (Reynolds, 2006). En réalité, les organismes phytoplanctoniques présentent différentes stratégies métaboliques et sont capables de produire des déplacements actifs horizontaux et verticaux dans le milieu hydrique à micro et méso-échelle spatiale, ou de contrôler leur flottabilité grâce à des stratégies adaptatives développées pour la vie dans la colonne d'eau. Toutefois, malgré la présence d'une variété de stratégies adaptatives, le phytoplancton est associé à la production primaire de matière organique à travers le processus de photosynthèse et responsable de presque la moitié (49%) de la production primaire nette mondiale (Field et al., 1998). La moitié de l'oxygène que l'on respire dérive aussi de l'activité photosynthétique du phytoplancton (Naselli-Flores & Padisák, 2022). Les communautés phytoplanctoniques jouent donc un rôle fondamental dans les cycles biogéochimiques et dans le transfert de matière et énergie. La **production** primaire est définie **nouvelle** quand elle est permise par l'utilisation de composés azotés qui proviennent de l'extérieur du système, par exemple des stocks profonds dérivant du sédiment (Glibert, 2016). À cette production s'oppose la **production régénérée**, permise par l'utilisation de l'azote dérivant des rejets azotés produits par les organismes au sein du système (Glibert, 2016). Selon la localisation, les flux d'eau et de nutriments et les saisons, cette production varie donc de façon importante, en fonction de la stratification de la colonne d'eau et de la disponibilité de lumière (Naselli-Flores & Padisák, 2022; Reynolds, 2006). Des relations complexes s'établissent entre le phytoplancton et les autres organismes (virus, bactéries, mais aussi zooplancton et organismes supérieurs), constituant des associations qui déterminent les cycles globaux des nutriments à différentes échelles temporelles (Naselli-Flores & Padisák, 2022). Le phytoplancton agit principalement sur des temps courts, mais il constitue la majorité des producteurs en milieu aquatique et joue un rôle essentiel dans la régulation et le soutien de la biosphère, dont la fixation du carbone (Naselli-Flores & Padisák, 2022). Cette productivité positionne le phytoplancton à la base du réseau trophique et est subordonnée à la disponibilité de nutriments dans la colonne d'eau et de lumière, ce qui implique une réactivité de ces organismes aux apports en

nutriments et changements du milieu. Comme les organismes phytoplanctoniques réagissent rapidement aux changements environnementaux, ils sont les premiers à répondre aux modifications, et toute altération de la structure communautaire ou de ses dynamiques peut se répercuter aux niveaux trophiques supérieurs (Margalef, 1978; Cloern, 1999; Loureiro et al., 2006; Reynolds, 2006).

1.2 Diversité et dynamiques : un outil indicateur du milieu

Le phytoplancton est caractérisé par une grande variabilité en termes de forme, morphologie, taille et phylogénétique. En effet, la gamme de diversité au sein du compartiment phytoplanctonique est comparable à celle qui peut être trouvée dans une forêt entre un arbre et un brin d'herbe (Reynolds, 2006). La distinction entre un arbre et un brin d'herbe paraît claire et fournit immédiatement des indications par rapport aux catégories fonctionnelles des deux organismes au sein de leur milieu. Par analogie, il paraît logique l'intérêt de trouver un moyen pour distinguer rapidement les groupes phytoplanctoniques et leur fonctionnalité, notamment sur la base d'un caractère relativement simple à repérer, comme la dimension (Reynolds, 2006). La nomenclature basée sur la classification par taille, développée par Sieburth et al. (1978) (Tableau 1), se base sur ce principe et est largement utilisée en écologie pour discriminer des groupes fonctionnels au sein du phytoplancton (Reynolds, 2006). Selon les classes de taille qui peuvent être identifiées, le picophytoplancton, comprenant les organismes de plus petite taille (Tableau 1), est dominant dans les eaux océaniques oligotrophes, alors que le nano- et le microphytoplancton (Tableau 1) sont plutôt associées aux eaux eutrophes (Reynolds, 2006; Bec et al., 2011).

Tableau 1 Classification du phytoplancton selon la nomenclature par classe de taille, établie par Sieburth et al. (1978).

Classe de taille	Nom de la catégorie
0.2-2 μM	picophytoplancton
2-20 μM	nanophytoplancton
20-200 μM	microphytoplancton
200 μM -2 mm	mesophytoplancton
> 2 mm	macrophytoplancton

Sournia et al. (1991) ont estimé l'existence d'environ 5000 différentes espèces phytoplanctoniques marines. En effet, le phytoplancton est constitué de plusieurs groupes taxonomiques (Figure 1). Il comprend des organismes eucaryotes, représentant la majorité du nano- et microphytoplancton, et procaryotes, surtout dans le compartiment picophytoplanctonique (Reynolds, 2006). Cette diversité est supportée

par une diversité morphologique, fonctionnelle, de distribution et de stratégies adaptatives de vie et métaboliques (Reynolds, 2006; Glibert, 2016). Les **diatomées**, autrement dit les organismes appartenant à la classe des **Bacillariophyceae**, constituent le groupe principal du phytoplancton en milieu marin et côtier (Figure 1 ; Avancini et al., 2006; Lee, 2008). Ces microalgues sont caractérisées d'une paroi siliceuse, appelée « frustule », et jouent donc un rôle fondamental dans le cycle de la silice en milieux aquatiques (Reynolds, 2006). Ces organismes, souvent de grande taille et à croissance rapide, sont fondamentaux pour le soutien de la productivité du système et de grand intérêt pour le maintien des ressources halieutiques (Dupuy et al., 2000; Pernet et al., 2012). Un autre groupe très dominant en milieu marin et côtier est celui des **dinoflagellés** (ou **Dinophyceae**, Figure 1). Ce groupe présente une très forte variété en termes de morphologie et physiologie. Les dinoflagellés sont caractérisés par la présence de deux flagelles qui leur confèrent une bonne capacité de motilité dans la colonne d'eau (Avancini et al., 2006; Lee, 2008; Reynolds, 2006). Certains organismes de ce groupe présentent une stratégie alimentaire, dite mixotrophie, selon laquelle ils sont capables d'autotrophie, mais peuvent aussi être hétérotrophes (Reynolds, 2006). Parallèlement, certaines espèces sont capables de produire des kystes de résistance qui germent seulement quand les conditions du milieu sont favorables. Toutes ces caractéristiques rendent les dinoflagellés très résistants au stress environnemental et leur confèrent donc un avantage compétitif sur d'autres organismes dans les milieux perturbés (Aligizaki et al., 2009; Skarlato et al., 2018a, 2018b; Fischer et al., 2020). Certaines espèces, surtout appartenant aux Dinophyceae, sont capables de produire des toxines qui peuvent provoquer des empoisonnements parfois très graves ou létaux chez la faune et chez l'homme (Smayda, 1997a). D'autres groupes phytoplanctoniques sont moins dominants sur les communautés marines. Les euglènes (**Euglenophyceae**, Figure 1) présentent des caractéristiques très particulières qui ont rendu difficile leur classification taxonomique. Les organismes appartenant à ce groupe peuvent être capables d'effectuer la photosynthèse, mais parfois de se nourrir par hétérotrophie et phagotrophie (Reynolds, 2006). Ces organismes sont donc actuellement classés sous les protozoaires, dans le phylum Euglenozoa (Figure 1). En raison de leurs capacités trophiques, plusieurs espèces d'euglènes sont associées aux systèmes enrichis en nutriments, comme les lacs et les lagunes (Reynolds, 2006). D'autres groupes phytoplanctoniques, notamment en milieu côtier et lagunaire, comme les **Chlorophyta** et les **Cryptophyceae** (Figure 1) sont associés aux apports en eau douce, et les Cryptophyceae sont en particulier associées aux eaux turbides, en raison de leur photosensibilité (Gregor & Maršálek, 2004; Lee, 2008; Catherine et al., 2012; Garrido et al., 2016). Enfin, les **cyanobactéries** font aussi partie du phytoplancton et sont donc considérées des microalgues, mais appartiennent au domaine des procaryotes, sous le Règne Bacteria (Figure 1). La plupart du picoplancton

est constitué de cyanobactéries, avec deux espèces principales, *Prochlorococcus* et *Synechococcus*, l'une dominante en milieu océanique et l'autre surtout dans les eaux côtières et lagunaires, plus riches en nutriments, en raison de son besoin nutritionnel plus élevé (Xia et al., 2017 et références citées). D'autres cyanobactéries font partie du microphytoplancton et peuvent parfois produire des colonies visibles à l'œil. Les cyanobactéries sont capables de fixer l'azote atmosphérique et ont donc un rôle essentiel dans le cycle de l'azote (Avancini et al., 2006; Reynolds, 2006; Lee, 2008). En outre, grâce à cette caractéristique, les cyanobactéries souvent prolifèrent en association avec des conditions dégradées de dystrophie, avec de faibles concentrations en azote et oxygène et un milieu réducteur (Pulina et al., 2011; Caroppo, 2015; Albrecht et al., 2017; Pasqualini et al., 2017).

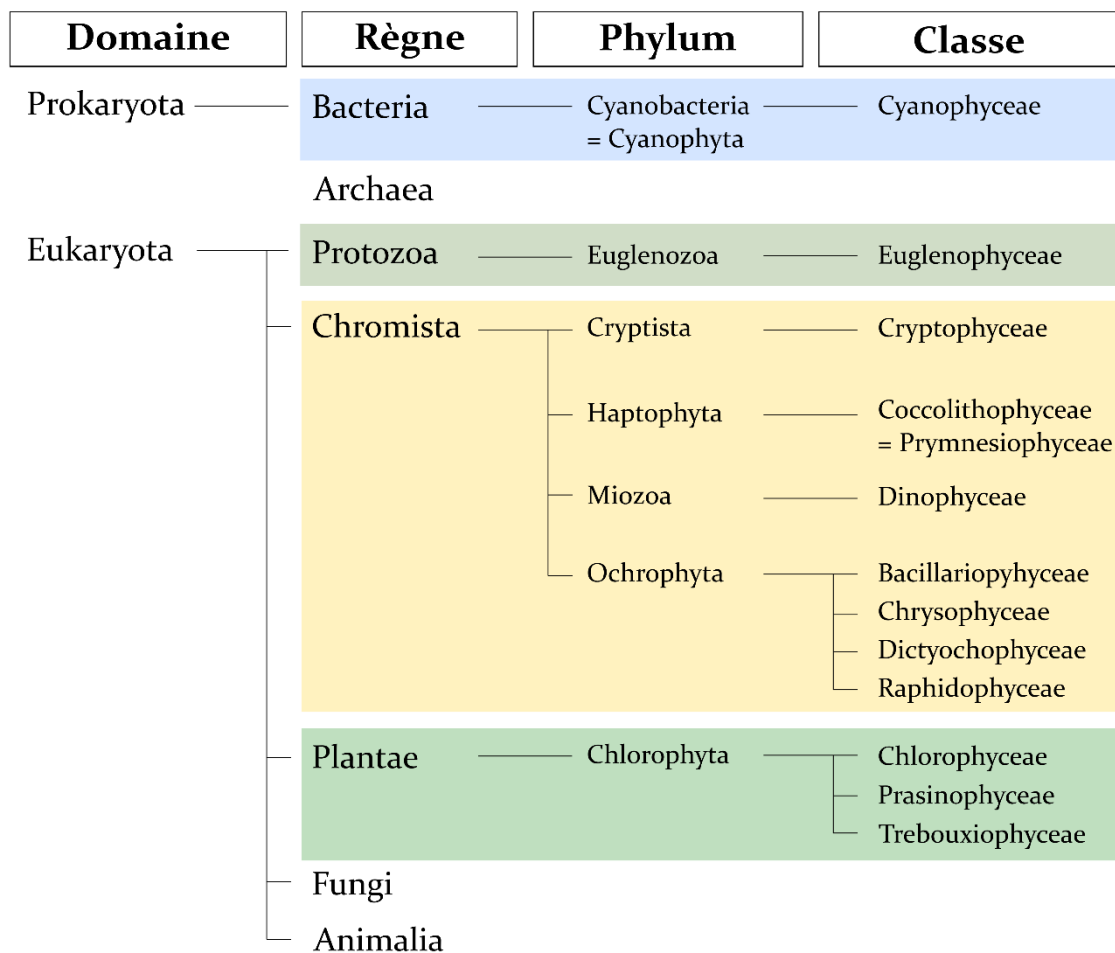


Figure 1 Classification simplifiée des principales classes phytoplanctoniques, selon la classification de Ruggiero et al. (2015).

Les dynamiques des communautés phytoplanctoniques sont gouvernées par plusieurs facteurs environnementaux, dont la lumière, la température, la disponibilité de nutriments, la salinité et la turbulence (Margalef, 1978; Cloern, 1996, 1999; Reynolds,

2006). Ces paramètres varient, entre autres, en fonction de saisons, par conséquent, les communautés phytoplanctoniques présentent une **saisonnalité** et plusieurs théories ont été donc développées pour en décrire les dynamiques (voir synthèses Reynolds, 2006; Trombetta et al., 2019). Ces théories se basent sur la stratification de la colonne d'eau et d'autres facteurs liés, comme la disponibilité de nutriments, la pénétration de la lumière et la régulation « *top-down* », liée à la présence de prédateurs (Margalef, 1958, 1978; Reynolds, 2006; Winder & Sommer, 2012; Pulina et al., 2012). Dans les eaux côtières et lagunaires, les modifications des propriétés de la colonne d'eau sont complexes et rapides, notamment pour les apports en nutriments et eau douce des bassins versants. Les efflorescences massives de phytoplancton, dites **blooms**, sont fréquentes dans ces milieux si dynamiques, et constituent un important évènement supportant la productivité primaire annuelle et le transfert d'énergie pour le réseau trophique (Hallegraeff, 1993; Smayda, 1997b, 1997a). Dans les systèmes côtiers, ces évènements typiquement se produisent au printemps et automne, en relation avec une augmentation de l'irradiation et des apports en nutriments (Margalef, 1958, 1978; Reynolds, 2006; Trombetta et al., 2019). Toutefois, les observations sur le terrain sont difficilement correspondantes aux théories et plus de connaissances sont nécessaires pour compléter la compréhension de ces dynamiques, en particulier dans les milieux forts instables, comme le milieu lagunaire (Trombetta et al., 2019).

Le phytoplancton, grâce à sa diversité, sa capacité de réponse rapide aux variations environnementales et sa position basale au sein des réseaux trophiques, est considéré un **excellent indicateur** de l'état et du fonctionnement des milieux aquatiques, souvent utilisé dans les normes de gestion environnementale (European Union (EU), 2000; Birk et al., 2012). La diversité du phytoplancton fournit des indications sur l'état du système et sur ses potentielles évolutions : les groupes taxonomiques que l'on retrouve dans le milieu reflètent ses caractéristiques en raison des préférences liées aux dynamiques de la colonne d'eau, à la température et la salinité, à la disponibilité en nutriments, etc., qui sont à leur tour influencées par les conditions météorologiques et, en milieu côtier et lagunaire en particulier, pas les apports du bassin versant et de la mer. Par exemple, de façon générale les dinoflagellés préfèrent des conditions eutrophes et une colonne d'eau stable et stratifiée, grâce à la présence des flagelles, qui leur confèrent une grande capacité de motilité, alors que les diatomées profitent des conditions de mélange des eaux (Margalef, 1978; Reynolds, 2006). D'autres groupes, typiquement en milieu lagunaire, sont associés à des conditions spécifiques du milieu, comme les chlorophycées aux arrivées d'eau douce et les cryptophytes à de faibles salinités également et à de fortes turbidités, alors que les cyanobactéries sont plutôt associées à des températures et concentrations en nutriments élevées (Paerl et al., 2003; Gregor & Maršálek, 2004; Bec et al., 2011; Catherine et al., 2012; Coelho et al., 2015).

De plus, les différents groupes fournissent un apport varié à la productivité et donc des changements en termes de diversité et de composition peuvent apporter des informations sur de potentiels impacts aux niveaux trophiques supérieurs. Par exemple, des modifications des espèces composantes les communautés peuvent amener à des variations en termes de taille, qui sont importantes et ont un impact sur le zooplancton et d'autres planctivores en raison de la relation de taille proie-prédateur et de la prédation sélective (Reynolds, 2006). Ensuite, des variations en termes de composition spécifique peuvent aussi avoir des effets à des niveaux trophiques supérieurs, car les différents groupes phytoplanctoniques ont de différentes valeurs nutritionnelles. Notamment, les diatomées et les Cryptophytes sont des groupes hautement nutritifs, surtout en termes de contenu en acides gras, nécessaires pour la croissance, la reproduction et le développement de moyens défensifs à plusieurs niveaux trophiques supérieurs ; au contraire, les Chlorophytes et les Chrysophyceae ont une valeur nutritionnelle modérée (Taipale et al., 2013; Astorg et al., 2022).

Les proliférations phytoplanctoniques, en particulier de diatomées, sont essentielles pour le soutien de la productivité, et ont donc également un intérêt en termes de services écosystémiques, notamment dans un cadre d'exploitation halieutique (Pernet et al., 2012). Néanmoins, dans certains cas, ces blooms peuvent constituer une menace au fonctionnement écosystémique et aux services fournis, et prennent le nom de **Harmful Algal Blooms** (HABs). Ces HABs compromettent la qualité du système à travers la perturbation du réseau trophique, la consommation d'oxygène, les dommages aux branchies des poissons en cage et la production de toxines, parfois létales pour la faune et l'homme (Figure 2; Hallegraeff, 1993; Smayda, 1997b). Parmi les groupes phytoplanctoniques, les dinoflagellés représentent 75 % des espèces phytoplanctoniques capables de produire de toxines (Smayda, 1997a). Toutefois, certaines diatomées, notamment certaines espèces du genre *Pseudo-nitzschia* sp., cyanobactéries et quelques espèces des groupes Raphidophyceae et Haptophyta (Figure 1) sont aussi capables de produire différents types de toxines (Lee, 2008). Les HABs sont historiquement connus, mais récemment se vérifient de façon plus fréquente et intense dans les côtes et les lagunes au niveau mondial (Smayda, 1997a; Hallegraeff, 2010; Kudela et al., 2015). Leur lien avec les perturbations d'origine anthropique, notamment l'eutrophisation, et le changement climatique, rendent ces phénomènes des indicateurs d'une dynamique déséquilibrée du système, sans compter les pertes économiques conséquentes la perte de valeur commerciale des produits halieutiques (Smayda, 1997b; Salcedo-Garduño et al., 2019).

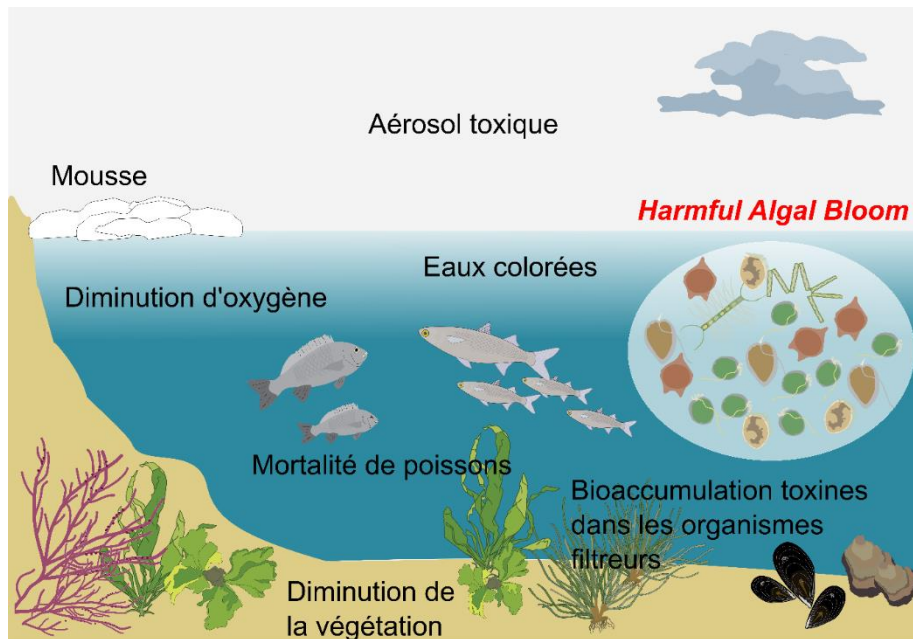


Figure 2 Schéma représentant un phénomène de HAB et les possibles conséquences sur le milieu.

1.3 Ressource biotechnologique

Au-delà de la production de toxines, le phytoplancton constitue une excellente ressource grâce à ses capacités métaboliques et la capacité de produire de nombreuses molécules de potentiel intérêt biotechnologique. En effet, les microalgues constituent un élément prioritaire émergent dans le secteur de la bioéconomie (Rizwan et al., 2018; Fernández et al., 2021). Le spectre des possibilités est extrêmement vaste, allant de la production de biomatériaux (e.g. bioplastiques), de biocarburants, de biofertilisants et de molécules utilisés dans le domaine de la médecine, des cosmétiques, de la nutrition et de la santé humaine et animale, jusqu'à de services de bioremédiation environnementale, traitement des eaux usées et contrôle de la qualité de l'eau (Rizwan et al., 2018; Han et al., 2019; Fernández et al., 2021). En particulier, l'un des majeurs domaines d'application des microalgues est celui de l'aquaculture, où elles sont utilisées pour améliorer la couleur de certaines espèces exploitées (salmonidés, crevettes), pour stabiliser et améliorer le milieu de culture, pour augmenter les défenses immunitaires des animaux exploités (et donc réduire l'utilisation d'antibiotiques et médicaments), mais surtout comme nourriture, car particulièrement appréciées pour les apports en lipides essentiels et autres molécules d'intérêt (Rizwan et al., 2018; Han et al., 2019). Différentes espèces sont utilisées dans ce secteur, dont principalement les Chlorophytes *Chlorella* et *Tetraselmis*, les Haptophytes *Isochrysis* et *Pavlova*, l'Ochrophyte *Nannochloropsis*, et les diatomées *Phaeodactylum*, *Chaetoceros*, *Skeletonema* et *Thalassiosira* (Rizwan et al., 2018).

2. LES LAGUNES CÔTIÈRES MÉDITERRANÉENNES : DES SYSTÈMES COMPLEXES

2.1 Définition et services écosystémiques fournis

Dans un monde en constant changement, les systèmes côtiers sont particulièrement fragiles ; les activités humaines, l'expansion de l'urbanisation et les effets du changement climatique se concentrent sur les côtes, provoquant une soustraction progressive d'habitats, connue sous le nom de *coastal squeeze*, qui impacte le fonctionnement naturel des systèmes côtiers (Chacón Abarca et al., 2021).

Les lagunes côtières sont des zones humides littorales communes dans le monde entier et constituent 13% des surfaces côtières mondiales (Nixon, 1982; Kjerfve, 1994). Malgré une connaissance encore limitée et fragmentée, on estime que dans la région méditerranéenne plus de 400 lagunes sont présentes et couvrent environ 6400 km² (Cataudella et al., 2015). Les côtes méditerranéennes ont une histoire anthropique millénaire et sont sujettes à une urbanisation croissante (Aurelle et al., 2022). De plus, la Méditerranée est considérée comme un *hotspot* pour le changement climatique selon les projections (MedECC, 2020; Cos et al., 2022). Les lagunes côtières, qui sont des milieux de transition entre terre et mer, caractérisées par des fortes dynamiques et instabilités naturelles, sont donc particulièrement fragiles face à ces pressions croissantes, en particulier en Méditerranée (MWO, 2018; Chacón Abarca et al., 2021).

Les lagunes côtières sont définies comme des plans d'eau littoraux et peu profonds, séparés de la mer par une barrière, connectés au moins de façon intermittente avec la mer à travers des ouvertures restreintes, et généralement orientés parallèlement à la côte (Kjerfve, 1994). Toutefois, ces milieux présentent de formidables différences en fonction de leurs origines géologiques et de leurs tailles, de leurs gradients physico-chimiques et de leurs connectivités aux systèmes adjacents, ce qui entraîne des difficultés au niveau de leur classification et l'existence de nombreux termes pour les définir, souvent liés au contexte régional : lagunes, étangs, *ponds*, *marsh*, marais, *stagni*, *sacca*, SECS (*Semi-Enclosed Costal Systems*) ou, plus récemment, ICOLLs (*Intermittently Closed and Opened Lakes and Lagoons*) (Tagliapietra et al., 2009; Newton et al., 2014; Cataudella et al., 2015). Le terme « lagune » est souvent utilisé comme une extension de langage pour représenter tous ces milieux.

Les lagunes méditerranéennes, comparées à celles atlantiques par exemple, sont moins influencées par les variations de marée, mais dépendent en forte mesure des apports en eau douce de leurs bassins versants (Figure 3). Des échanges avec la mer se font à travers la ou les ouvertures, dites *graus*, qui percent la barrière sableuse de séparation, appelée *lido* en Méditerranée. Cet équilibre dynamique entre les apports d'eau douce du bassin versant et d'eau salée de la mer fait que les eaux lagunaires montrent de forts gradients de salinité et une grande variabilité, qui confère aux systèmes des caractères allant d'oligohalins (salinité de 0,5 à 5), mésosalins (5 à 18), polyhalins (18 à 30), euhalins (30 à 40) jusqu'à hyperhalins (salinité > 40) (Venice System, 1958).

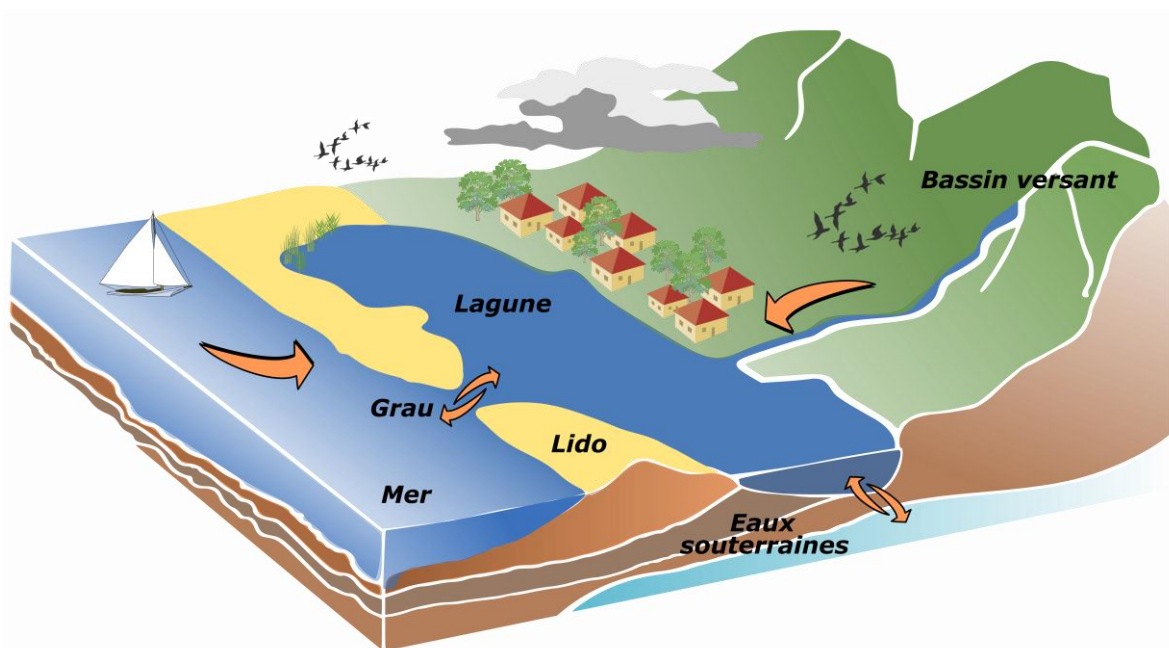


Figure 3 Représentation schématique d'une lagune et de ses connexions (flèches) avec les systèmes adjacents (bassin versant, milieu marin, eaux souterraines).

En raison de leur localisation, les lagunes côtières sont des systèmes à plusieurs interfaces, dont le fonctionnement dépend fortement des interactions du plan d'eau avec les conditions climatiques locales, les flux d'eaux douces du bassin versant et des eaux souterraines, les échanges avec la mer, les interactions avec les sédiments (Pérez-Ruzafa et al., 2011c, 2019b). Ces interfaces multiples, associées aux volumes relativement faibles des masses d'eau, rendent les lagunes extrêmement réactives aux changements environnementaux et typiquement caractérisées de gradients physico-chimiques importants et d'une forte variabilité spatiale et temporelle (Pérez-Ruzafa et al., 2019b). Cette complexité hydrologique et fonctionnelle est aussi couplée à certaines restrictions aux flux énergétiques, sous forme de barrières physiques naturelles et propres de la morphologie lagunaire (communication restreinte avec la mer à travers les graus, végétation, rochers) ou artificielles (digues, bordigues) (Pérez-Ruzafa et al., 2018). Ces

situations particulières et uniques permettent d'avoir des systèmes extrêmement riches et productifs dans lesquels des configurations physiques, hydrologiques et biologiques très hétérogènes se forment, rendant les systèmes lagunaires particulièrement complexes, ce qui les différencie des simples estuaires (Pérez-Ruzafa et al., 2011c).

La richesse et la complexité de ces milieux induisent la présence de mosaïques d'habitats fortement propices à accueillir une biodiversité importante (Pérez-Ruzafa et al., 2011a). Cette biodiversité est aussi un « réservoir » d'importance capitale pour de nombreuses espèces : des poissons, mollusques et crustacés se reproduisent, s'alimentent ou vivent leur phase larvaire au sein des lagunes. De plus, ces systèmes constituent des zones d'alimentation, de reproduction, d'hivernage ou de passage pour plusieurs espèces d'oiseaux et des habitats idéaux pour reptiles et amphibiens (Pearce & Crivelli, 1994; MWO, 2018).

Au-delà de leur importance biologique, les lagunes ont aussi un intérêt écologique, économique et social non négligeable (Pérez-Ruzafa et al., 2020). En effet, grâce à leur spécificité et grande richesse, les lagunes assurent de nombreuses fonctions et rendent d'importants services écosystémiques aux populations humaines (Newton et al., 2018; Pérez-Ruzafa et al., 2019b).

Quatre grandes catégories de services écosystémiques sont identifiées en relation avec les supports fournis au bien-être humain (Figure 4 ; MEA, 2005). En premier lieu, les lagunes fournissent des services d'**auto-entretien** et de **régulation**, tels que les cycles des nutriments, les formations des sols, la production primaire et fixation du carbone et la recharge des nappes phréatiques (MEA, 2005; Pérez-Ruzafa et al., 2019b). Ensuite, elles contribuent à la régulation du climat local et régional, à l'épuration des eaux et protègent les côtes et les berges des phénomènes de crue et d'inondation ainsi que des tempêtes et de l'érosion côtière, grâce à leur capacité d'absorption et d'accumulation de sédiments (Figure 4 ; Barbier et al., 2011; Newton et al., 2018; Pérez-Ruzafa et al., 2019). Ces fonctions sont aussi de grand intérêt au regard du changement climatique, car elles vont pouvoir fournir une protection du littoral des phénomènes d'érosion et d'inondation qui seront de plus en plus fréquents et intenses selon les projections.

Grâce à leur grande productivité, les lagunes fournissent également des services d'**approvisionnement**, étant historiquement exploitées pour la pêche, l'aquaculture et la conchyliculture typiquement, mais aussi à travers leur rôle de nourricerie, zone d'alimentation et de reproduction pour de nombreuses espèces marines d'intérêt commerciale (Figure 4 ; Elliott et al., 2007b; Barbier et al., 2011; Newton et al., 2014). Finalement, les lagunes ont aussi une valeur paysagère liée à l'esthétique et à leur richesse et fournissent donc des services **culturels et patrimoniaux**, tels que des opportunités pour l'éducation, des lieux de loisir, d'inspiration artistique et de tourisme,

mais aussi des opportunités d'emploi liées aux activités développées autour de ces milieux (Figure 4 ; Barbier et al., 2011; Newton et al., 2018; Pérez-Ruzafa et al., 2019). Les lagunes côtières font partie des habitats qui rendent le plus de services écosystémiques au monde (Anthony et al., 2009; Newton et al., 2018).

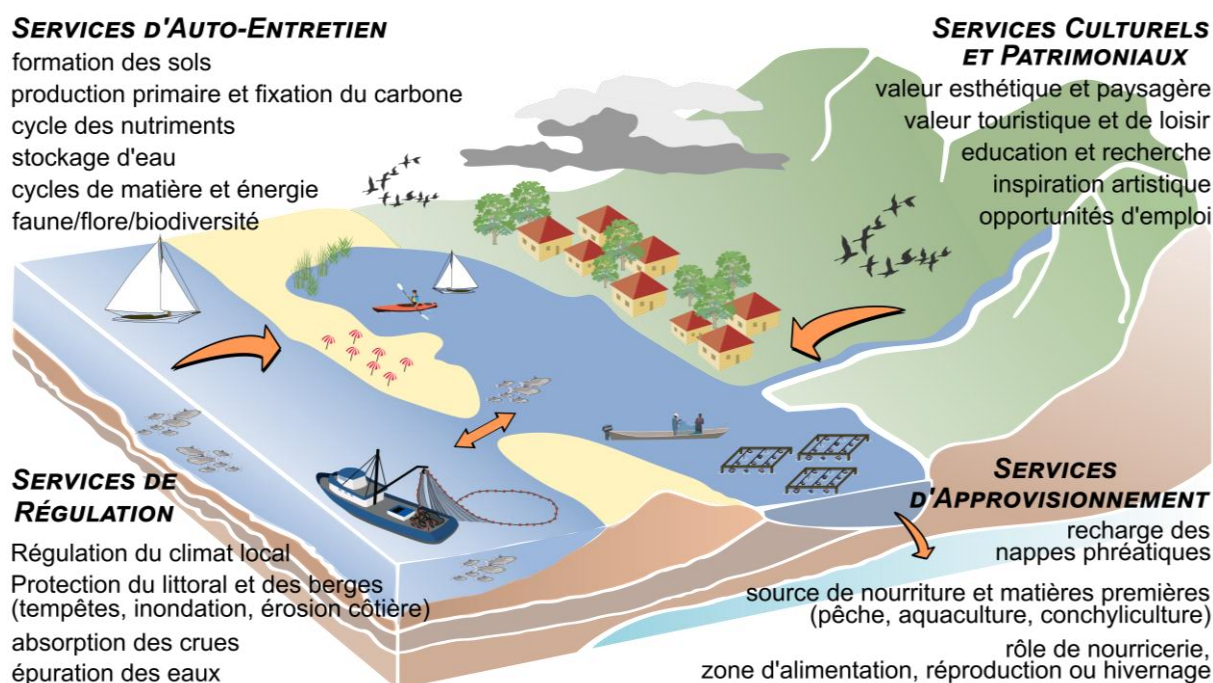


Figure 4 Schéma des principaux services écosystémiques fournis par les milieux lagunaires, selon la classification établie par le *Millennial Ecosystem Assessment Program* (MEA, 2005) et Newton et al. (2018). Les flèches indiquent les principaux échanges en eau, matière ou organismes, entre la lagune, la mer, le bassin versant et les eaux souterraines.

2.2 Menaces

Malgré leurs intérêts, les lagunes côtières comptent aussi parmi les écosystèmes les plus menacés et sont en voie de disparition (Pérez-Ruzafa et al., 2011a; Ferrarin et al., 2014; Birch et al., 2022). Historiquement ces systèmes étaient même considérés comme insalubres, car associés à la prolifération de certaines maladies, comme le paludisme, et pendant plusieurs siècles ils ont été comblés (Cizel, 2017). Les premiers textes sur la pratique de l'**assèchement des zones humides** datent du XVI^e siècle et font référence à la nécessité hygiénique de mettre fin à l'insalubrité de ces milieux et au besoin de récupérer des terres afin de pouvoir les exploiter pour l'agriculture (Cizel, 2017). Malgré le fait que le comblement des zones humides est à ce jour fortement règlementé, en France, Espagne, Italie et en Grèce, une perte de plus qu'un tiers des zones humides a eu lieu pendant les deux dernières générations à cause de cette pratique, qui a affecté en particulier des lagunes de petite surface (Diamantopoulou et al., 2008; Cizel, 2017).

Les principales menaces directes d'origine anthropique sont aujourd'hui **l'urbanisation** et **l'artificialisation** (MWO, 2018; Chacón Abarca et al., 2021; Aurelle et al., 2022). Ces phénomènes, ainsi que les activités industrielles et agricoles qui se développent souvent sur les bassins versants des lagunes, entraînent la dégradation et la perte d'habitat, à travers la modification de l'hydrologie et les rejets. La substitution de la végétation aux alentours des lagunes pour créer des espaces urbains ou agricoles, ainsi que la création de chenaux d'irrigation, modifient le fonctionnement hydrique des systèmes lagunaires et le ruissellement, pouvant entraîner des modifications importantes des milieux (Fichez et al., 2017; Pérez-Ruzafa et al., 2019b). Parallèlement, les rejets d'origine urbaine, industrielle ou agricole, apportent des polluants de différentes origines (i.e. détergents, hydrocarbures, contaminants pharmaceutiques) et des quantités importantes de matière organique et de nutriments (Pérez-Ruzafa et al., 2019b). Une des problématiques les plus importantes en milieu lagunaire est en effet **l'eutrophisation**, un enrichissement excessif des eaux consécutif à des apports massifs en nutriments (Cloern, 2001; Lloret et al., 2008; Zaldívar et al., 2008; Padedda et al., 2019). Une des sources les plus importantes d'azote (N) et de phosphore (P) dans les milieux aquatiques côtiers sont les activités agricoles, notamment à cause des engrais synthétiques et des élevages, et urbaines, surtout des rejets des eaux usées et des émissions des combustibles fossiles, relâchant de l'azote (Cloern, 2001; Zaldívar et al., 2008; Malone & Newton, 2020). À l'échelle globale, à partir des années 1920, l'augmentation d'engrais artificiellement enrichis en azote et l'augmentation des apports en azote et phosphore dans les bassins versants ont amené à un enrichissement des systèmes côtiers et à un déséquilibre des rapports N:P, en raison de la différente réactivité de ces éléments et de leurs interactions avec le compartiment biotique (Cloern, 2001; Zaldívar et al., 2008). Ces éléments peuvent en effet être introduits dans les systèmes sous des formes différentes, interagir avec l'environnement et passer sous plusieurs processus de transformation. Généralement, l'azote sous forme d'ammonium (NH_4^+) est un marqueur de rejets des stations d'épuration, d'excrétion animale et de décomposition bactérienne de la matière organique, notamment au niveau des sédiments (Orsoni, 2001; Bec et al., 2005). Les nitrites (NO_2^-) sont une forme intermédiaire entre l'azote réduit (NH_4^+) et la forme oxydée des nitrates (NO_3^-) (Orsoni, 2001). Ces derniers indiquent typiquement des pollutions de type agricole, par lessivage des engrais, et urbaines, notamment des systèmes d'assainissement, donc ils sont souvent utilisés comme marqueurs d'impact anthropique dans les eaux de surface et souterraines (Appelo & Postma, 2005; Re et al., 2017; Vystavna et al., 2017; Erostate et al., 2018). Les enrichissements en phosphore, deuxième acteur en jeu dans le processus d'eutrophisation, dérivent principalement des engrais synthétiques, mais les dynamiques de cet élément sont compliquées, car il a la tendance à s'accumuler dans les

sédiments et son relargage dépend fortement de la température (Orsoni, 2001; Bec et al., 2005). Depuis plusieurs années, des efforts importants ont été mis en place pour contraster le processus d'eutrophisation dans les milieux lagunaires et les résultats semblent être à ce jour encourageants, avec plusieurs lagunes, au moins à l'échelle française, qui sont passées à une trajectoire d'oligotrophisation (Leruste et al., 2016, 2018, 2019; Derolez et al., 2020a). Toutefois, l'eutrophisation est toujours considérée une cause majeure de dégradation des lagunes méditerranéennes. Elle constitue un risque écologique, car elle favorise les crises dystrophiques et des phénomènes d'anoxie, liés à la consommation de la matière organique et donc de potentiels cas de mortalité de la macrofaune, entraînant une dégradation du milieu et la perte de services écosystémiques (Cloern, 2001; Zaldívar et al., 2008; Newton et al., 2014).

Parallèlement à ces problématiques, le **changement climatique** en progression impacte également les systèmes côtiers lagunaires : les températures augmentent progressivement et les périodes pluvieuses se réduisent de plus en plus à des phénomènes de courte durée et forte intensité (Cos et al., 2022; MedECC, 2020). Il a été estimé que les impacts sur les milieux lagunaires seront amplifiés par rapport au milieu marin, avec des températures des eaux jusqu'à 15 % plus élevées et des augmentations de salinité plus de quarante fois plus fortes qu'en mer pour les lagunes méditerranéennes (Ferrarin et al., 2014). Les changements climatiques impactent donc directement l'hydrologie des systèmes lagunaires, mais également indirectement sur le long terme, à travers des évaporations de plus en plus importantes et une diminution de la disponibilité et des flux d'eau douce, qui compromettent la connectivité des lagunes aux milieux adjacents.

Les perturbations d'origine anthropique et le changement climatique agissent conjointement et sont souvent le moteur des changements des compartiments biologiques. En particulier en milieu lagunaire, l'action combinée des menaces anthropiques, notamment l'eutrophisation, et du changement climatique favorise le développement de certains organismes, comme le phytoplancton. Souvent des phénomènes de *bloom*, c'est-à-dire des proliférations massives de ces microorganismes, ont été liés aux causes précédemment citées (Fischer et al., 2020; Hallegraeff, 2010; Kudela et al., 2015; Pulina et al., 2012; Trombetta et al., 2019). Si des **HABs** se produisent, ils peuvent constituer une menace pour la santé humaine, notamment dans des cas d'exploitation aquacole, par bioaccumulation des toxines dans les organismes commercialisés (Smayda, 1997b; Zingone et al., 2021). Ces phénomènes peuvent donc entraîner une perte de services écosystémiques à travers des arrêtés d'interdiction de pêche ou de vente de produits halieutiques et aquacoles pour précaution envers les

potentielles conséquences sanitaires sur l'homme (Hallegraeff, 1993; Smayda, 1997b, 1997a).

La dégradation progressive des systèmes lagunaires sous les menaces croissantes entraîne une simplification des communautés biologiques et une **homogénéisation** biotique et abiotique, qui rendent les milieux de plus en plus fragiles. Cette fragilité joue un rôle fondamental dans une des autres grandes problématiques émergentes, particulièrement importantes au niveau des lagunes : l'**invasion biologique** (Elmqvist et al., 2003; Boudouresque & Verlaque, 2012; Tordoni et al., 2019). L'introduction d'espèces non natives est une des majeures sources de pollution biologique, particulièrement dans le monde globalisé du Nouveau Millénaire (Elliott, 2003; Occhipinti-Ambrogi et al., 2011; Boudouresque & Verlaque, 2012). Les systèmes côtiers et lagunaires sont parmi les plus envahis (Dawson et al., 2017; Tordoni et al., 2019). Souvent ces espèces envahissantes en milieu lagunaire profitent des conditions dégradées et deviennent parfois invasives, en provoquant des dégâts au niveau écologique, mais aussi économique (Boudouresque & Verlaque, 2012; Katsanevakis et al., 2014). Elles peuvent modifier la diversité, soutenir l'homogénéisation biotique et la dégradation ultérieure, modifier le fonctionnement écologique à travers des relations de prédation et compétition, et finalement impacter de façon directe ou indirecte les activités humaines, comme la pêche ou le tourisme (Boudouresque & Verlaque, 2012; Katsanevakis et al., 2014).

2.3 Trajectoires d'évolution et fonctionnement

Les trajectoires de dégradation des systèmes lagunaires sont bien connues et elles peuvent être décrites à travers différentes étapes de succession de producteurs primaires, particulièrement réactifs aux changements du milieu et dont les dynamiques sont contrôlées principalement par la lumière et la disponibilité de nutriments (Figure 5 ; Schramm, 1999; De Wit et al., 2017; Pasqualini et al., 2017). Dans des conditions de bon état du milieu, caractérisé par de faibles teneurs en nutriments inorganiques et une faible turbidité, les producteurs primaires sont dominés par des macrophytes benthiques pérennes, telles que les phanérogames *Ruppia* et *Zostera* spp., qui stabilisent le substrat (Figure 5 ; Schramm, 1999; Pergent-Martini et al., 2005; Pergent et al., 2006). En fonction de l'augmentation progressive des concentrations en nutriments, le système passe à travers des étapes successives : initialement a lieu une limitation lumineuse due au développement d'organismes épiphytes opportunistes sur les feuilles des phanérogames, qui subissent donc un progressif déclin ; ensuite, des macroalgues opportunistes, telles que *Gracilaria*, *Ulva* et *Cladophora* spp., se développent, jusqu'à atteindre finalement un état turbide dominé par le phytoplancton au fur et à mesure de

l'augmenter de la dégradation (Figure 5 ; Schramm, 1999; Bec et al., 2011; De Wit et al., 2017; Le Fur et al., 2018).

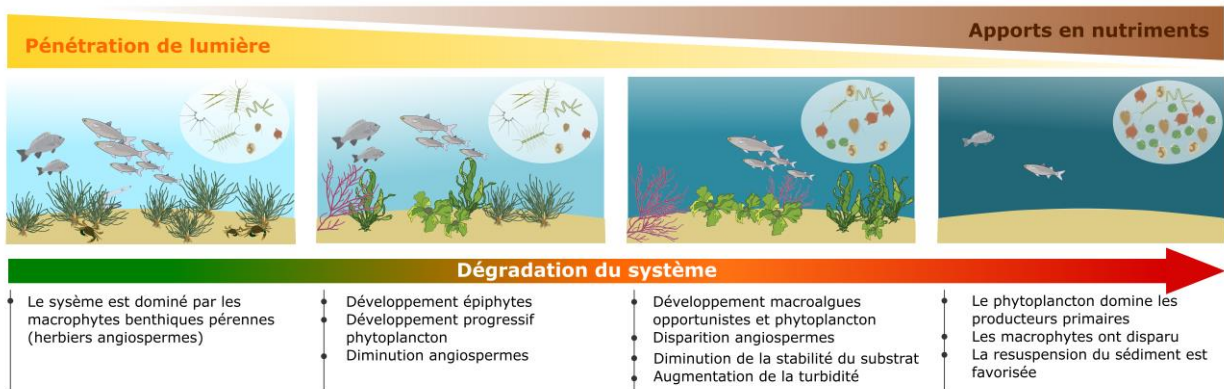


Figure 5 Modèle conceptuel des différentes étapes du processus de dégradation en milieu lagunaire, suivant les modifications typiques de la dominance des producteurs primaires et des paramètres structurants associés (d'après Schramm, 1999; Le Fur et al., 2018).

Toutefois, les trajectoires d'évolution des écosystèmes ne suivent pas des parcours linéaires. Ils existent des seuils critiques tels qu'une fois dépassés, le système tombe brusquement dans un nouvel état, selon un processus par saut, qui est nommé « *regime shift* » (Scheffer et al., 2001; Scheffer & Carpenter, 2003). Si le système est proche d'un point de rupture (Figure 6a, le point F₂), un petit changement des conditions peut le faire tomber dans un état alternatif plus bas (« *forward shift* », Figure 6a). Le *forward shift* peut être provoqué par une perturbation, si elle est suffisamment puissante à dépasser le seuil critique (Figure 6b). Pour revenir à un état « plus haut », il faut que le système subisse un « *backward shift* » (Figure 6a). Toutefois, les différents états alternatifs du système présentent des bassins d'attraction plus ou moins profonds, qui en déterminent la stabilité (Figure 6c) : par exemple, une perturbation assez puissante à amener le système au-delà du bord du bassin d'attraction peut déterminer un *shift* (Figure 6c et b), par contre, dans un cadre de trajectoire de dégradation, si le nouvel état dégradé possède un bassin d'attraction profond (il s'agira donc d'un « état stable alternatif »), il faudra beaucoup d'énergie pour reconvertir le système, donc le *backward shift* se produira seulement si le changement des conditions sera inversé suffisamment pour atteindre un nouveau point de bifurcation (Figure 6a, le point F₁).

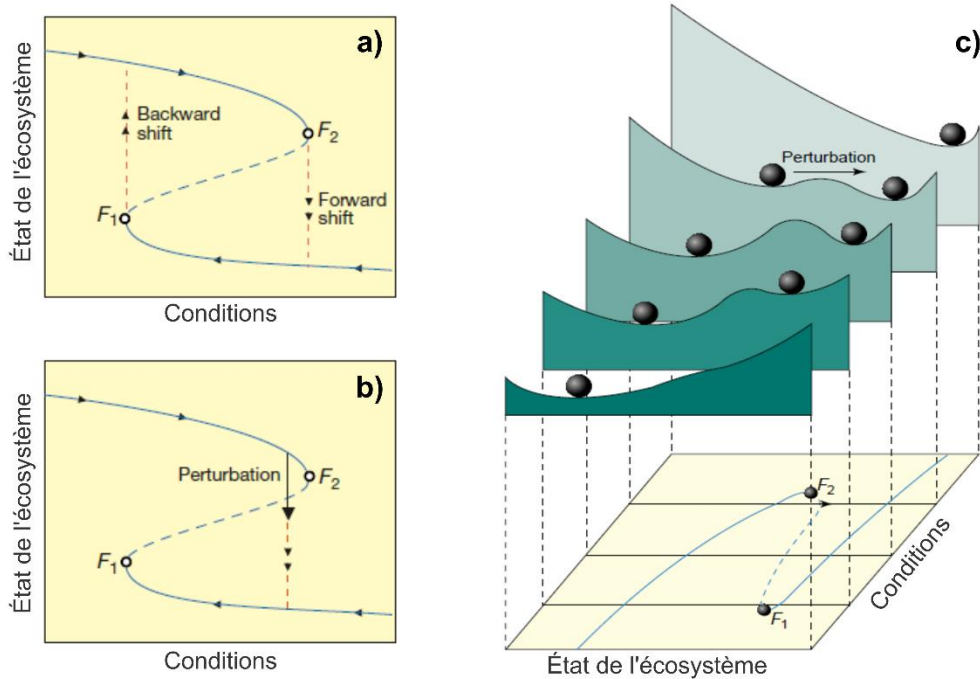


Figure 6 Schémas représentant les dynamiques de shift des systèmes et le principe des bassins d'attraction. À gauche, deux processus de shift vers des états alternatifs. a) Représentation du « *forward shift* » et « *backward shift* » du système entre différents états en fonction du changement des conditions et des respectifs points de bifurcation (F_2 et F_1). b) Exemple de *forward shift* provoqué par une perturbation. c) Représentation des bassins d'attraction de l'état du système sous de cinq différentes conditions (d'après Scheffer et al., 2001; Scheffer & Carpenter, 2003).

Le concept des bassins d'attraction est utile pour comprendre les notions de résilience, résistance et hystérésis, développées en écologie pour la description et compréhension des trajectoires d'évolution des écosystèmes. La **résistance** est définie comme la capacité du système à ne pas subir d'altération de son état face à une perturbation ou changement (Folke et al., 2004; Elliott et al., 2007a). La **résilience** est classiquement définie comme la capacité du système de revenir à l'équilibre dans un état précédent une perturbation, mais cette notion a désormais évolué vers un concept plus large, défini comme la capacité du système de subir une perturbation sans perdre sa fonction et son identité (Walker et al., 2006; Cote & Nightingale, 2012). En effet, si l'écosystème subit un retour complet à son état initial, la résilience est complète (Figure 7, Résilience (a)), mais le système peut basculer sur un état intermédiaire, en fonction d'une résilience incomplète (Figure 7, Résilience (b)). Dans les trajectoires d'évolution des écosystèmes, la résilience des différents états possibles est influencée donc par leurs bassins d'attraction : plus le bassin est profond, plus la résilience est forte. Le fait qu'il soit difficile de revenir à un état précédent et qu'on ait plutôt plusieurs états alternatifs intermédiaires est dû à l'hystérésis. Cette propriété est liée à l'inertie du système, qui a un délai de réponse aux changements, par exemple suite à la diminution de pression

(Figure 7, hystérésis I) et qui peut donc déterminer un écart entre l'état atteint et l'état initial (Figure 7, hystérésis II) (Elliott et al., 2007a).

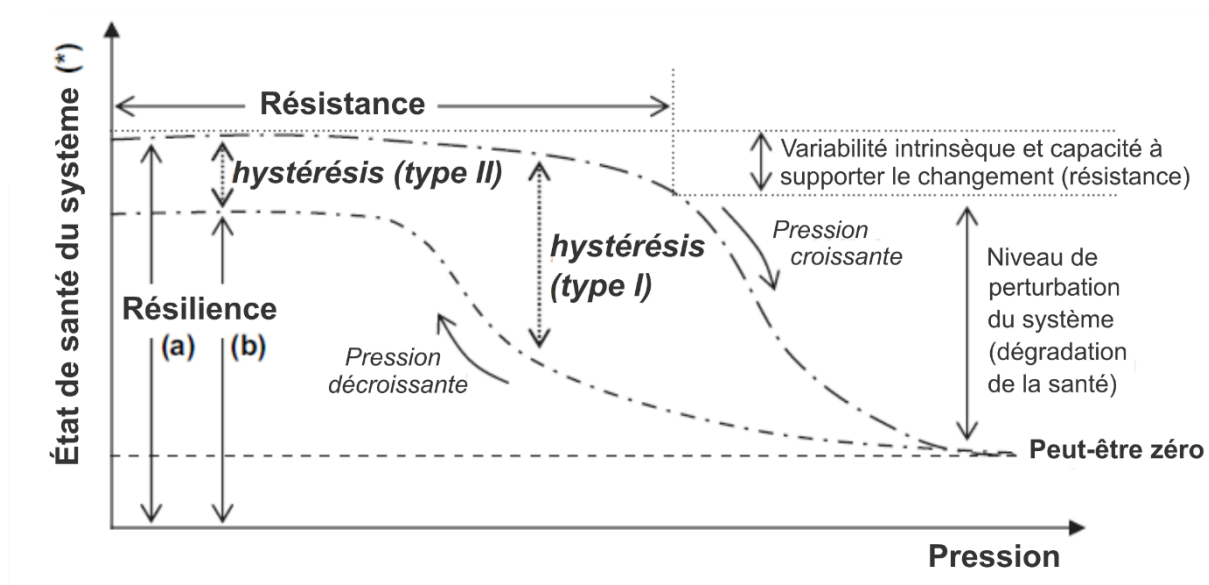


Figure 7 Modèle conceptuel des dynamiques de changement d'état d'un écosystème en fonction d'un gradient de pression croissante ou décroissante. (*) État de santé du système défini selon un indicateur de structure ou de fonction ; (a) Résilience complète ; (b) Résilience incomplète ; d'après Elliott et al., 2007a).

Ces notions et propriétés des écosystèmes sont fondamentales dans la gestion environnementale. En effet, elles font que les trajectoires de restauration des systèmes dégradés ne suivent pas le parcours inverse des trajectoires de dégradation. Les trajectoires de restauration sont donc beaucoup plus imprévisibles et elles sont moins connues par rapport à la dégradation, notamment en milieu lagunaire, où les études à cet égard ont commencé à apparaître assez récemment (Leruste et al., 2016; De Wit et al., 2017). En matière de gestion, il est possible d'effectuer quand cela est nécessaire une restauration passive ou active en fonction d'un **état de référence** (Figure 8). La procédure de restauration écologique prévoit l'identification d'un état de référence, ensuite la description d'un **état désiré**, qui soit proche ou pas de l'état de référence, et enfin la mise en place de stratégies pour converger vers cet état (De Wit et al., 2020). Généralement, la **restauration est dite « passive »** quand l'action humaine se limite à la réduction des pressions agissantes sur le milieu et se base sur la capacité naturelle de résilience du système, pour rétablir spontanément son équilibre (De Wit et al., 2017, 2020). Souvent des actions plus drastiques peuvent être amenées pour améliorer l'état du système ou réduire les temps du processus de convergence vers l'état désiré, en complément d'une restauration passive (De Wit et al., 2017, 2020). Ces actions consistent en des opérations d'éco-ingénierie, par exemple la transplantation de phanérogames

pour reconstituer des herbiers rapidement, et constituent la **restauration active** (De Wit et al., 2017, 2020).

Une question importante de la gestion environnementale réside dans le fait que les définitions d'état de référence et d'état désiré font l'objet de débat : idéalement le premier correspond à un état historique non contaminé, qui est souvent difficile à identifier et à être reflété dans un état désiré. Pour cette raison, la définition de l'état désiré est très importante dans une optique de gestion. Dans un cadre anthropocentrique, où l'objectif de durabilité est central, cette définition a donc une vaste ampleur et doit englober des concepts sociaux, comme la préservation de certains services écosystémiques considérés d'importance par la société (Folke, 2016; Grafton et al., 2019; Walker, 2020). Toutefois, l'état désiré peut être défini sur la base d'indicateurs spécifiques et de standards de qualité imposés par les cadres normatifs (De Wit et al., 2020). Ces cadres normatifs sont utiles pour plusieurs raisons, dont la définition des objectifs, des priorités et des décisions à prendre pour la conservation des écosystèmes.

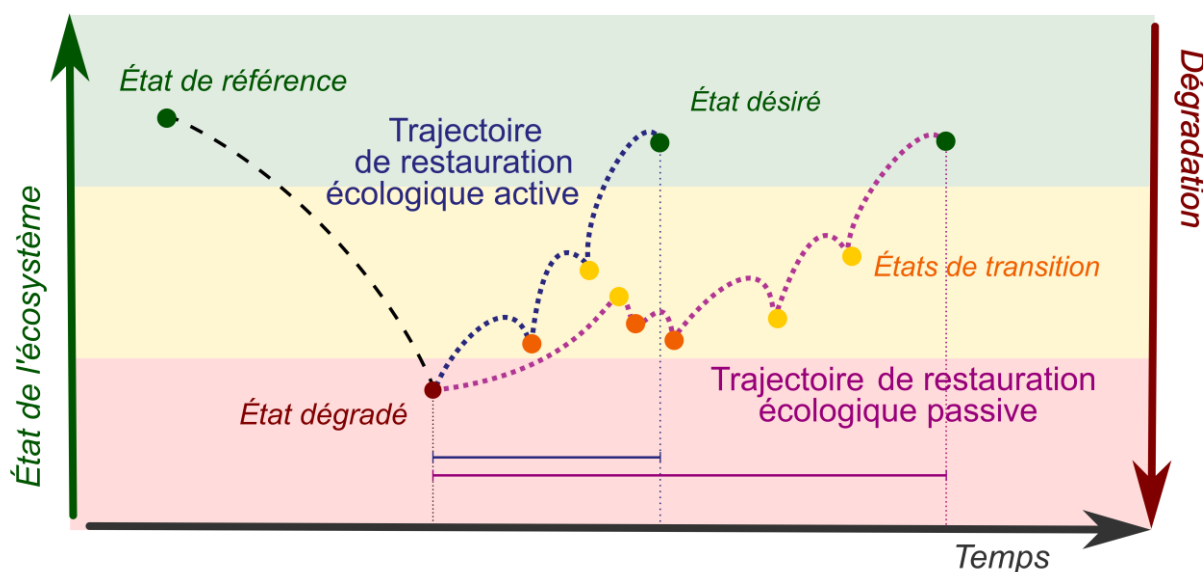


Figure 8 Représentation des trajectoires de restauration du milieu suite à une dégradation. L'écosystème peut évoluer vers l'état désiré avec des trajectoires variables en fonction d'une restauration active (i.e. éco-ingénierie) ou passive (réduction des pressions agissantes), qui sont fréquemment couplées pour accélérer et optimiser la récupération.

2.4 Gestion durable des lagunes côtières : vers un enjeu multifacette

En raison de l'importance et de l'intérêt pour l'homme, ainsi que de leur vulnérabilité, il y a une préoccupation croissante par rapport à la protection et à la gestion des milieux lagunaires. Les études sur les lagunes côtières se sont développées principalement entre les années 60 et 90, mais depuis ces années, les théories initialement développées par rapport aux processus et au fonctionnement des lagunes

côtières ont évolué très rapidement. Considérés comme des milieux simples et gouvernés par des processus physiques, ils sont aujourd'hui étudiés comme des systèmes à haute complexité, présentant de fortes diversités intra et inter -lagunes, et gouvernés par des interactions complexes d'une multitude de facteurs (Pérez-Ruzafa et al., 201b). Pour gérer ces systèmes, il faut comprendre comment ils fonctionnent et il est donc essentiel d'améliorer les connaissances sur les différents compartiments en jeu, ainsi que les relations entre les altérations des processus écologiques et les activités humaines ou autres menaces (Pérez-Ruzafa et al., 201b). Parallèlement, en raison de la grande diversité des lagunes côtières (morphologique, hydrologique, biologique, d'usages, etc.), il y a aussi un besoin d'évaluer ces aspects dans toute la gamme des conditions écologiques que ces systèmes peuvent offrir (Pérez-Ruzafa et al., 201b).

En Europe, plusieurs mesures ont été développées dans l'optique de garantir une protection des milieux lagunaires, comme l'institution de parcs naturels, réserves naturelles, statuts de sites d'intérêt classés « Natura 2000 » et « Ramsar ». Malgré l'application de ces mesures, la plupart des sites demeurent toujours en danger et sont soumis à une dégradation à cause des pressions anthropiques et d'un manque de mesures de gestion contraignantes et efficaces (Zaldívar et al., 2008; Cizel, 2017; De Wit et al., 2017; Grafton et al., 2019; Pérez-Ruzafa et al., 2020; Popoff et al., 2021). De ce fait, en raison de l'importance écologique et socio-économique de ces milieux et de leur fragilité, les États Membres de l'Union Européenne ont implémenté les mesures de conservation des lagunes côtières à travers la Directive Cadre sur l'Eau (DCE; WFD, 2000/60/EC ; European Union (EU), 2000). Dans le cadre de cette directive, des interventions humaines de restauration passive ou active sont envisagées pour pouvoir accélérer les processus de réhabilitation des milieux et attendre l'objectif de « bon état » selon les échéances imposées (De Wit et al., 2017). Malgré cela, beaucoup de sites en France restent encore loin de cet objectif (De Wit et al., 2020). De plus, plusieurs sites restent exclus, car une définition légale de « lagune » n'est pas fournie par la DCE, et donc les lagunes temporaires et de petites surfaces (< 50 ha) ne sont pas prises en compte. En Europe, une autre norme définit des objectifs de conservation pour les lagunes côtières avec une approche différente : la Directive Habitats Faune Flore (DHFF ; European Union (EU), 1992). Cette norme inclue les lagunes méditerranéennes sous la définition d'habitat 1150*-2, ne présente pas de limite de surface et prévoit une série d'indicateurs qui ne correspond pas de façon identique à ceux de la DCE (Barre et al., 2020). Par conséquent, le « bon état » écologique d'une masse d'eau selon la DCE est nécessaire, mais pas forcément suffisant pour que l'habitat de cette même masse d'eau soit qualifié d'un état de conservation favorable par la DHFF, selon laquelle d'autres indicateurs doivent être pris en compte dans l'évaluation de l'état de conservation (Barre et al., 2020).

Cette complexité dans les définitions et les normes de conservation, avec la tendance globale à la dégradation des lagunes, fait qu'il existe un fort besoin de connaissances de base sur les masses d'eau lagunaires et sur leur qualité. La compréhension de l'état et du fonctionnement écologique de ces milieux est un prérequis essentiel pour pouvoir implémenter leur conservation et fournir des outils d'aide à la décision dans leur gestion.

2.4.1 Dynamiques sur le long terme et variations saisonnières

Un des premiers aspects à considérer dans ce *challenge* est l'évaluation des trajectoires sur le long terme. Les suivis de surveillance sont un élément clé pour l'évaluation de l'état du système, mais ils fournissent également des données essentielles pour la reconstruction des trajectoires à long terme, qui sont fondamentales pour comprendre les dynamiques et le fonctionnement du milieu (Biggs et al., 2015; De Wit et al., 2020). En particulier, les études sur le long terme sur le phytoplancton, indicateur précoce du changement, sont informatives sur les trajectoires des milieux et permettent de mettre en évidence les conséquences des processus ou pressions en action, notamment le changement climatique, des actions humaines ou des trajectoires d'eutrophication ou d'oligotrophisation (Pulina et al., 2012; Hernández-Fariñas et al., 2014; Carstensen et al., 2015; Mariani et al., 2015; Derolez et al., 2020b). De nombreuses études ont déjà été réalisées sur les dynamiques à long terme des communautés phytoplanctoniques, toutefois certains aspects demeurent encore méconnus, notamment leur saisonnalité et leurs évolutions dans des lagunes profondes oligotrophes. La majorité des études de ce genre se focalise sur la saison estivale, considérée comme étant la période à plus haute productivité et plus à risque en termes de HABs (Souchu et al., 2010; Bec et al., 2011; Leruste et al., 2016, 2019; Derolez et al., 2020b). Pourtant, l'importance des processus saisonniers n'est pas négligeable : par exemple, des *shifts* dans la saisonnalité des *blooms* phytoplanctoniques printaniers ont déjà été identifiés et mis en relation avec la progression du changement climatique (Pulina et al., 2012; Trombetta et al., 2019). Cela indique que la modification de dynamiques des communautés phytoplanctoniques peut avoir des répercussions sur les saisons suivantes et donc que cet aspect de saisonnalité doit être pris en compte pour une compréhension profonde du fonctionnement du milieu, en particulier dans le cadre du changement climatique et ce d'autant plus en région méditerranéenne.

2.4.2 Approche globale et intégrée

Malgré le rôle d'excellent indicateur du phytoplancton, la complexité des lagunes fait qu'il est parfois compliqué de réduire les analyses et interprétations à ce seul

compartiment, surtout en raison du contexte fortement anthropisé dans lequel ces milieux s'insèrent. Il convient alors d'avoir un regard plus large et de prendre en compte d'autres compartiments biotiques et leurs interactions avec les variations des paramètres du milieu. Par exemple, toujours au niveau des producteurs primaires, les macrophytes sont indicatrices des trajectoires de dégradation et restauration (Schramm, 1999). À différents niveaux trophiques, les invertébrés benthiques sont très sensibles aux variations environnementales (salinité, confinement, eutrophie et crises dystrophiques, type de sédiment...) et peuvent être utiles pour identifier des stress d'origines anthropiques ou liés au changement climatique (Lardicci et al., 1997; Kemp et al., 2005; Basset et al., 2012; Pitacco et al., 2018, 2019). En effet, ils sont des excellents indicateurs de l'état écologique des milieux lagunaires et des trajectoires de restauration, ainsi, ils font aussi partie des indices biologiques pris en compte dans le cadre de la DCE (Simboura & Reizopoulou, 2008; Munari et al., 2009; Basset et al., 2012; Pitacco et al., 2019). En particulier, les huîtres et les filtreurs benthiques sont fortement affectés par des apports nutritifs excessifs, les modifications du système et les exploitations halieutiques (Kemp et al., 2005). Encore, la DCE inclut aussi un indice basé sur la faune piscicole, elle aussi indicatrice de l'état et du changement des milieux : des changements dans les communautés piscicoles ont été mis en relation avec la diminution de la qualité des eaux, les bouleversements hydrologiques (parfois entraînés par des actions de gestion) et les variations de salinité, le changement climatique, l'exploitation de pêche et la perte d'habitat (Kemp et al., 2005; Elliott et al., 2007b; Pérez-Ruzafa et al., 2007; Prestrelo & Monteiro-Neto, 2016; Ilarri et al., 2022). Également, les oiseaux d'eau, en particulier en milieu lagunaire, couvrent un rôle essentiel dans les processus écologiques et répondent aux variations induites par des pressions, anthropiques et non, comme l'eutrophisation, le changement climatique, les espèces invasives, les activités de pêche et les altérations des stocks de poissons (Aymerich & Celdrán, 2011). Malgré le fait que les oiseaux d'eau soient exclus des indices biotiques imposés par la DCE, ils sont des bons indicateurs de l'état et du fonctionnement des milieux lagunaires et peuvent constituer des signaux précoces de changement indésirable (Aymerich & Celdrán, 2011). Finalement, les espèces invasives donnent des informations importantes sur les trajectoires et les états écologiques des systèmes aquatiques et lagunaires en particulier, et constituent notamment des symptômes, mais aussi des *drivers* de la dégradation du système (Boudouresque & Verlaque, 2012; Tordoni et al., 2019).

Pour comprendre efficacement les dynamiques des communautés biotiques et les variations environnementales au sein des systèmes lagunaires, il est essentiel de considérer les échanges et les connexions avec les hydrosystèmes adjacents, autrement dit, le bassin versant et la mer, qui façonnent les caractéristiques du plan d'eau lui-même. Ce regard global et intégré sur le système, avec ses différentes composantes

biotiques et abiotiques et les interrelations qui viennent s'y constituer, engendre une **approche écosystémique (Ecosystem-based Approach – EBA)**, indispensable pour la compréhension du fonctionnement écologique (Berkes, 2012; Boudouresque et al., 2020).

Cette approche globale, incluant différents systèmes et compartiments, amène logiquement à la prise en compte de la composante humaine dans les écosystèmes (Walker et al., 2006; Hobbs et al., 2009; Cote & Nightingale, 2012; Folke, 2016; Elmqvist et al., 2019; Grafton et al., 2019; Walker, 2020). Malgré les débats, toujours d'actualité, sur la séparation des systèmes sociaux et des systèmes naturels, notamment par rapport à des problématiques de gestion environnementale, les observations de la réalité montrent que cette démarcation ne peut pas exister : l'histoire de l'humanité est intrinsèquement dépendante de la nature, qui a été, certes, modifiée par les activités anthropiques, mais qui a aussi forgé la société humaine (Berkes et al., 2003). L'Homme est une composante des systèmes écologiques et les façonne à son tour, avec ses activités d'exploitation, comme, pour les lagunes, la pêche ou l'aquaculture, les activités sur les bassins versants et les interventions de gestion (Cote & Nightingale, 2012).

L'augmentation constante des populations humaines et de leurs activités entraîne une dégradation des lagunes côtières, qui parfois amène à un *shift* de ces systèmes dans des états alternatifs dégradés, difficiles à reconvertir (Scheffer et al., 2001; Carpenter et al., 2012; Nyström et al., 2012; Pérez-Ruzafa et al., 2018). Parallèlement, la présence humaine implique aussi une multitude de services écosystémiques à préserver, en fonction des acteurs en jeu sur le système, dans une optique de durabilité qui est d'importance centrale pour la prise de décisions dans le cadre de la gestion (Cote & Nightingale, 2012; Grafton et al., 2019; Walker, 2020). Ce côté socio-économique ne peut donc pas être écarté, car il joue un rôle fondamental pour la compréhension des caractères qui confèrent résistance et résilience au milieu et des mécanismes et actions humaines qui promeuvent (ou épuisent) ces capacités (Folke et al., 2010; Walker, 2020). En raison de ces fortes interactions avec l'Homme, les systèmes lagunaires sont donc considérés comme des **socio-écosystèmes (Figure 9)**, autrement dit des systèmes complexes où les composantes « naturelle » et « humaine » coexistent dans un même environnement et interagissent entre-elles (Redman et al., 2004). Dans cette optique, la vision socio-écosystémique est un prérequis essentiel pour la conservation des lagunes côtières (Folke, 2006; Folke et al., 2010; Folke, 2016; Walker, 2020) et, par conséquent, une approche écosystémique globale, du bassin versant, avec les activités et les pressions exercées, jusqu'à la mer, en lien notamment avec les activités halieutiques, est fondamentale (Lloret et al., 2008; Biggs et al., 2015; Jones et al., 2018; Erostate et al., 2019; Jaunat et al., 2019; De Wit et al., 2020; Erostate et al., 2020).

Souvent, la préservation de la capacité de résilience des milieux naturels est considérée comme la solution optimale pour garantir la persistance du système et des services écosystémiques fournis (Pérez-Ruzafa et al., 2018). Toutefois, il y a un risque de confondre l'écologie avec le point de vue purement humain dans l'action pratique de restauration écologique, ce qui implique un besoin de connaissance approfondie sur le fonctionnement du milieu afin d'aider la prise de décision dans un cadre de gestion (Bullock et al., 2011).

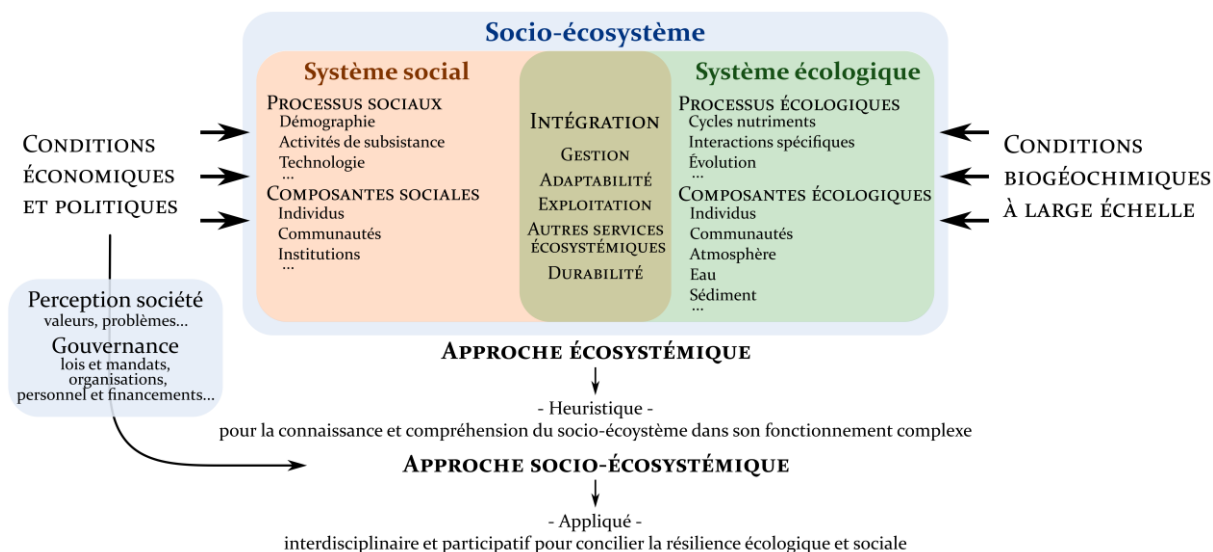


Figure 9 Schéma représentant la complexité des socio-écosystèmes et les éléments principaux des approches écosystémique et socio-écosystémique qui peuvent être appliqués (inspiré et adapté de Virapongse et al., 2016; conceptualisation sur la base de Redman et al., 2004; Benessaiah & Sengupta, 2014; Virapongse et al., 2016; Boudouresque et al., 2020).

Le défi de la gestion consiste en concilier l'adaptabilité et la durabilité des écosystèmes, en garantissant leur capacité à soutenir le développement de la société à travers la conservation des services écosystémiques fournis, face au changement et à l'instabilité (Berkes et al., 2003). Dans la « gestion écosystémique », avec l'application de l'approche écosystémique et du « *resilience thinking* », l'écosystème est analysé dans sa complexité et la composante humaine est prise en compte dans la quête de connaissance et d'apprentissage sur le fonctionnement du système et sa gestion (Redman et al., 2004; Crowder et al., 2006; Cote & Nightingale, 2012). Cette approche écosystémique fournit donc une alternative heuristique et préalable à sa suite logique : l'**approche socio-écosystémique** (*Social-ecological approach*) (Figure 9). Ce dernier diffère de l'approche écosystémique pour le poids qui est donné aux dynamiques sociales, et au pouvoir (politique-économique-culturel) en particulier (Figure 9; Robards et al., 2011; Berkes, 2012; Benessaiah & Sengupta, 2014). L'approche socio-écosystémique intègre l'aspect appliqué et pratique des problématiques sociales, de la perception de la société, de l'autorité et du pouvoir (notamment dans la définition des états désirés : « *Resilience*

for whom and at what cost to which others ? » Cote & Nightingale, 2012), à travers l'implication des sciences sociales (Figure 9 ; Redman et al., 2004). Dans ce cadre, l'interdisciplinarité et l'approche participative sont essentielles pour réfléchir à la favorisation synergique de la résilience sociale et écologique, et pour balancer des problématiques culturelles et de pouvoir (Figure 9 ; Folke et al., 2001; Ostrom, 2009). L'approche écosystémique est donc une étape préliminaire et exploratoire pour développer des connaissances, des analyses spatiales et temporelles à différentes échelles, pour favoriser donc les travaux interdisciplinaires et pour attirer l'attention vers la nécessité d'améliorer la communication entre les différentes parties prenantes (scientifiques ou pas) et utilisateurs des systèmes (Folke et al., 2001; Ostrom, 2009).

2.4.3 Changement climatique et variations de salinité

Dans ce cadre, déjà très complexe et riche d'interactions entre plusieurs facteurs et disciplines, un autre grand défi pour la conservation des lagunes côtières concerne la nécessité de prendre en considération que le monde dans lequel on opère se situe dans un contexte de changement continu et progressif, montrant une rapidité jamais observée avant (Aurelle et al., 2022). Les lagunes côtières, grâce à leur complexité, sont d'excellents laboratoires naturels pour l'étude d'une multiplicité de processus (au niveau des individus, des espèces, des populations, des communautés, des écosystèmes), ainsi que l'impact des activités humaines et du changement climatique (Pérez-Ruzafa et al., 2011b). Grâce à leur réactivité et instabilité naturelle, elles sont des sentinelles de changement global, mais elles sont aussi vulnérables face à ces menaces (Robert & Mazzilli, 2007; Ferrarin et al., 2014).

Comme précédemment évoqué, les problématiques dérivantes du changement climatique impliquent des altérations hydrologiques qui impactent fortement les milieux lagunaires, parmi d'autres milieux aquatiques, en raison de la réactivité de ces systèmes. Les lagunes sont de base soumises à de fortes variations de salinité, en fonction de leurs connexions à la mer et des arrivées des bassins versants. Parfois ces connexions peuvent être altérées par des actions humaines, qui entraînent donc des fluctuations de la salinité. De plus, les variations de salinité, déjà fortement variables dans les cycles saisonniers des lagunes méditerranéennes, sont prévues tendre vers une augmentation de plus de quarante fois plus fortes qu'en mer, en lien avec le changement climatique (Ferrarin et al., 2014). Avec l'augmentation des températures et la diminution des pluies, les lagunes seront de plus en plus soumises à de fortes évaporations entraînant des augmentations remarquables de la salinité. Toutefois, parallèlement, l'augmentation de la fréquence des phénomènes de *flash flood*, autrement dit des événements de pluie extrêmes, va induire des diminutions de salinité très soudaines et intenses dans les

milieux lagunaires. Ces variations ne peuvent qu'être accompagnées par des changements au niveau biologique aussi : notamment, la salinité est l'un des principaux facteurs structurant les communautés phytoplanctoniques (Margalef, 1978; Cloern, 1996, 1999; Reynolds, 2006). Les augmentations de salinité ont souvent été mises en relation avec des variations dans la composition et la richesse des communautés phytoplanctoniques, la parution ou la prolifération de certaines espèces tolérant le stress et parfois potentiellement toxiques (Carrada et al., 1991; Fraga et al., 1995; Schallenberg et al., 2010; Islabão & Odebrecht, 2015; D'ors et al., 2016; Skarlato et al., 2018a). Cela suggère de potentielles futures altérations au niveau écosystémique dans le cadre du changement climatique. Pourtant, contrairement aux augmentations de température, l'impact des fortes et brusques variations de salinité, surtout dans le cadre du changement climatique, reste encore méconnu (Dube et al., 2010; Pulina et al., 2012). Il y a donc un besoin de pouvoir prévoir de potentielles réponses des systèmes lagunaires aux changements futurs et pouvoir donc appliquer une gestion proactive pour préserver ces milieux (Chapman, 2012; Pérez-Ruzafa et al., 2019b; Taylor et al., 2021).

2.4.4 Ressources pour de potentielles applications biotechnologiques

Comme précédemment évoqué, la conservation des lagunes côtières n'est pas seulement liée à l'évident intérêt écologique : au-delà des nombreux services écosystémiques fournis, la complexité de ces systèmes peut se révéler une ressource fondamentale à préserver. L'instabilité et l'importante dynamique des lagunes côtières imposent des facteurs environnementaux contraignants pour les organismes et résultent donc en une forte capacité d'adaptation et de résistance des espèces que ces milieux abritent (Tzovenis et al., 2009). Ces propriétés peuvent alors avoir un potentiel économique remarquable pour des applications biotechnologiques. Notamment, dans le domaine de l'aquaculture, les variations de salinité, irradiation et nutriments sont souvent problématiques pour les cultures de microalgues, utilisées comme nourriture pour les espèces en élevage (Hotos & Avramidou, 2021). Il existe donc un besoin d'isoler de nouvelles souches pour augmenter le potentiel d'application industrielle et les souches issues du milieu naturel peuvent représenter une bonne solution pour obtenir une résistance majeure et des propriétés nutritionnelles plus performantes (Eryalçın et al., 2015; Jusoh et al., 2020; Hotos & Avramidou, 2021). Comme les lagunes subissent des fluctuations intenses et fréquentes en termes de salinité, lumière, température, apports en nutriments, pollution, etc., il est logique de s'attendre que des espèces prévenantes de ces milieux soient plus résistantes et qu'elles puissent produire des molécules d'intérêt, avec de potentielles propriétés particulières, en raison de leur adaptation au changement constant (Hotos & Avramidou, 2021). En effet, certaines espèces issues des milieux lagunaires ont montré des caractéristiques différentes par rapport à leurs

contreparties pélagiques, montrant donc un potentiel biotechnologique avancé (Fisher & Schwarzenbach, 1978; Tzovenis et al., 2009; Hotos & Avramidou, 2021). De plus, si les espèces sont exploitées à l'échelle locale, l'avantage d'utiliser des souches issues du milieu naturel peut être aussi une meilleure adaptation aux conditions environnementales locales, dans le cadre par exemple des systèmes de culture en plein air (Tzovenis et al., 2009). Dans ce contexte, les organismes phytoplanctoniques des lagunes côtières ont donc non seulement un intérêt de type biochimique, avec le potentiel physiologique et nutritionnel, mais aussi une valeur ajoutée de valorisation locale, à travers un développement plus rentable de l'industrie locale et l'affranchissement des importations des souches de l'étranger (Tzovenis et al., 2009).

3. LES LAGUNES CÔTIÈRES DU LITTORAL CORSE

3.1 La Corse comme site d'intérêt

La Corse offre plusieurs avantages pour l'étude et la compréhension des systèmes lagunaires côtiers : l'île peut être considérée un modèle pour les systèmes lagunaires côtiers de la Méditerranée (Ghilardi, 2021; Di Rita et al., 2022).

En raison de sa localisation, la Corse présente un climat méditerranéen, elle est relativement peu impactée des pollutions ou activités anthropiques et donc conserve toujours une richesse écologique remarquable, mais elle présente toutefois des menaces croissantes, notamment l'urbanisation côtière et une pression touristique de plus en plus élevée sur certains secteurs, qui la rendent représentative du système côtier méditerranéen. En outre, l'île est riche de lagunes sur ses 1000 km de côte, mais une estimation précise de la quantité et de la qualité de ces systèmes est toujours manquante (Ghilardi, 2021; Di Rita et al., 2022).

La plupart des lagunes côtières en Corse sont situées sur la côte orientale de l'île, en particulier, les quatre grandes lagunes les plus importantes : Biguglia, Diana, Urbino et Palo (Figure 10). Ces quatre lagunes sont les seules en Corse à dépasser le seuil des 50 ha de surface et à rentrer donc dans les critères imposés par la DCE (SDAGE, 2021). Le reste des lagunes est constitué d'un grand nombre de lagunes qui présentent une petite surface. Celles-ci sont localisées tout autour de l'île, mais se concentrent en particulier sur la côte est et surtout dans le sud (Figure 10).

La multitude des systèmes lagunaires sur l'île présente une grande variabilité en termes d'origine, de morphologie, d'hydrologie et fonctionnement, de taille, de contextes anthropiques et usages, de biodiversité.

Certaines lagunes, de type « lagune *sensu stricto* » (ou sédimentaires) ou d'origine deltaïque (Perthuisot & Guelorget, 1992), comme l'étang de Biguglia, au nord-est, les petites lagunes d'Arasu et de Santa Giulia et le delta du Stabiacciu, en Corse-du-Sud (Figure 10), sont typiquement peu profondes et fortement influencées par les apports de leurs bassins versants. D'autres lagunes, comme l'étang de Balistra en Corse-du-Sud et l'étang de Terrenzana (Figure 10), présentent au contraire un caractère estuarien. Toutefois, sur l'île sont présentes aussi deux lagunes d'origine tectonique (les étangs de Diana et Urbino ; Figure 10), dites de type « *bahira* », « petite mer » en langue arabe (Perthuisot & Guelorget, 1992). Comme ce nom l'indique, il s'agit de lagunes fortement influencées par le milieu marin adjacent, montrant des communautés biotiques proches de celles marines et des profondeurs plutôt importantes, de l'ordre de 10 m, généralement peu communes en milieu lagunaire. En effet, le niveau de connectivité au milieu marin et au bassin versant détermine les caractéristiques de ces milieux lagunaires, principalement en termes de salinité et variabilité. Encore une fois, la Corse présente des lagunes côtières d'une multitude de configurations, allant de lagunes très peu salées, en raison d'une connexion à la mer faible ou temporaire, comme les lagunes de Barcaggio, Lavu Santu, Padulatu, Padulatu Tortu et une partie de l'étang de Pinarellu, jusqu'à des milieux poly- à hyperhalins, comme le delta du Stabiacciu (Figure 10). Ces équilibres entre apports d'eaux douces et d'eau marine et les niveaux de connexion entraînent une variabilité considérable intra-lagune, comme c'est le cas de l'étang de Pisciu Cane qui subit de fortes fluctuations du niveau d'eau en fonction des conditions et des saisons, et interlagunes, notamment avec certaines lagunes qui peuvent être considérées temporaires en raison de leurs assèchements réguliers en lien avec la saison, comme les lagunes de Barcaggio, Crovani et Lavu Santu (Figure 10). Parfois, ces variations font partie de la variabilité naturelle des systèmes, quand ceux-ci sont complètement naturels et très peu impactés par l'Homme, par exemple Barcaggio, Crovani et Pisciu Cane (Figure 10). Dans d'autres cas, ces lagunes ont subi des modifications artificielles et leur histoire anthropique passée a laissé une trace marquante dans leur fonctionnement actuel : par exemple l'étang Del Sale (Figure 10), exploité au Moyen-Âge pour l'extraction du sel, a été remanié pendant des siècles dans l'objectif de le combler pour assainir la zone et lutter contre le paludisme. Les ouvrages d'ingénierie hydraulique appliqués ont donc séparé l'étang du milieu marin. Ce milieu naturellement salé, de son ancienne exploitation pour le sel, a été transformé par l'action de l'Homme en une lagune limnohaline, abritant à ce jour la plus grande roselière de Corse. D'autres lagunes ont subi l'action humaine, comme Terrenzana, Pinarellu, Arasu, San Ciprianu et Canettu, qui ont été modifiées et coupées par la construction de routes et barrages et qui montrent encore aujourd'hui des plans d'eau fragmentés (Figure 10).

Il apparait clairement que les lagunes côtières en Corse présentent une grande variété de contextes anthropiques. Au-delà des artificialisations passées et malgré le grand nombre de sites peu impactés par la présence humaine, d'autres lagunes corses sont à ce jour soumises à des pressions anthropiques croissantes, comme le tourisme, l'urbanisation, le risque d'incendie, l'impact du pâturage et des rejets dans des zones d'élevage et agricoles, en particulier, mais non seulement, en Corse-du-Sud (e.g. Arasu, San Ciprianu, Balistra, Diana, Urbino, Biguglia ; [Figure 10](#)). De plus, les lagunes corses abritent aussi des activités humaines de grande importance économique et sociale. Les quatre plus grandes lagunes sont connues pour leur exploitation halieutique centenaire dans certains cas, comme la conchyliculture à Diana, déjà exploitée pour la récolte de mollusques à l'époque romaine ([Figure 10](#)). La pêche artisanale est traditionnellement réalisée sur plusieurs étangs, notamment ceux de grande taille (Biguglia, Diana, Urbino et Palo; [Figure 10](#)), mais aussi sur certaines lagunes de petite surface, par exemple Santa Giulia sur laquelle un pêcheur professionnel exerce son activité ([Figure 10](#)).



Figure 10 Localisation des quatre grandes lagunes du littoral corse le long de la plaine orientale (incluses dans le cadre de la DCE) et des nombreuses lagunes de petites surfaces, principalement dans le sud de la Corse. La carte a été réalisée sur la base de données fournies par le Pôle Relais Lagunes Méditerranéennes – Tour du Valat (PRLM/TDV).

Cette grande diversité d'écosystèmes et de contextes anthropiques permet d'avoir une multitude de situations et configurations qui rend la Corse un excellent exemple d'étude pour l'acquisition de connaissance et le transfert à d'autres systèmes similaires ailleurs en Méditerranée et dans le monde.

3.2 Lagunes de petites surfaces : une problématique émergente

Seulement quatre des nombreuses lagunes présentes sur l'île, Biguglia, Diana, Urbino et Palo, ont une surface supérieure à 50 ha et sont donc incluses dans la DCE déclinée à l'échelle nationale française (SDAGE, 2021). En général, ces grandes lagunes attirent plus d'intérêt par rapport à celles de petites surfaces en raison de leurs usages et activités commerciales, qui leur confèrent une nette valeur économique. Ces lagunes sont relativement bien connues et étudiées, grâce au fait que l'on dispose de longues séries de données et suivis historiques qui dérivent surtout des suivis scientifiques effectués dans les cadres de gestion, notamment la DCE.

Malheureusement, des séries de données et observations sur de longues échelles temporelles ne sont pas toujours disponibles. Notamment, les lagunes de petites surfaces, souvent exclues des normes de gestion, comme la DCE. De plus, elles attirent moins d'intérêt financier que les grandes lagunes, et demeurent toujours méconnues. Cette approche sur le long terme n'est donc pas applicable. À ce jour, en raison d'un manque d'information, il n'a pas été mis en évidence de différence substantielle entre ces lagunes de petites surfaces et les grandes lagunes. Toutefois, dans les systèmes continentaux d'eau douce, les lacs de petite taille présentent des distinctions par rapport aux grands lacs, comme une biodiversité plus élevée, un dynamisme plus marqué et un rôle clé dans les processus à large échelle (Downing, 2010). De plus, ces petites lagunes sont des systèmes fréquents dans le monde, par exemple sur la côte occidentale de l'Afrique et de l'Amérique du Nord, sur les côtes sud-orientales de l'Amérique et de l'Australie et en particulier dans la région méditerranéenne (Suzuki et al., 1998; Dye & Barros, 2005; Tuncel et al., 2007; Moreno et al., 2010; Camacho et al., 2012; Mitchell et al., 2017; Doughty et al., 2019). Parmi les Pays de la côte méditerranéenne, au moins quatre, l'Italie, la Grèce, la Turquie et l'Espagne, abritent un grand nombre de lagunes de surface inférieure à 50 ha (Cataudella et al., 2015).

Historiquement, ces petits systèmes étaient souvent considérés insalubres et comblés. Notamment, un grand nombre de lagunes de petites surfaces ont disparu à cause de cette pratique en France, Espagne, Italie et Grèce (Diamantopoulou et al., 2008; Cizel, 2017). La Corse ne fait pas exception, car des tentatives de comblement ont historiquement eu lieu sur certaines lagunes de petite surface, comme l'étang Del Sale (Figure 10). Toutefois, à ce jour ces lagunes sont considérées de grande importance : elles sont censées fournir au minimum les mêmes services écosystémiques que les lagunes de grande taille et, en analogie avec les lacs continentaux, potentiellement avoir des caractéristiques particulières, comme une biodiversité majeure (Downing, 2010).

Par conséquent, l'attention des gestionnaires a commencé à se tourner vers ces écosystèmes sur lesquels il y a un fort besoin de quantifier et qualifier les masses d'eaux, ainsi qu'une nécessité d'acquérir des connaissances sur leurs état et fonctionnement écologique et sur l'impact des pressions croissantes ou l'identification de sites à préserver (Latron et al., 2022). L'avantage dans ce cas est que les acquisitions de connaissances peuvent débiter avec une sorte de « maturité écologique » selon laquelle la démarche à travers une approche multidisciplinaire et globale comprenant le système et ses connexions aux systèmes adjacents est indispensable pour une gestion efficace et intégrée (Walker et al., 2006; Hobbs et al., 2009). Ceci implique aussi la prise en compte du contexte anthropique présent (et passé, quand traçable) avec ce regard global à la continuité hydrologique du système bassin versant – lagune – mer pour comprendre efficacement le fonctionnement de l'écosystème. De plus, si l'on considère l'analogie avec les connaissances sur les lacs, les lagunes de petites surfaces sont attendues avoir un potentiel de mitigation plus faible et une réactivité plus importante comparées à celles de grande surface (Downing, 2010). Cela les rend particulièrement fragiles face au changement climatique, mais aussi intéressantes en tant que sentinelles : comprendre le fonctionnement et les potentielles réponses aux bouleversements des lagunes, et en particulier celles de petites surfaces, est un outil primordial pour pouvoir en garantir la conservation et prévoir leur avenir dans une optique de gestion proactive.

Étant donné que la Corse est extrêmement riche en lagunes de petites surfaces (Figure 10), elle peut être considérée comme un site d'intérêt pour l'étude de ces systèmes. La plupart de ces lagunes ne sont pas encore reconnues à l'échelle régionale et il existe de nombreuses lacunes par rapport aux connaissances sur l'état, la qualité et le fonctionnement de ces milieux.

3.3 Particularité de la propriété foncière

Historiquement en Corse, les milieux lagunaires ont eu depuis des siècles une importance centrale pour la population, surtout en lien avec des exploitations halieutiques et donc les commerces et activités économiques de la région. Notamment, on dispose d'une riche connaissance historique pour les trois plus grandes lagunes de l'île, Biguglia, Urbino et Diana, qui ont été exploitées pour la pêche et/ou l'aquaculture depuis des siècles et elles le sont toujours. Cette situation spéciale a amené à un contexte de propriété très particulier par rapport aux lagunes de la France continentale (De Wit et al., 2021). En effet, historiquement les lagunes corses étaient entièrement des propriétés privées (De Wit et al., 2021). Sur le continent, la plupart des lagunes côtières font partie du *Domaine Publique Maritime* (DPM), mais en Corse, suite à l'annexion de l'île à la France en 1768, la propriété privée des lagunes est respectée et ce statut a perduré

pendant longtemps, jusqu'à récemment (De Wit et al., 2017). Ensuite, avec la création du *Conservatoire du Littoral* en 1975, organisme français public dédié à la conservation des systèmes naturels côtiers, des acquisitions de certaines lagunes ont été réalisées (De Wit et al., 2021). Malgré cette situation, le contexte historique particulier de l'île fait que, à ce jour, les lagunes corses sont souvent soumises à un statut de propriété entièrement privée, comme c'est le cas pour la lagune de Balistra et l'étang de Diana. D'autres lagunes, comme l'étang d'Urbino et la lagune de Santa Giulia, ont été entièrement achetées par le *Conservatoire du Littoral* et font donc actuellement partie du *Domaine Public du Conservatoire*. Finalement, dans d'autres cas, l'achat partiel de la part du *Conservatoire du Littoral* résulte en des propriétés multiples et mixtes, c'est-à-dire partagées entre des propriétaires privées et publiques, comme c'est le cas pour la lagune d'Arasu, qui compte une vingtaine de propriétaires, dont le *Conservatoire du Littoral*.

Ces différents statuts de propriété, également souvent partagée avec plusieurs municipalités, entraînent fréquemment des problématiques de gestion, en raison de la difficulté à partager et échanger des informations, à mobiliser des ressources et à atteindre des solutions concertées entre les différents acteurs en jeu. Ces situations de propriétés fragmentées et la dispersion des organismes dévolus à la gestion en Corse, mais également dans d'autres régions comme en région Occitanie, constituent des enjeux d'importance centrale pour la conservation de ces milieux et doivent être prises en compte pour en envisager une gestion efficace (De Wit et al., 2021).

4. OBJECTIFS ET ORGANISATION DE LA THÈSE

Les pressions croissantes sur les systèmes lagunaires côtiers compromettent le fonctionnement naturel de ces écosystèmes et leurs capacités de faire face aux bouleversements. Cela rend les lagunes particulièrement fragiles au regard du changement climatique et aux pressions anthropiques. Le risque de perdre les services écosystémiques que ces milieux fournissent gratuitement pour supporter le bien-être humain entraîne la nécessité de mettre en place des mesures de protection et de gestion efficaces. Les gestionnaires de ces milieux demandent de plus en plus de connaissances sur leurs fonctionnements et leurs potentielles réponses aux changements pour prévoir leur avenir et envisager une gestion intégrée et proactive.

Cette thèse se développe sur plusieurs fronts. Elle ambitionne d'apporter un soutien aux politiques publiques pour la restauration et la conservation des lagunes côtières, mais également à rechercher de potentielles valorisations de ces ressources. Dans un premier temps, les travaux visent à approfondir les connaissances sur les trajectoires d'évolution des communautés phytoplanctoniques et des lagunes côtières

du littoral corse, (i) en questionnant l'évolution des variations saisonnières face aux paramètres abiotiques, mais également l'impact des variations de salinité, notamment dans le cadre du changement climatique, sur de grandes lagunes et/ou des lagunes de petite taille et (ii) en testant différentes approches globales et intégrées avec la prise en compte de l'impact de l'homme, du bassin versant jusqu'à la mer. Dans un deuxième temps, les travaux visent à identifier les potentialités biotechnologiques d'une diatomée isolée dans une lagune du littoral corse. Pour répondre à ces objectifs, des suivis *in situ* et des expérimentations en microcosme et en laboratoire sont envisagés.

Les deux grands objectifs visent à :

1. **Apporter des connaissances sur le fonctionnement des lagunes côtières méditerranéennes face aux pressions anthropiques et au changement climatique afin de fournir un aide à la décision en matière de gestion durable et de conservation de ces milieux.**

Les investigations, réalisées sur six lagunes de Corse choisies selon les objectifs visés, sont présentées sous forme de quatre questionnements ou chapitres et détaillées ci-dessous :

- **Chapitre I** : Ce chapitre évalue les **trajectoires d'évolution sur le long terme** des communautés phytoplanctoniques, en questionnant spécifiquement la **saisonnalité** et les facteurs impliqués dans le déclenchement des ***blooms***.

Les deux lagunes, Diana et Urbino ([Figure 10](#)), sont choisies en raison de la disponibilité de données anciennes et de leur caractère de **lagunes profondes** et **oligotrophes d'origine tectonique**, pour lesquelles les dynamiques saisonnières demeurent encore méconnues.

- **Chapitre II** : Ce chapitre questionne l'intérêt d'une **approche écosystémique** appliquée à l'étude des **trajectoires d'évolution** des communautés phytoplanctoniques, où le système lagunaire est considéré comme un *continuum* avec son bassin versant et le milieu marin adjacents, dans une optique de **socio-écosystème** comprenant l'Homme.

L'étang de Biguglia ([Figure 10](#)) est choisi comme site d'étude en tant que site extrêmement bien documenté, du point de vue historique et dans ses différents

compartiments biotiques et abiotiques, ainsi qu'en raison de son contexte et de son importance (présente et passée) au niveau socio-économique.

- **Chapitre III** : Ce chapitre vise à étudier les **lagunes côtières de petite taille**, à ce jour méconnues, par une **approche multidisciplinaire éco-hydrogéologique** et en gardant une optique globale et intégrée du système qui est considéré comme un socio-écosystème.

Le travail est mené sur trois études de cas : les lagunes d'Arasu, Santa Giulia et Balistra (Figure 10). Ces lagunes ont été prises comme exemples parmi les nombreuses lagunes de petite taille en Corse, en raison de leurs tailles comparables, de leur localisation proche et de leurs différents cadres hydrogéomorphologiques et anthropiques, représentatifs des petits systèmes lagunaires côtiers.

- **Chapitre IV** : Ce chapitre interroge l'impact des variations de **salinité** sur les communautés phytoplanctoniques des lagunes côtières de petites surfaces dans des conditions extrêmes (sécheresse et inondation), en lien avec le **changement climatique**.

L'étude est menée à travers deux expérimentations en microcosmes sur des communautés phytoplanctoniques naturelles issues de la lagune de Santa Giulia (Figure 10), choisie en raison de sa sensibilité au réchauffement et aux phénomènes d'assèchement.

Ces quatre chapitres sont entrelés du fil rouge de la saisonnalité et sont présentés dans cette thèse suivant une logique d'évolution chronologique. Les premières investigations se focalisent sur une approche rétrospective avec la reconstruction de l'évolution passée des communautés phytoplanctoniques ; le deuxième travail intègre à l'approche rétrospective une approche écosystémique pour produire une image holistique du système et de son évolution dans le passé ; le troisième travail s'affranchit de l'histoire du système, indisponible sur des milieux peu connus, et se focalise sur une caractérisation de l'état actuel du milieu, mais implémente le concept de vision globale sur l'écosystème avec une approche interdisciplinaire éco-hydrogéologique et des éléments de raisonnement socio-écosystémique ; enfin le quatrième travail se projette sur le futur des systèmes lagunaires en essayant d'anticiper de potentielles réponses de ces systèmes face au changement climatique en progression.

2. Identifier des potentialités biotechnologiques et d'application d'une souche issue d'une lagune de Corse dans le domaine aquacole, afin d'exploiter et valoriser une ressource naturelle et locale.

Ce deuxième objectif est étudié à travers un travail d'expérimentation réalisé sur des cultures monospécifiques en laboratoire. Il s'insère dans la suite des chapitres précédents en portant une interrogation spécifique sur la valorisation de ressources phytoplanctoniques locales dans une optique de développement. Ce travail fait donc l'objet du cinquième et dernier chapitre de cette thèse et son objectif est détaillé ci-dessous :

- **Chapitre V** : Ce chapitre vise à comprendre les **dynamiques de croissance** et les **caractéristiques physiologiques et biochimiques** d'une espèce phytoplanctonique issue du milieu naturel lagunaire.

L'étude porte sur une souche de la diatomée *Chaetoceros tenuissimus*, issue de la lagune de Diana ([Figure 10](#)). L'intérêt d'utiliser une espèce de cette lagune est lié surtout à l'exploitation conchylicole de l'étang, dans une optique de future application biotechnologique d'une ressource locale, en particulier dans le domaine de l'aquaculture.

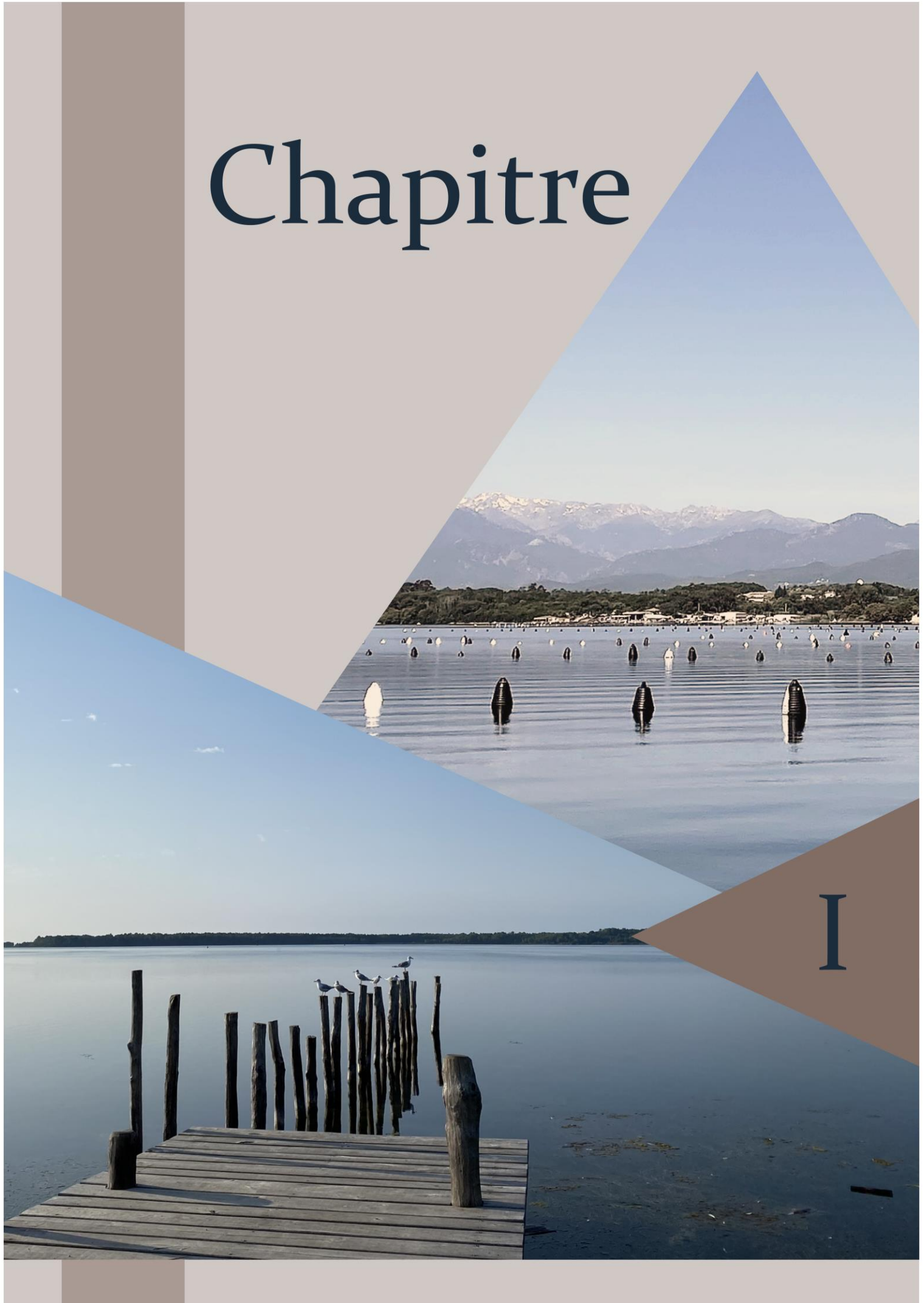
La structure des différents chapitres, avec les principales questions scientifiques et méthodologies ou approches appliquées, est schématisée dans la [Figure 11](#).

Dans ce manuscrit, les cinq chapitres sont présentés, rédigés en anglais, sous forme d'articles scientifiques publiés, en cours de publication ou en cours de rédaction. Enfin, une dissertation sur l'ensemble des résultats obtenus, les limites des études et les potentiels développements pour des recherches futures est discutée dans la section « Discussion et Perspectives », tandis qu'une synthèse des apports à la communauté scientifique des travaux réalisés est présentée dans la partie « Conclusion générale ».

	PRINCIPALES QUESTIONS SCIENTIFIQUES	APPROCHE et MÉTHODE	OBJET D'ÉTUDE	ZONE D'ÉTUDE
ÉCOLOGIE ET GESTION				
CHAPITRE I	<ul style="list-style-type: none"> • Quelles trajectoires saisonnières peuvent être décrites sur le long-terme ? • Quelles sont les évolutions des <i>blooms</i> ? • Quels facteurs contrôlent ces trajectoires et les <i>blooms</i> et quelles potentielles évolutions peuvent être attendues dans un cadre de changement climatique ? 	Données anciennes (1998-2019) et approche saisonnière sur le long-terme	Communautés phytoplanctoniques	Lagunes de Diana et Urbino
CHAPITRE II	<ul style="list-style-type: none"> • Quelles trajectoires écologiques peuvent être décrites sur la base des connaissances historiques, dans un point de vue socio-écosystémique ? • Quelles sont les capacités de résistance et résilience du milieu et comment ont évolué au fil du temps ? • Quels facteurs influencent ces capacités et quels éléments peuvent apporter de l'aide à la gestion ? 	Données anciennes (2000-2021), suivi <i>in situ</i> (2020) et approche écosystémique sur le long-terme	Communautés phytoplanctoniques, Macrophytes, Espèces invasives, Pêche, Apports du bassin versant, Actions de gestion	Étang de Biguglia
CHAPITRE III	<ul style="list-style-type: none"> • Quelle est l'importance des lagunes, surtout celles de petite surface, en termes de quantité et qualité au niveau régional et méditerranéen ? • Quelles différences de fonctionnement écologique peuvent être décrites sous différents contextes hydrologiques et anthropiques ? • Quels éléments peuvent apporter de l'aide à la gestion ? 	Suivi saisonnier <i>in situ</i> (2020-2021) et approche intégrée (hydrogéologie, système bassin versant-lagune-mer)	Communautés phytoplanctoniques, Eaux de surface et souterraines, Contexte anthropique	Lagunes de Arasu, Santa Giulia et Balistra
CHAPITRE IV	<ul style="list-style-type: none"> • Quelles potentielles réponses peuvent être attendues des écosystèmes lagunaires au regard du changement climatique ? • Quelles implications faut-il prendre en compte pour envisager une gestion proactive ? 	Expérimentation en microcosmes à différentes saisons (été et automne 2021)	Communautés phytoplanctoniques	Lagune de Santa Giulia
APPLICATION BIOTECHNOLOGIQUE				
CHAPITRE V	<ul style="list-style-type: none"> • Quelles sont les caractéristiques biochimiques et physiologiques d'une espèce phytoplanctonique locale issue du milieu lagunaire ? • Quelles peuvent être ses potentielles applications en aquaculture ? • Quels éléments peuvent constituer un avantage par rapport à une espèce issue des collection et donc apporter une valorisation de ressources locale ? 	Expérimentation en culture (2020)	<i>Diatomées</i> : <i>Chaetoceros tenuissimus</i> (de la lagune de Diana) et <i>Chaetoceros simplex</i> var. <i>calcitrans</i> (souche de collection)	Lagune de Diana

Figure 11 Schéma de la structure de la thèse, avec les questions scientifiques posées et les approches appliquées pour chaque chapitre.

Chapitre



I

PHYTOPLANKTON DYNAMICS AND BLOOM EVENTS IN OLIGOTROPHIC MEDITERRANEAN LAGOONS: SEASONAL PATTERNS BUT HAZARDOUS TRENDS

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CONTEXTE GÉNÉRAL ET RÉSUMÉ

Les trajectoires d'évolution saisonnières dans les lagunes profondes oligotrophes sont peu connues, en raison de l'attention plus marquée sur la période estivale, très productive, et la présence mineure de ce type de lagunes. L'observation de *shifts* saisonniers dans la composition des communautés et dans la fréquence des événements de *bloom*, ainsi que la mise en relation de ces phénomènes avec le changement climatique, rendent particulièrement nécessaire et importante l'analyse des dynamiques saisonnières du phytoplancton dans des lagunes profondes oligotrophes.

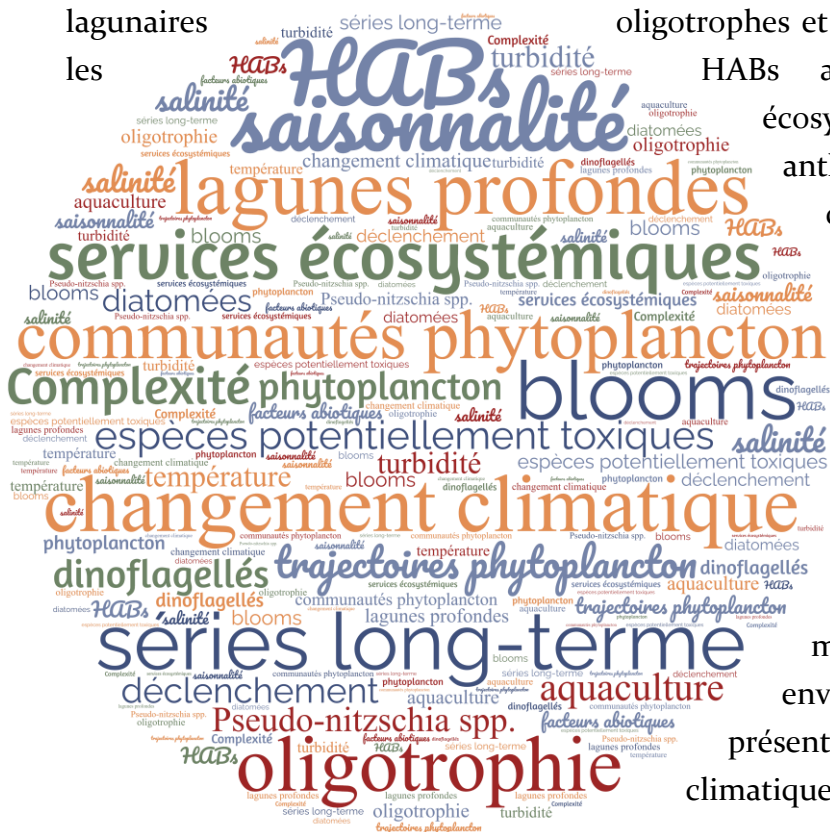
À travers cette étude, les variations saisonnières des communautés phytoplanctoniques des étangs oligotrophes de Diana et Urbino, sur la plaine orientale de la Corse, ont été analysées grâce à des bases de données sur le long terme (20 ans), afin de déterminer si les patterns de composition des communautés et des événements de *bloom* présentent une saisonnalité. De plus, les trajectoires des communautés phytoplanctoniques ont été étudiées afin d'identifier de potentielles tendances significatives et de repérer les facteurs abiotiques structurants.

Les résultats montrent une composition phytoplanctonique similaire entre les deux lagunes, mais des différences en termes d'abondances, temporalité, magnitude et occurrence des unités taxonomiques considérées et de l'occurrence de *blooms*. Le groupe dominant, les diatomées, a montré une saisonnalité bien précise, avec de hautes contributions de *Skeletonema* sp. pendant l'hiver et le printemps, et d'autres unités taxonomiques montrant une affinité pour les saisons chaudes (e.g. *Chaetoceros* spp.) ou une absence de saisonnalité marquée (e.g. *Pseudo-nitzschia* spp.). Pour le groupe des dinoflagellés, des proliférations ponctuelles ont été observées sporadiquement, sans un lien direct à la saisonnalité, mais de fortes contributions ont été observées presque systématiquement en automne. Pour l'étang de Diana, la salinité a été identifiée comme le paramètre environnemental le plus influant sur les dynamiques des communautés phytoplanctoniques, alors qu'à l'étang d'Urbino celles-ci sont surtout contrôlées par la turbidité. Une trajectoire alarmante de la diatomée potentiellement toxique *Pseudo-nitzschia* spp., liée aux variations de salinité et température, a été détecté dans les deux lagunes, indiquant une relation avec le changement climatique et une potentielle menace pour les activités halieutiques.

Cette étude a mis en évidence une difficulté dans la capacité d'expliquer les données biologiques relatives aux communautés phytoplanctoniques à travers peu de facteurs abiotiques. Les nombreux facteurs en jeu dans les systèmes lagunaires et les interactions entre plusieurs compartiments biotiques, notamment le contrôle *top-down* des prédateurs zooplanctoniques et piscicoles, rendent difficiles les interprétations des

dynamiques du phytoplancton. Cela suggère qu'il est nécessaire d'aller plus loin dans le fonctionnement du système et de prendre en compte plusieurs facteurs biotiques et abiotiques pour expliquer efficacement les dynamiques des communautés phytoplanctoniques. Souvent, il est difficile de disposer de données sur le long terme comprenant une multitude de paramètres. Pour ces raisons, cette étude met en évidence la nécessité de poursuivre les suivis réguliers des systèmes lagunaires et de promouvoir la réalisation de suivis de plusieurs paramètres, afin de pouvoir construire des bases de données exhaustives pour étudier la complexité du milieu. Toutefois, l'étude constitue un excellent point de départ pour la compréhension du fonctionnement des systèmes lagunaires

les oligotrophes et suggère des relations clés liant les HABs au fonctionnement de ces écosystèmes. Malgré les contextes anthropiques différents, des changements des communautés phytoplanctoniques sont en cours dans les deux lagunes étudiées, en indiquant donc qu'un important impact sur les dynamiques du phytoplancton et le déclenchement des blooms dans les lagunes méditerranéennes peut être envisagé dans le cadre du contexte présent et futur des changements climatiques.



MOTS CLÉS

Dynamiques saisonnières phytoplancton · Variations long-terme · Bloom · Harmful Algal Blooms (HAB) · *Pseudo-nitzschia* spp. · Lagunes côtières méditerranéennes · Corse

1. INTRODUCTION

The Mediterranean region is expected to be specifically affected by climate change in future projections (Giorgi, 2006; Lejeusne, 2010). This, together with eutrophication observed on aquatic ecosystems during the past 50 years (Cloern, 2001; De Jonge et al., 2002), results in considerable threats to Mediterranean coastal lagoons. Nevertheless, coastal lagoons are very productive ecosystems hosting a high degree of biodiversity and provide numerous ecosystem services for human wellbeing (Barbier et al., 2011). There is an urgent need to better understand the functioning of coastal lagoons and the response of biological communities to current and future global and local changes, particularly with regard to their vulnerability. Beside biomass, the relative species abundance and the community composition are the main metrics for characterizing phytoplankton assemblages; their evolution can result in cascading effects at higher trophic levels (Goberville et al., 2010). Phytoplankton dynamics are driven by multiple environmental factors, mainly temperature and salinity, turbulence, nutrient availability and irradiance (Cloern, 1999), but also by trophic strategies, allelopathic interactions and grazing, which determine together the community composition, algal populations growth and species succession (Armi et al., 2010; Garrido et al., 2016). These factors lead to recurrent patterns of phytoplankton composition observed at different temporal scales (Cloern, 1996).

Most phytoplankton species can grow under a wide range of environmental conditions. The structure of the assemblage will therefore depend on the trade-off among several complex chemical, physical and biological factors (Naselli-Flores et al., 2021).

Analyses of phytoplankton composition and long term studies on phytoplankton assemblages' variations are extremely important for a better understanding of coastal lagoons biogeochemistry. Despite a consistent amount of studies on long-term phytoplankton variations in the Mediterranean lagoon environment, most of them are focused on summer period (Bec et al., 2011; Derolez et al., 2019, 2020b). The interest on this specific season resides in its maximal productivity in lagoons, due to optimal light and temperature conditions (Souchu et al., 2010; Bec et al., 2011; Leruste et al., 2016, 2019; Derolez et al., 2020b), which frequently results in high frequency of bloom occurrence (Bec et al., 2011). However, phytoplankton communities exhibit seasonal patterns that are crucial to understand, especially in relation to the driving factors involved and because some bloom events can occur all year round (Bec et al., 2005; Pulina et al., 2018; Silkin et al., 2019; Trombetta et al., 2019). Trombetta et al. (2019) already highlighted winter blooms as high as spring blooms and linked to increase in temperature in a Mediterranean coastal lagoon (France). Pulina et al. (2012) described a shift in the annual

peak density from summer-autumn to winter-spring period over long-term analysis in another Mediterranean coastal lagoon (Cabras Lagoon, Italy). General common seasonal patterns have already been identified, with diatoms (most adapted to exploit a large continuum of environmental conditions and usually exhibiting fast growth) being observed during winter, spring and autumn, and dinoflagellate blooms generally occurring in summer, even though spatial and temporal variability is important (Armi et al., 2010; Carstensen et al., 2015). The dinoflagellates, representing 75% of toxin-producing phytoplankton species (Smayda, 1997a), can also bloom in other periods than summer, and often peak in autumn (Carrada et al., 1991; Caroppo et al., 2018).

Among diatoms, some groups are recurrent in a specific season due to their ecological niche: winter and spring blooms are frequently dominated by *Skeletonema* spp. worldwide, while *Chaetoceros* spp., *Leptocylindrus* spp., *Nitzschia* spp. and *Cerataulina* sp. are mostly found in warmer seasons (Sarno et al., 1993a; Dupuy et al., 2000; Gilabert, 2001; Gle et al., 2007). Proliferations of diatoms are essential as they sustain trophic network and are the major resource in aquaculture exploitation (Pernet et al., 2012). However, some blooms can be dangerous for the environment. Such hazardous blooms, under the name of Harmful Algal Blooms (HABs), are historically known to occur and can bring about disruption in the ecosystem functioning (e.g. disturbances in both pelagic and benthic trophic networks, damage to fish gills or oxygen depletion; Hallegraeff, 1993). These events can sometimes be especially concerning as some species are able to produce toxins which can be detrimental and even lethal for wildlife and humans (Smayda, 1997b). HABs recently gained attention, mainly due to their impact on economy, especially in respect of aquaculture exploitation (Zingone et al., 2021). Caged fish are very susceptible to non-toxic HABs provoking mechanical or chemical gills damage, but toxic HABs are even more underhand threat especially in shellfish farming, as filter-feeding molluscs can concentrate toxins through bioaccumulation in their tissues and lose their commercial values (Smayda, 1997b; Salcedo-Garduño et al., 2019). In the last few decades, HABs have shown an increasing trend in multiple environments, especially in coastal zones and noticeably around Mediterranean margins (Smayda, 1997b; Hallegraeff, 2010; Kudela et al., 2015; Cecchi et al., 2016). Indeed, proliferation of some species, mainly from the Amnesic Shellfish Poisoning (ASP) toxins-producer *Pseudo-nitzschia* genus, are known to produce blooms at all seasons in lagoon environment (Bouchouicha Smida et al., 2014; Delegrange et al., 2018; Melliti Ben Garali et al., 2020). Moreover, *Pseudo-nitzschia* spp. blooms have already been shown to be increasing in frequency and magnitude over the Mediterranean basin (Husson et al., 2016; Melliti Ben Garali et al., 2020).

At present, lagoons functioning and evolutions still remain imperfectly understood, especially with regard to phytoplankton communities' seasonal dynamics, bloom events and hazardous taxa. The main objective of this study was thus to characterize the seasonality of the phytoplankton community structure (i.e. abundance, bloom events, relation to environmental factors) in two nearby oligotrophic Mediterranean coastal lagoons using long-term data series. We hypothesized that seasonal phytoplankton community patterns can be identified and that environmental and biological long-term trajectories can be highlighted on seasonal basis. The main questions addressed are the following: (i) Are there seasonal environmental and phytoplankton communities' long-term evolutions and which structuring environmental drivers can be identified? (ii) Is it possible to highlight significant trends (blooms occurrence, composition and magnitude, nature of toxic taxa) by season, what are their dependence on environmental factors, and which possible implications of climate change on phytoplankton communities can be identified?

2. MATERIALS AND METHODS

2.1 Study sites

Diana and Urbino lagoons are located on the oriental coast of Corsica island (Mediterranean Sea), not far from each other (< 10 km; [Figure 1](#)).

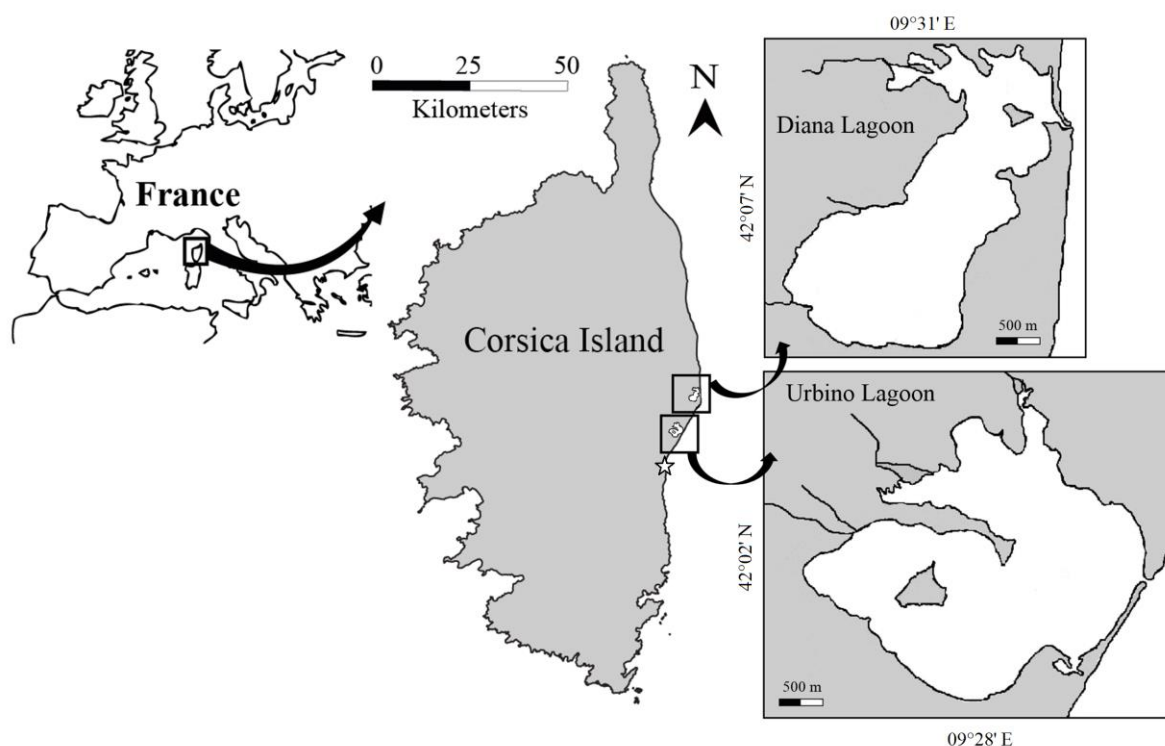


Figure 1 Location of the two study sites: Diana and Urbino lagoons. The white star indicates Solenzara meteorological station (Météo-France).

They share some common characteristics, such as same tectonic origin, geomorphological features, hydrological functioning, oligotrophic status and dominant fauna and flora (Table 1).

Nevertheless, these lagoons exhibit some major differences (renewal rate; watershed size and percentage of agricultural exploitation, degree of the communication with the sea) while also submitted to contrasting anthropogenic histories and current human impacts. Diana lagoon is owned and managed by multiple private enterprises exploiting it for fishing and for shellfish and fish farming, while no aquaculture activities are carried out in Urbino lagoon nowadays, as they were gradually stopped from 2000 (Table 1). Moreover, Urbino lagoon, which is the property of Conservatoire du Littoral since 2007, is recognized as Natura 2000 site since 2004 and Ramsar wetland conservation site since 2009.

Table 1 Characteristics of Diana and Urbino lagoons.

		Diana (42°07' N, 09°31' E)	Urbino (42°02' N, 09°28' E)
General features (1), (2), (3)	Surface	570 ha	790 ha
	Volume	33x10 ⁶ m ³	38x10 ⁶ m ³
	Mean depth	6 m	5 m
	Maximal depth	11 m	9 m
	Salinity	35-39 PSU	35-39 PSU
	Property	Private	Public (<i>Conservatoire du Littoral</i>)
	Management	By aquaculture exploiters	By managers of Corsican region
	Main protection status	ZNIEFF site, Natural site	Natura 2000 Site, Ramsar site
Hydrology (1), (4)	Watershed	62 km ² ; Some dwelling and factories have individual sanitary systems (sewage leaking into the soil)	31 km ² ; Some dwelling and factories have individual sanitary systems (sewage leaking into the soil)
	Freshwater	Three main streams, runoff from watershed	Two main streams, runoff from watershed and peripheral marshes
	Sea channel	Located in the northern part, regularly entertained by the aquaculture exploiters.	Located in the northern part, occasionally cleaned by managers
	Renewal	19 months	57 months
Dominant fauna & flora (2), (5)	Aquatic fauna	Mulletts, seabass, sole, eels, ...	Mulletts, seabass, eels, <i>Aphanius spp.</i> , ...
	Terrestrial fauna	Great cormorants, laridae, shorebirds, large waders, ...	Great cormorants, shorebirds, waders, black-headed gulls, ...
	Aquatic flora	Aquatic phanerogams (<i>Cymodocea nodosa</i>) and macroalgae	Aquatic phanerogams (<i>Cymodocea nodosa</i>) and macroalgae
	Terrestrial flora	Shores composed of glasswort, inulas, reeds, phragmites.	Shores composed of glasswort, tamarisks, reeds.
Human activities (1), (6), (7), (8)	Watershed	Agriculture (about 10%), mainly vineyard, low urbanization.	Agriculture (about 45%), mainly vineyards, low urbanization.
	Lagoon	The lagoon is exploited for shellfish (oysters, mussels) and fish farming (seabream, seabass) and fishing activities. Estimated production in 2020: 150t oysters and 800t mussels.	Intensive shellfish farming was carried out from 1990 to 2000. Nowadays, activities on the lagoon are limited to traditional fishing. Mean production during exploitation: 100t/year oysters and 130t/year mussels.

Data were obtained from different sources: (1) Bouchoucha (2010), (2) Pergent-Martini et al. (1997), (3) Souchu et al. (2010), (4) Orsoni et al. (2003), (5) Garrido et al. (2013b), (6) Orsoni, (2004), (7) Orsoni (2001), (8) Frisoni, (1984)

2.2 *Long-term analysis*

Daily rainfall and daily mean air temperature data were collected from Météo-France at Solenzara weather station (41°55'19" N, 9°24'03" E), which was chosen to represent meteorological conditions of the area, based on its proximity to the study sites (20 km South; [Figure 1](#)). Cumulative monthly rainfall and mean monthly air temperature were calculated to characterize meteorological conditions from January 1998 to December 2019. Environmental parameters (salinity, temperature, turbidity, dissolved oxygen concentration and nutrients (Dissolved Inorganic Nitrogen (DIN), Dissolved Inorganic Phosphorus (DIP) and silicates)) and biotic data (microphytoplankton (generally > 20 µm) abundances and chlorophyll *a* (Chl *a*) concentrations), were collected from the REPHY—French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters—monitoring network ([REPHY, 2019](#)). For each lagoon, one single surface sampling station was available: “Diana centre” and “Urbino centre”; however, they were considered representative of the entire basins as internal spatial homogeneity is well known for both lagoons ([Frisoni, 1984](#)). Environmental parameters datasets from January 1998 to September 2019 (Diana) and August 2018 (Urbino) based on monthly medians ([Derolez et al., 2020b](#)) were used for long-term analyses.

For microphytoplankton, two different datasets are available, according to the strategy applied for cell counting. A first strategy consisted in the counting of all identifiable taxa present in a sample, regardless of their concentration: the associated Total Flora database (FLORTOT) contains thus a representative estimate of all taxa present, so of community diversity and composition ([Belin & Neaud-Masson, 2017](#)). The second strategy aimed at monitoring a certain number of taxa on a selected list defined by the Water Framework Directive (WFD): the associated Indicator Flora database (FLORIND) produces thus a restricted description of the community present in the sample.

A regular monitoring of certain selected toxic taxonomic groups (*Pseudo-nitzschia*, *Alexandrium*, *Dinophysis*, *Ostreopsis*) was systematically carried out, regardless of their concentration (FLORTOX), while some other non-toxic taxa were included only when their concentration exceeded the threshold of 100 000 cell L⁻¹, defining a bloom event ([Belin & Neaud-Masson, 2017](#)).

Based on the extensiveness of REPHY databases, our work allowed different long-term analyses of phytoplankton communities, depending on the availability of

monitoring strategies data, for the two lagoons studied (a summary description of the databases used is available in Supplementary Material – Annexe I – [Table S1](#)):

(1) Diana lagoon analysis on total phytoplankton community has been performed, as FLORTOT dataset was available between January 2001 and September 2019, with monthly to three times per month sampling frequency. FLORTOT dataset was used to describe seasonal evolution of total phytoplankton community over a longer timescale, as well as to identify driving environmental parameters involved;

(2) In order to analyse and compare phytoplankton communities in the two lagoons (Diana and Urbino), the FLORIND database was used. FLORIND data were available all year round from January 2008 to December 2015 and sampling frequency varied from monthly to five times per month. FLORIND dataset exploitation allowed to compare bloom events between lagoons over a longer time-scale and to investigate potential relation with environmental drivers;

(3) FLORIND strategy is constantly evolving in time to satisfy sanitary regulations evolution and WFD requirements. Hence, longer series concerning only selected toxic species were available, from January 1998 to September 2019 for Diana lagoon and to April 2017 for Urbino lagoon; sampling frequency varied from monthly to five times per month. This longer series, hereafter referred to as FLORTOX, allowed to target and analyse the evolution of the potentially toxic taxon *Pseudo-nitzschia* spp. in the two lagoons (Diana and Urbino).

For all datasets, phytoplankton cellular densities were grouped in Taxonomic Units (T.U.s) in order to homogenize data and reduce classification confusion, as suggested by other studies involving REPHY datasets ([Gailhard et al., 2002](#); [Guarini et al., 2004](#); [Hernández-Fariñas et al., 2014](#)). Taxonomic groups were aggregated to the lowest common taxonomic level ([Table 2](#)).

Table 2 List and codes of the most frequent taxonomic units of major groups observed at Diana and Urbino stations (bloom-forming taxa for the FLORIND dataset, and taxa with frequency of occurrence > 15% in each season for the FLORTOT dataset).

Group	Code	Taxonomic unit	Grouping Taxonomic level
Diatoms	ASTE	<i>Asterionella</i> spp.	Family: Fragilariaceae
Diatoms	CERA	<i>Cerataulina</i> spp.	Genus: <i>Cerataulina</i>
Diatoms	CHAE	<i>Chaetoceros</i> spp.	Genus: <i>Chaetoceros</i>
Diatoms	CYLI	<i>Cylindrotheca</i> spp.	Family: Bacillariaceae
Diatoms	DACT	<i>Dactyliosolen</i> spp.	Genus: <i>Dactyliosolen</i>
Diatom	DIATind	Unidentified diatoms	Class: Bacillariophyceae
Diatoms	DITY	<i>Ditylum brightwellii</i>	Species: <i>D. brightwellii</i>
Diatoms	GUIN	<i>Guinardia</i> spp.	Genus: <i>Guinardia</i>
Diatoms	HEMI	<i>Hemiaulus</i> spp.	Genus: <i>Hemiaulus</i>
Diatoms	LEPT	<i>Leptocylindrus</i> spp.	Genus: <i>Leptocylindrus</i>
Diatoms	NAVI	<i>Navicula</i> spp., <i>Fallacia</i> spp., <i>Haslea</i> spp., <i>Lyrella</i> spp., <i>Petronis</i> spp.	Superorder: Bacillariophycanae
Diatoms	NITZ	<i>Nitzschia</i> spp., <i>Hantzschia</i> spp.	Family: Bacillariaceae
Diatoms	ODON	<i>Odontella</i> spp.	Genus: <i>Odontella</i>
Diatoms	PLEU	<i>Pleurosigma</i> spp., <i>Gyrosigma</i> spp.	Family: Pleurosigmataceae
Diatoms	PROB	<i>Proboscia</i> spp.	Genus: <i>Proboscia</i>
Diatoms	PSNI	<i>Pseudo-nitzschia</i> spp.	Genus: <i>Pseudo-nitzschia</i>
Diatoms	RHIZ	<i>Rhizosolenia</i> spp.	Genus: <i>Rhizosolenia</i>
Diatoms	SKEL	<i>Skeletonema costatum</i>	Species: <i>S. costatum</i>
Diatoms	THAL	<i>Thalassionema</i> spp., <i>Thalassiothrix</i> spp., <i>Lioloma</i> spp.	Family: Thalassionemataceae
Dinoflagellates	APHD	<i>Amphidinium</i> spp.	Genus: <i>Amphidinium</i>
Dinoflagellates	DPHY	<i>Dinophysis</i> spp.	Genus: <i>Dinophysis</i>
Dinoflagellates	DPLS	<i>Diplopsalis</i> spp., <i>Diplopelta</i> spp., <i>Diplopsalopsis</i> spp., <i>Preperidinium</i> spp., <i>Oblea</i> spp.	Family: Protoperidiniaceae
Dinoflagellates	GYMN	Gymnodiniales, <i>Gymnodinium</i> spp.	Order: Gymnodiniales
Dinoflagellates	GYRO	<i>Gyrodinium</i> spp.	Genus: <i>Gyrodinium</i>
Dinoflagellates	KARE	<i>Karenia</i> spp., <i>Centrodinium</i> spp.	Genus: <i>Karenia</i>
Dinoflagellates	PROR	<i>Prorocentrum</i> spp.	Genus: <i>Prorocentrum</i>
Dinoflagellates	PROP	<i>Protoperidinium</i> spp., <i>Peridinium</i> spp., <i>Protoperidinium</i> spp., <i>Archaeperidinium minutum</i>	Order: Peridinales
Dinoflagellates	SCRI	<i>Scripsiella</i> spp., <i>Ensiculifera</i> spp., <i>Pentapharsodinium</i> spp.	Family: Peridiniaceae
Euglenophyceae	EUGL	<i>Euglena</i> spp., Euglenoidea, <i>Eutreptia</i> spp.	Class: Euglenophyceae
Cryptophyceae	CRYP	Cryptophyceae	Class: Cryptophyceae
Others	HERM	<i>Hermesinum adriaticum</i>	Species: <i>H. adriaticum</i>
Others	DICT	<i>Dictyocha</i> spp., Dictyochaceae, Dictyochophyceae, Pe- dinellales	Class: Dictyochophyceae

2.3 Statistical analysis

All data were analysed with the statistical R software (RStudio Team, 2016; version 4.0.2).

To evaluate long-term changes of the two lagoons, a seasonal approach was carried out to analyse the historical databases obtained. Seasons were determined as follows: Winter as December, January and February, Spring as March, April and May, Summer as June, July and August and Autumn as September, October and November.

For both lagoons, deviations of mean annual values from averages over the period were considered for cumulative rainfall, mean air temperature, salinity and water temperature. Mann–Kendall (MK) trend tests (*modifiedmk* package in R; Patakamuri &

O'Brien, 2020) were also applied on seasonal annual medians of the same parameters with the aim of detecting potential monotonic trends over the period considered for each season separately. To avoid serial autocorrelation drawbacks, a modified Mann–Kendall test was performed (Hamed & Rao, 1998). If the MK test was significant (i.e. P-value < 0.05), Theil-Sen's slope estimator was provided.

In order to describe temporal evolution of phytoplankton communities in the two lagoons, multiple approaches were carried out. Before analysis, as phytoplankton counts are generally subjected to a limit in cell detection, a threshold of 100 cell L⁻¹ was set up and used to describe abundances of non-detected T.U.s, whose concentration was then considered to be below this threshold (Derolez et al., 2020b). This detection limit was taken into account when the calculation of annual seasonal medians was needed, thanks to the application of the Robust Regression on Order Statistics method (ROS) (Helsel & Cohn, 1988; Lee & Helsel, 2007).

A first in depth analysis was performed on Diana lagoon on FLORTOT dataset to investigate total phytoplankton community seasonal evolution on the long term and to identify potential environmental drivers. Long-term changes in Chl *a* concentrations and total cellular densities of dominant classes, i.e. diatoms and dinoflagellates, were analysed with Mann–Kendall trend test applied to annual medians by season. Then, for each season separately, annual contribution of most frequent T.U.s (frequency of occurrence > 15% on total samples and for each season) to total microphytoplankton abundance was studied.

Relationships between phytoplankton community and environmental variables were analysed through Canonical Correspondence Analysis (CCA) on the overall dataset: cellular densities of the 25 most frequent T.U.s (frequency of occurrence > 15% and total abundance > 80% in each season) were log₁₀(x + 1) transformed and analysed together with four environmental variables (rainfall, salinity, water temperature and turbidity). Mean air temperature was not included in the analysis as it showed strong significant correlation with water temperature. Seasonal differences were demonstrated through Permutational Multivariate Analysis Of Variance (PERMANOVA) test. Significant effects were furtherly investigated through PAIRWISE test and similarity percentages test (SIMPER), in order to identify differences between groups and major T.U.s contributing to these differences.

Further analysis focusing on bloom events on both lagoons was based on FLORIND databases over the 2008–2015 period, in order to compare long-term bloom events seasonal patterns and potential links to environmental factors in the two lagoons. In this study, “bloom events” corresponded to blooms of one T.U. with concentrations

exceeding 100 000 cell L⁻¹. Frequency of occurrence of blooms was analysed (number of blooms over total number of samplings), considering each season separately, and contribution of each T.U. to bloom occurrence was expressed in terms of percentage proportion. To analyse and compare magnitude of blooms occurring in the lagoons, mean bloom densities were calculated for each season on overall bloom events. Maximal bloom-forming T.U.s were also noted, as well as the abundances reached. A similar approach was applied to analyse blooms produced by the potentially toxic taxon *Pseudo-nitzschia* on the overall FLORTOX period. Then, seasonal monotonic trends on the abundance of this taxon were also investigated through Mann–Kendall trend tests applied on annual medians. For significant MK test (i.e. P-value < 0.05), Theil-Sen's slope estimator was provided.

General Linear Model (GLM) was used in order to assess possible links between environmental parameters (salinity, water temperature and turbidity) and bloom events at different seasons and to describe the triggering factors in the two lagoons. A first GLM model was used to test the effects of the three environmental parameters, of season (winter, spring, summer or autumn) and of site (Diana or Urbino lagoon). Separate GLM models were then applied for each lagoon in order to test the effects of environmental factors and season. Interactions between variables were also tested and the best models were selected according to the Akaike information criterion (AIC).

3. RESULTS

3.1 Environmental variables

The long-term analysis (from 1998 to 2019) of meteorological conditions revealed that major rainfall events were concentrated in autumn, winter and spring depending on the year but with an important interannual variability in terms of intensity (Supplementary – Annexe I – [Figure S1a](#), [Figure S1b](#)). No monotonic trend could be identified over the period (Mann–Kendall trend test). Mean air temperature showed a typical seasonal trend (Supplementary – Annexe I – [Figure S1c](#)) and positive anomalies occurred almost systematically at all seasons from 2014 (data not shown).

Significant monotonic increasing trends in mean air temperature were detected in spring (MK P = 0.005) and summer (MK P = 0.028) over the period, with an annual increase of 0.08 °C and 0.07 °C respectively (Sen's Slope = 0.08 and 0.07) ([Table 3](#)). The two lagoons showed different salinity patterns, with variations of higher amplitude at Urbino lagoon (Supplementary – Annexe I – [Figure S1d](#)). Mann–Kendall trend tests did not reveal any significant monotonic trends for this parameter ([Table 3](#)). Water temperatures followed typical seasonal trend with similar variation patterns for both

lagoons (Supplementary – Annexe I – Table S2). Significant monotonic increasing trends were detected for water temperature in winter at Diana lagoon (MK P = 0.03, Sen’s Slope = 0.07) and spring for both lagoons (Diana: MK P < 0.001, Sen’s slope = 0.13; Urbino: MK P < 0.001, Sen’s Slope = 0.22) (Table 3). Highest mean turbidity and lowest mean dissolved oxygen values were found in autumn and summer respectively at both lagoons (Supplementary – Annexe I – Table S2) that were not different to each other.

Nutrient data were available only for summer season (Supplementary – Annexe I – Table S2). Dissolved Inorganic Phosphorus (DIP) and Dissolved Inorganic Nitrogen (DIN) concentrations showed a similar temporal pattern for both lagoons (not shown), except a peak of DIP at Diana lagoon in 2008 (1.69 μM). A sharp increase in DIN was registered between 2017 and 2018, reaching over 1.00 μM on annual median at both lagoons. Silicate concentration was more elevated in Urbino lagoon over the period (Supplementary – Annexe I – Table S2), especially after 2010, reaching a seasonal peak in 2013 at 92.70 μM . Maximal Silicate concentration values were found in July 2013 for both lagoons.

Table 3 Summary of statistical results of Mann–Kendall trend tests performed on annual medians of meteorological variables (cumulative rainfall, mean air temperature), salinity and water temperature for Diana and Urbino lagoons, chlorophyll a concentrations, diatoms and dinoflagellates abundances from

		Mann Kendall trend test					
		p-value		Sen's slope	Trend		
Cumulative rainfall 1998-2019	Winter	0.398	-1.65				
	Spring	0.955	-0.04				
	Summer	0.756	0.14				
	Autumn	0.822	-0.47				
Mean air temperature 1998-2019	Winter	0.236	0.05				
	Spring	0.005	0.08				↗
	Summer	0.028	0.07				↗
	Autumn	0.055	0.05				
		Diana			Urbino		
		p-value	Sen's slope	Trend	p-value	Sen's slope	Trend
Salinity 1998-2019 (Diana) 1998-2018 (Urbino)	Winter	0.088	0.07		0.315	0.08	
	Spring	0.099	-0.06		0.243	-0.13	
	Summer	0.638	-0.02		0.867	0.01	
	Autumn	0.432	0.02		0.401	0.06	
Water temperature 1998-2019 (Diana) 1998-2018 (Urbino)	Winter	0.032	0.07	↗	0.069	0.07	
	Spring	0.000	0.13	↗	0.000	0.22	↗
	Summer	0.264	0.04		0.070	0.08	
	Autumn	0.904	0.01		0.649	0.05	
Diatoms abundance 2001-2019	Winter	0.294	-23461.54				
	Spring	0.208	1764.29				
	Summer	0.001	24460.00	↗			
	Autumn	0.093	6316.67				
Dinoflagellates abundance 2001-2019	Winter	0.528	81.82				
	Spring	0.079	210.00				
	Summer	0.506	200.00				
	Autumn	0.054	1511.11				
Chlorophyll a 2001-2019	Winter	0.000	0.03	↗			
	Spring	0.272	0.02				
	Summer	0.256	-0.02				
	Autumn	0.471	0.02				

FLORTOT dataset of Diana lagoon. Significant P-values of Mann–Kendall tests are reported in bold and trend direction represented by arrows.

3.2 Long-term phytoplankton dynamics in Diana lagoon

The FLORTOT series available for Diana allowed the long-term analysis of phytoplankton assemblages (Supplementary – Annexe I – Table S1). From 2001 to 2019, Chl *a* concentration ranged between 0.03 $\mu\text{g L}^{-1}$ in January 2004 and 13.4 $\mu\text{g L}^{-1}$ in February 2001 (Supplementary – Annexe I – Table S3), and a significant increasing trend was detected in winter (Table 3; MK $P < 0.001$, Sen's slope = 0.03). From 2001 to 2019, Diana's phytoplankton community was largely dominated by diatoms representing up to 90% of total abundances at all seasons except autumn, where they represented 69.8% of total abundances. In autumn, dinoflagellates exhibited their highest contribution to total abundances of the 2001–2019 period, reaching 19.2%. The long-term analyses on diatoms' abundances highlighted high intra- and interannual variations (Figure 2a). Nevertheless, a significant increasing trend could be identified in summer season (Table 3; MK $P = 0.001$, Sen's slope = 2.5×10^4), where median total diatom abundances increased from 1.8×10^4 cell L^{-1} in 2001 to 1.8×10^6 cell L^{-1} in 2019 (Figure 2a). No monotonic long-term trends in abundances were detected for dinoflagellates, although higher densities for this class were observed in the most recent years at all seasons, reaching up to 3.2×10^6 cell L^{-1} in September 2019 (Figure 2b).

The composition of phytoplankton assemblages has also experienced a wide variability among years and seasons (Figure 2c). In winter, *Skeletonema* sp. was the major contributor to total abundances in 2001 and 2002. Other T.U.s, mainly *Leptocylindrus* spp., *Pseudo-nitzschia* spp., *Chaetoceros* spp., Thalassionemataceae and *Nitzschia* spp. were alternatively dominant over the period. From 2005 to 2009, the Cryptophyceae class showed high contribution to total abundances, reaching a peak in December 2007, at 2.7×10^6 cell L^{-1} . Some T.U.s of the dinoflagellates (*Prorocentrum* spp., *Protoperidinium* spp. and *Scrippsiella* spp.) were present in 2005, 2006 and 2009, but their abundances never reached the bloom threshold (i.e. 100 000 cell L^{-1}). During spring, *Skeletonema* sp. exhibited again high dominance in 2008, 2015 and 2019. *Chaetoceros* spp. was systematically present from 2010, constituting an important part of total abundances especially between 2010 and 2012 (> 29%). Dinoflagellate contribution was also quite important especially in 2003, 2007 and 2009, where multiple taxa like Gymnodiniales, *Protoperidinium* spp. and *Scrippsiella* spp., and potentially toxic taxa such *Dinophysis* spp. and *Prorocentrum* spp., appeared, but they did not reach bloom density threshold. The years 2006 and 2007 showed greater diversity in terms of composition but no single T.U. clearly dominated the community, while in 2007 the lowest concentrations of diatoms (Figure 2a) and dinoflagellates (Figure 2b) over the entire study period were recorded. The only bloom of Euglenophyceae (over the entire period) occurred in March 2013 (1.1×10^5 cell L^{-1}).

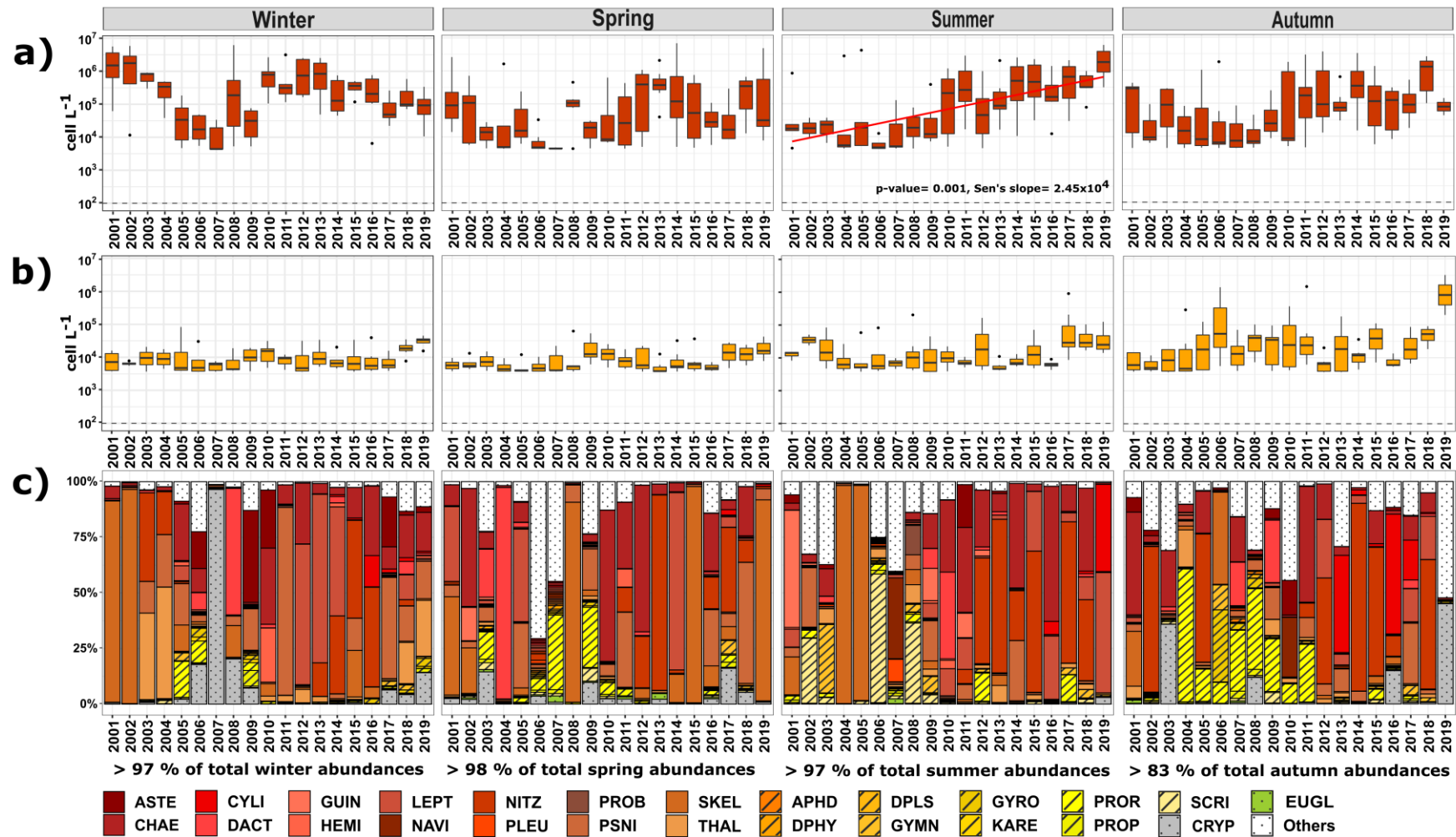


Figure 2 Box and whiskers plots showing long-term seasonal evolution of dominant phytoplankton classes of 2a) diatoms and 2b) dinoflagellates at Diana lagoon, based on FLORTOT dataset (2001–2019). Mann–Kendall trend test significant P-value and Sen’s slope value are reported for diatoms in summer (2a). Contributions (%) of major T.U.s (frequency of occurrence > 15% in each season; see Table 2 for T.U.s codes) to total annual abundance is shown for each season (2c): diatoms are shown with colours only, dinoflagellates with hatched coloured bars and other classes with dotted coloured bars.

Summer season was characterized by a dichotomous distribution: the phytoplankton community showed higher diversity before 2012 (except for 2004 and 2005 with a total *Skeletonema* sp. dominance). Then, after 2012, *Nitzschia* spp., *Chaetoceros* spp., *Leptocylindrus* spp. and *Pseudo-nitzschia* spp. were systematically the most dominant T.U.s. This structural shift corresponds to the increasing dominance trend of diatoms underlined in [Figure 2a](#) for this season.

Some dinoflagellates were also detected, particularly in 2002, 2006 and 2008, when *Scrippsiella* spp. also bloomed at 1.8×10^5 cell L⁻¹. Other dinoflagellate blooms were recorded in 2012 (*Prorocentrum* spp.) and 2017 (*Prorocentrum* spp. and Gymnodiniales). Most of dinoflagellate blooms were observed in autumn. Particularly, between 2004 and 2011, this class highly contributed to total abundances and was sometimes dominating. Multiple *Prorocentrum* spp. blooms occurred in 2004, 2005, 2006, 2010 and 2011, reaching up 1.4×10^6 cell L⁻¹ in November 2011. Other punctual bloom events were due to rarer taxa, such as Gymnodiniales and *Gyrodinium* spp. in 2006, *Heterocapsa* spp. in 2013 and *Heterocapsa* spp. and *Tripos* spp. in 2019. From 2012, diatoms were always dominant and *Nitzschia* spp. and *Chaetoceros* spp. showed a marked presence. The Cryptophyceae class also bloomed in 2003, 2013 and 2019 (reaching its maximum on the overall period at 3.0×10^5 cell L⁻¹ in September 2019) and appeared to be important on total abundance, as well as in 2008 even if no bloom density was reached.

Relationships between Diana phytoplankton community and environmental variables (rainfall, water temperature, salinity and turbidity) were investigated through CCA ([Figure 3](#)). The model was significant ($P = 0.001$) and the first two significant canonical axes ($P < 0.01$) explained 52.5 and 21.3% of the total variance respectively and were used to summarize variation in community composition. The first axis was positively correlated with salinity and water temperature, corresponding to samples collected during summer and autumn, while the second axis was positively correlated with turbidity and rainfall, corresponding to samples collected during spring and autumn. In the CCA tri-plot, four main quadrants can be identified that corresponded to the four seasons represented by their centroids ([Figure 3](#)). Diatoms were almost centred on the tri-plot as they were dominant whatever the season. A seasonality can be identified for the main diatom T.U.s: on the left part *Pseudo-nitzschia* spp. and *Skeletonema* sp. seemed to be favoured by lower salinity and temperature and associated to spring and winter seasons. At the opposite side, *Leptocylindrus* spp. and *Nitzschia* spp. were favoured by higher temperatures and salinity and mostly associated with the summer season. Gymnodiniales and *Scrippsiella* spp. appeared also to be more favoured by higher salinities and temperatures, without clear influence of rainfall and turbidity. *Chaetoceros* spp. and Thalassionemataceae were positioned in the bottom part of the plot, in opposition to high turbidity and rainfall levels, unlike *Prorocentrum* spp. and

Gyrodinium spp. which seemed to be mainly driven by turbidity and rainfall. Dinoflagellates were also located in the top-right quadrant, indicating their importance in autumn.

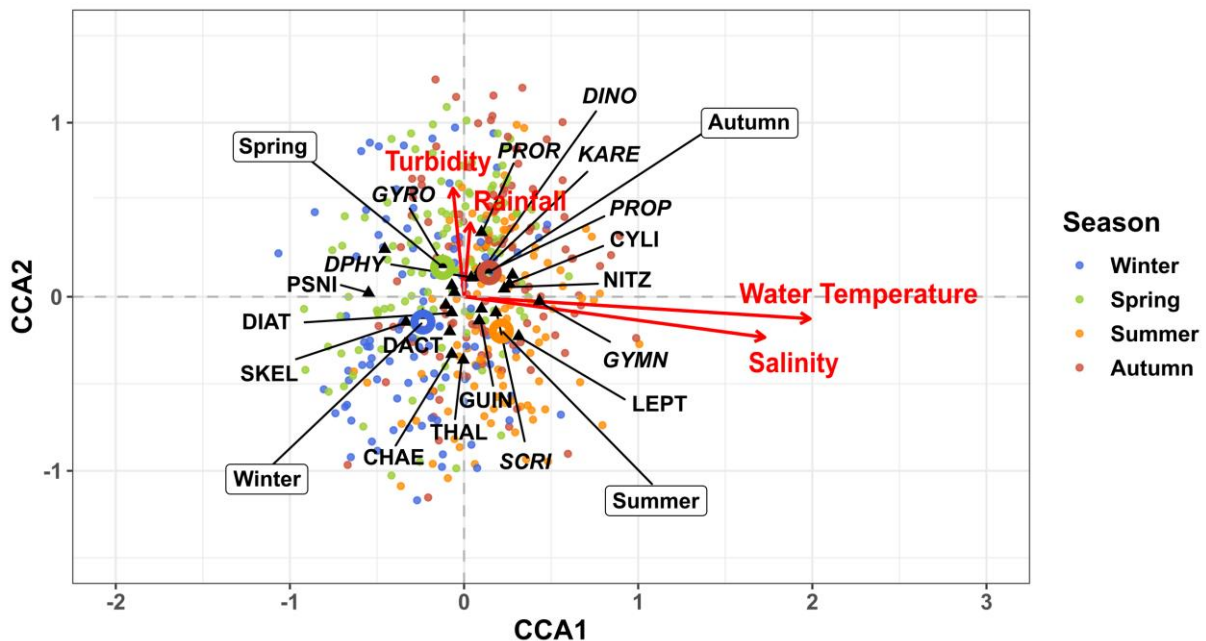


Figure 3 Tri-plot of the Canonical Correspondence Analysis (CCA) for samplings (points), environmental variables (arrows) and major phytoplankton T.U.s (triangles). Major T.U.s were selected as those showing frequency of occurrence > 15% all over the period, and representing at least 80% of total phytoplankton abundance in each season. Labels are displayed only for some selected T.U.s (representing > 70% of total abundance for each season), which were chosen inside the dominant classes of diatoms (regular font) and dinoflagellates (italic font) as those showing at least 20% frequency of occurrence in each season (see [Table 2](#) for codes, DIAT and DINO indicate total diatoms and dinoflagellates respectively). The points representing the samples are colour-coded based on season: blue for winter, green for spring, gold for summer, red for autumn. Centroids for each season are represented by large coloured and hollowed circles.

PERMANOVA investigation on phytoplankton assemblages highlighted significant effect of the season ($P = 0.001$) (Supplementary – Annexe I – [Table S4](#)). PAIRWISE test confirmed each season differed from the others ($P < 0.01$) (Supplementary – Annexe I – [Table S4](#)). From SIMPER test, spring showed overall 12% difference from other seasons, while other contrasts all showed 13% difference. *Chaetoceros* spp., *Pseudo-nitzschia* spp., *Nitzschia* spp., *Skeletonema* sp., Thalassionemataceae, diatoms, *Leptocylindrus* spp. and *Prorocentrum* spp. were systematically within the 10 more important contributors to diversity between seasons, representing at least 59% of the difference between groups. The general seasonal characterization emerging from the test showed that diatoms in general, *Skeletonema* sp. and *Pseudo-nitzschia* spp. in particular, as well as Cryptophyceae, were most important during cooler and rainy seasons, i.e. winter and spring. Other T.U.s like *Chaetoceros* spp. and *Leptocylindrus* spp. were generally more abundant in summer. Globally, dinoflagellates were most abundant during autumn and summer, like

Prorocentrum spp., *Scrippsiella* sp. and Gymnodiniales, this latter being, however, important in winter due to bloom formation.

In the contrast between summer and autumn, other dinoflagellates as *Proto-peridinium* spp., *Gyrodinium* spp., *Karenia* spp., *Diplopsalis* spp., *Dinophysis* spp. and *Amphidinium* spp. showed higher importance during autumn, despite being contributing less to overall difference between seasons.

3.3 Bloom events in Diana and Urbino lagoons

Blooms analysis over the 2008–2015 period for the two lagoons relied on the FLORIND dataset (Supplementary – Annexe I – Table S1). 212 events have been recorded, i.e. 26.5 blooms per season and per site on average, but with a lower occurrence in Urbino than in Diana (84 and 128 events, respectively) (Figure 4). High interannual variability, both in terms of bloom occurrence and T.U.s contributions to the blooms, was highlighted for both lagoons (Figure 4). Highest bloom frequency (number of blooms over total samplings per season) was found in winter at Diana lagoon (0.59) and in autumn and spring at Urbino lagoon (0.46 and 0.42, respectively) (Figure 4). At Diana lagoon, no bloom was recorded in 2008 during summer and autumn, in spring and autumn 2009 and in spring 2010. Urbino lagoon did not exhibit bloom events in winter for three consecutive years (2012, 2013 and 2014) and in summer 2012 (Figure 4). However, both lagoons reached the maximal bloom occurrence in winter 2008, with 11 and 7 bloom events for Diana and Urbino respectively. In Urbino lagoon, the maximal bloom occurrence (7 events) was also found in autumn 2013. Overall, despite seasonal variability, the regular occurrence of several dominant T.U.s was similar for the two lagoons.

Blooms of *Nitzschia* spp. have been systematically observed at both lagoons whatever the season (Figure 4). *Pseudo-nitzschia* spp. occurrence was particularly important in winter and spring, together with *Skeletonema* sp. (Figure 4). *Chaetoceros* spp. also constituted an important proportion of bloom events in both lagoons, all year round except in winter, and especially stood out in summer, together with *Leptocylindrus* spp. (Figure 4). Thalassionemataceae group seemed to be more important at Urbino lagoon but occurred at both lagoons in summer (Figure 4). Dinoflagellate blooms (*Prorocentrum* spp. and Gymnodiniales) constituted punctual events at both lagoons and were found only in autumn and winter. However, dinoflagellate blooms could reach important magnitude, like Gymnodiniales, which were responsible for the highest winter bloom recorded in Diana lagoon, at 6.9×10^6 cell L^{-1} in January 2008 (Figure 4). Generally, mean seasonal bloom magnitude for both lagoons was in the order of 10^5 cell L^{-1} , except for spring at Diana lagoon, where it was up

to 10^6 cell L^{-1} , with multiple dense blooms of *Skeletonema* sp., reaching up to a maximum of 2.1×10^7 cell L^{-1} in March 2015 (Figure 4).

During summer season, bloom frequency and mean magnitude were lower at Urbino lagoon (Figure 4).

Among the selected toxic taxa listed in the FLORIND dataset (2008–2015), *Pseudo-nitzschia* spp. was systematically present at both lagoons and contributed strongly to blooms occurrence. The analysis of FLORTOX data (1998–2019 at Diana and 1998–2017 at Urbino) revealed a higher *Pseudo-nitzschia* spp. bloom frequency at Urbino lagoon than at Diana lagoon in winter and spring seasons (Table 4). In general, blooms of *Pseudo-nitzschia* spp. were denser at Urbino site, with maximum blooms reaching 10^6 cell L^{-1} at all seasons except summer, while the same densities were reached only at the winter maximal bloom for Diana (Table 4). The Mann–Kendall trend test on annual median abundances detected significant increasing trends for this T.U. over the studied periods for winter and spring seasons at Diana lagoon ($P = 0.006$ and $P = 0.034$ respectively) and for autumn season at Urbino lagoon ($P = 0.034$) (Table 4).

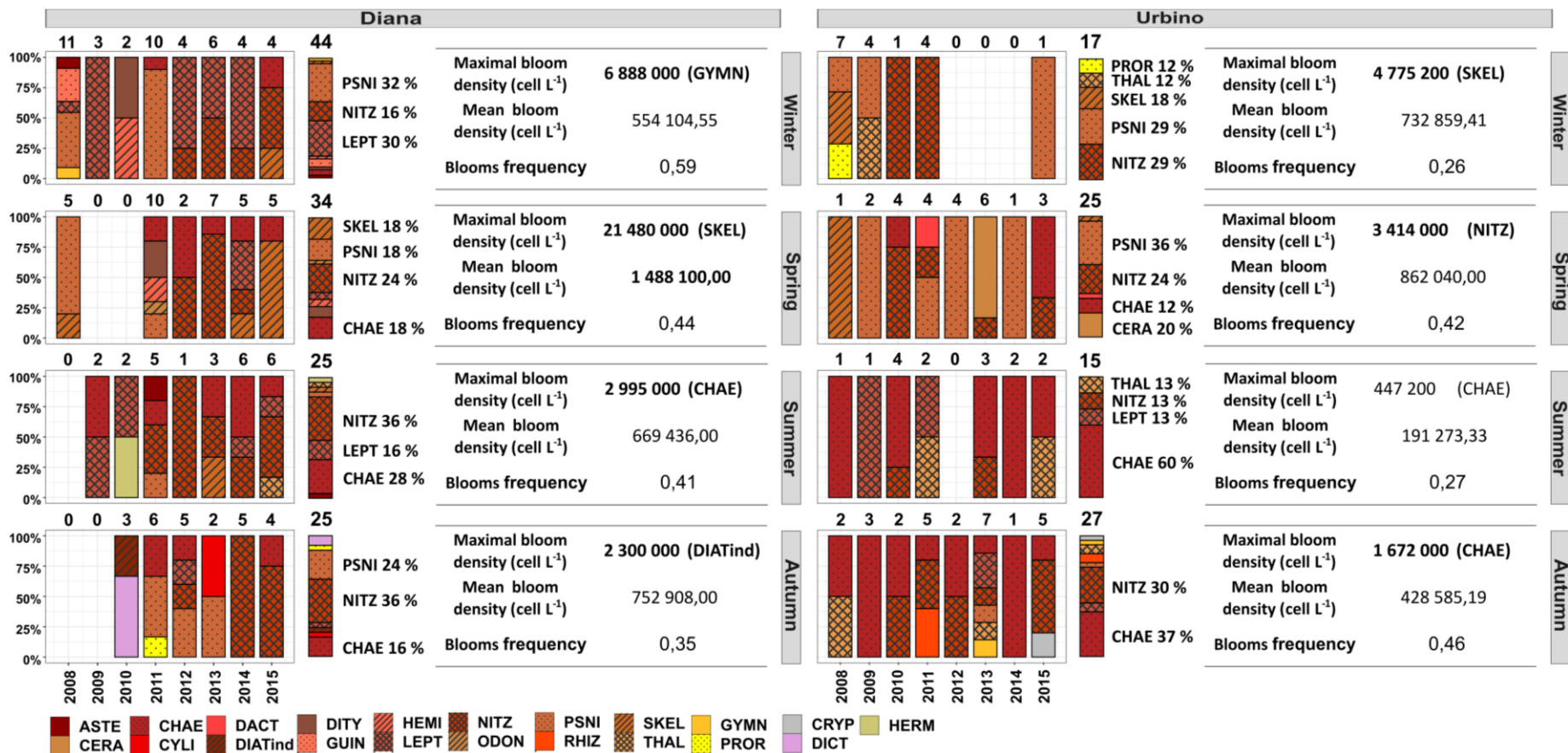


Figure 4 Blooms occurrence and contribution to annual and seasonal bloom events of FLORIND Taxonomic Units over the study period (2008–2015) in Diana and Urbino lagoons (See Table 2 for codes). Number of blooms per year and season are reported on top of corresponding bars. Percentage contribution of main dominant T.U.s on overall seasonal bloom events are shown. On the right, the maximal bloom magnitude (cell L⁻¹) and responsible T.U. are stated for each season, as well as the overall mean bloom magnitude and seasonal blooms frequency (number of blooms/total number of samples). Values over 1 000 000 cell L⁻¹ are highlighted in bold.

Table 4 Summary description of *Pseudo-nitzschia* spp. bloom events in Diana and Urbino lagoons, based on available FLORTOX data (left). Maximal density and mean density (sum of bloom densities over number of blooms) calculated on all bloom events registered during the considered period are reported (values over 1 000 000 cell L⁻¹ in bold). Bloom frequency was calculated as number of *Pseudo-nitzschia* spp. blooms (n) over the total number of samples (N) recorded for each season. Seasonal long-term trends of *Pseudo-nitzschia* spp. cellular densities over the sampling period are shown on the right (with significant P-values of Mann–Kendall trend tests in bold and trend direction represented by arrows).

		<i>Blooms description</i>						<i>Mann-Kendall trend test</i>		
		Maximal bloom density (cell/L)	Mean bloom density (cell/L)	N	n	Bloom frequency	p-value	Sen's slope	Trend	
<i>Diana</i>	FLORTOX 1998 - 2019	Winter	1 236 800	248 044	156	16	0.10	0.006	1043.199	↗
		Spring	334 400	182 211	182	9	0.05	0.034	214.084	↗
		Summer	117 100	112 000	139	2	0.01	0.449	32.948	
		Autumn	283 800	160 017	147	6	0.04	0.348	50.000	
<i>Urbino</i>	FLORTOX 1998 - 2017	Winter	8 060 000	3 013 756	167	23	0.14	0.093	190.614	
		Spring	3 185 600	819 774	175	23	0.13	0.185	311.400	
		Summer	201 200	158 100	137	2	0.01	0.449	-29.045	
		Autumn	2 543 000	912 500	142	6	0.04	0.034	144.881	↗

GLM models helped to understand bloom determinism. The first best GLM model tested on entire dataset (AIC = 710) highlighted a significant effect of the lagoon factor (Diana vs Urbino) in interaction with season and turbidity, and of the season factor in interaction with salinity (Table 5). Separate GLM models were then applied for each lagoon in order to better understand seasonal bloom dynamics and to identify major environmental factors involved. The best GLM for Diana lagoon (AIC = 401) indicated a significant effect of the interaction between the season and salinity. In particular, a decrease in salinity values during spring season significantly enhanced the probability of blooms occurrence (P = 0.018), while the opposite effect was found for autumn season (P = 0.037) (Table 5). Best GLM model for Urbino lagoon (AIC = 297) identified an important and significant role of turbidity on bloom events, in interaction with seasonal factor (Table 5). A negative effect of turbidity was found for both spring (P = 0.003) and autumn (P = 0.005), indicating an increase in bloom occurrence with decreasing turbidity at these seasons (Table 5). Temperature did not show any significant effect on bloom triggering for Diana and Urbino. Overall, bloom determinism seemed to be differently regulated within the two lagoons: mainly by salinity in Diana and mainly by turbidity in Urbino.

Table 5 Summary of statistical results from GLMs performed on binomial variable “bloom vs non-bloom events” against environmental variables (salinity: SALI, water temperature: TEMP and turbidity: TURB) for Diana and Urbino lagoons. Interactions are represented with the code “x”. Best models formulas and significant effects are reported. Based on the significance level, variables are reported with the following codes for P-values: ‘***’ 0,001; ‘**’ 0,01; ‘*’ 0,05. The best models were selected based on lowest Akaike information criterion (AIC).

Two Lagoons			
best model = blooms ~ Lagoon + Season + SALI + TEMP + TURB + Lagoonx-Season + LagoonxSALI + SeasonxSALI + LagoonxTEMP + LagoonxTURB + SeasonxTURB + SALIxTURB + LagoonxSeasonxSALI + LagoonxSeasonxTURB (AIC: 710)			
	Estimate	p-value	
Season Spring	15.74	0.012	*
Season Autumn	-29.38	0.043	*
Season SpringxSALI	-0.44	0.011	*
Season AutumnxSALI	0.75	0.046	*
Lagoon UrbinoxSeason AutumnxTURB	-1.41	0.030	*
Diana			
best model = blooms ~ Season + SALI + TEMP + SeasonxSALI (AIC: 401)			
	Estimate	p-value	
Season Spring	12.92	0.021	*
Season Autumn	-30.66	0.034	*
Season SpringxSALI	-0.38	0.018	*
Season AutumnxSALI	0.79	0.037	*
Urbino			
best model = blooms ~ Season + TURB + SeasonxTURB (AIC: 297)			
	Estimate	p-value	
(Intercept)	-2.80	0.000	***
Season Spring	2.88	0.000	***
Season Autumn	3.72	0.000	***
TURB	0.99	0.003	**
Season SpringxTURB	-1.24	0.003	**
Season AutumnxTURB	-1.73	0.000	***

4. DISCUSSION

4.1 Seasonal patterns and key taxonomic units

The two studied lagoons are set in a Mediterranean climate context, with two main rainy periods corresponding to autumn and spring, separated by a winter drier cold period, and an arid and hot period during summer (Aubin et al., 2019). Over the study period, some exceptionally rainy winters occurred (e.g. in 2008 and 2017), and the 2008–2015 period was generally cooler, with especially wet spring. Overall, the two lagoons exhibited some shared traits, like similar seasonal environmental dynamics and oligotrophic status, which is their main characteristic. From a general point of view, Chl *a* concentrations were consistent with observations relative to other Mediterranean oligotrophic lagoons (Souchu et al., 2010; Bec et al., 2011; Leruste et al., 2019). Microphytoplankton community was dominated by diatoms and dinoflagellates, which are known to be the dominant classes and major contributors to the phytoplankton communities of Mediterranean lagoons (Frisoni, 1984; Armi et al., 2010; Derolez et al., 2020b). The oligotrophic nature of these systems implies a tight dependence of

phytoplankton dynamics on nutrient fluctuations, typical for the Mediterranean region (Paches et al., 2019).

Seasonal nutrient patterns are therefore important for the understanding of phytoplankton seasonality. Several studies have described a typical DIN pattern in Mediterranean coastal lagoons (Collos et al., 2003; Bec et al., 2005). NO_3^- concentrations rising occurs mostly in humid seasons and is conventionally linked to inputs from rainfall and runoff, while a major contribution of NH_4^+ is observed in summer, and classically associated with in situ regenerated production (Bec et al., 2005) and/or release from the sediment production in warm period (Garrido et al., 2016).

Such shifts in nutrient sources could have affected the microphytoplankton composition we observed in our study. In winter, *Skeletonema* sp. showed an important contribution to total abundance at Diana lagoon, together with *Pseudo-nitzschia* spp. and *Nitzschia* spp. This is in accordance with other observations that detected especially *Skeletonema* spp. as an important contributor to winter blooms in coastal systems, linked to NO_3^- inputs from watershed following rainfall events (Sarno et al., 1993a; Gle et al., 2007; Collos et al., 2014). *Skeletonema* sp. success during winter might reside in its preference for high NO_3^- loads and for low temperatures (Collos et al., 2003; Derolez et al., 2020b).

In Diana lagoon, an association between *Skeletonema* sp. and *Pseudo-nitzschia* spp. abundances and lower salinity and temperature values emerged, related to winter conditions.

Skeletonema spp. is considered a generalist taxon that is highly tolerant to salinity variations. However, the link between *Pseudo-nitzschia* spp. and lower salinity is in contrast to other studies that have underlined positive correlation of this genus with salinity and temperature (Balzano et al., 2011; Bouchouicha Smida et al., 2014; Hernández Fariñas et al., 2015; Husson et al., 2016; Van Meerssche et al., 2018), although this may vary depending on species or genotype (Armi et al., 2008; D'Alelio et al., 2009).

Winter conditions detected in long-term analysis on Diana lagoon are also consistent with the presence and high contribution of Cryptophyceae class during this season, as they are known to be linked to freshwater inputs and turbid waters in other natural systems and lagoon environment (Gregor & Maršálek, 2004; Catherine et al., 2012; Garrido et al., 2016, 2019). Winter observations are also in accordance with Sarno et al. (1993), who found important abundances of small Cryptophyceae during winter together with *Skeletonema costatum* in an Italian coastal lagoon.

Spring microphytoplankton composition showed redundant high dominance and blooms of *Pseudo-nitzschia* spp. in both lagoons, together with *Chaetoceros* spp. and *Skeletonema* sp., which is in line with typical timing of these taxa (Sarno et al., 1993a; Gle et al., 2007). Some dinoflagellates were also found at Diana lagoon, even if not

blooming, mainly of the taxa *Dinophysis* spp., *Prorocentrum* spp., *Gymnodiniales* and *Scrippsiella* sp. This is in accordance with other observations stating that some of these organisms can be found all year round in oligotrophic waters, due to metabolic advantages of mixotrophy (Bec et al., 2011; Derolez et al., 2020b).

The microphytoplankton observed during summer season was mainly characterized by *Chaetoceros* spp., Thalassionemataceae, *Cerataulina* spp., *Nitzschia* spp. and *Leptocylindrus* spp. Dominant T.U.s detected were favoured by high temperature and salinity values, which can also explain the presence of some dinoflagellates, like *Scrippsiella* sp., sometimes associated with these conditions in Mediterranean lagoons (Dhib et al., 2013).

Generally, the summer phytoplankton composition described in this study was similar to that found in this season in other lagoon environments and especially in the French Mediterranean Thau lagoon, showing similar characteristics to the two studied lagoons (Dupuy et al., 2000; Collos et al., 2003; Souchu et al., 2010). Thalassionemataceae group was also found to increase over long-term summer survey in these different ecosystems (Dupuy et al., 2000; Derolez et al., 2020b).

A long-term increasing trend in diatom total densities was detected for Diana lagoon during summer.

Parallel to diatom abundances rise during summer, an increasing trend in air temperature was observed on the long term, suggesting a possible role of climatic factors in phytoplankton structure shifting. As summer is considered to be the most affected season by climate change in the Mediterranean region, with global temperature predicted to increase by 4–5 °C over the century (Giorgi & Lionello, 2008), possible effects of this factor seem already detectable on phytoplankton community structure and will probably intensify in the future. Temperature rise could also lead to increasing frequency of potentially toxic dinoflagellates already detected in this season, i.e. *Scrippsiella* spp., *Prorocentrum* spp. and *Gymnodiniales* (Reñé et al., 2011; Dhib et al., 2013; Sahraoui et al., 2013). Both community composition modification and the emergence of toxic taxa correspond to an alarming threat in sight of future climate change. A similar increasing trend in mean air and water temperature was also detected for spring. Even if no significant trend emerged from phytoplankton analysis, it may not be too long to see similar changes to those observed in summer with the exacerbation of climate change.

Autumn microphytoplankton community was mainly characterized by a stronger contribution of dinoflagellates. Despite being usually associated with summer conditions, some studies already underlined the presence and importance of dinoflagellates in oligotrophic lagoons, like Thau and Leucate lagoons (France,

Mediterranean Sea), and especially in autumn, thanks to their trophic abilities (Collos et al., 2009, 2014; Cecchi et al., 2016).

4.2 *Bloom dynamics and concerning trends*

For both lagoons, some years did not present blooms at each season, but there is no correspondence between lagoons nor with specific meteorological events, suggesting that local factors are primarily involved. Overall, despite high silicate concentrations and diatoms dominance, lower phytoplankton biomass and bloom occurrence were observed at Urbino than at Diana lagoon over the study. Generally, in oligotrophic lagoons, major primary producers are aquatic angiosperms and macroalgae (Duarte, 1995; Schramm, 1999; Souchu et al., 2010). Urbino lagoon is dominated by especially well-developed *Cymodocea nodosa* meadows (Garrido et al., 2013b).

The important presence of these phanerogams has already been proven to negatively impact the phytoplankton compartment due to competitive advantage over microalgae for environmental resource exploitation and through allelopathic regulation (De Wit et al., 2012; Laabir et al., 2013). However, this phenomenon could also be associated with the different exploitation carried out on the two lagoons. Indeed, intensive aquaculture performed in Diana lagoon certainly induces high inputs of organic matter (faecal pellets, other external food inputs) which can sustain a higher phytoplankton production (Mazouni et al., 1998).

Concerning the T.U.s seasonal repartition, a stronger contribution of *Skeletonema* sp. to blooms was found in spring at Diana than at Urbino lagoon. Parallel to that, an association between lower salinity and higher bloom probability was detected, diatoms being the most involved group in these events. This contrasts with previous studies, which highlighted positive correlation between diatom blooms and salinity (Mukherjee et al., 2018).

At Urbino lagoon, low turbidity was found to favour bloom occurrence during spring and autumn. Turbidity variations can either indicate water column stabilization or alternatively mixing with sediment inducing nutrients resuspension; thus, they greatly impact on fitness and composition of phytoplankton assemblages (Trombetta et al., 2021). The observed inverse relationship between blooms and turbidity in Urbino lagoon is in contrast with the common knowledge regarding diatom preference for well mixed waters; however, light penetration could play a role in this case, as spring blooms can be triggered by combined effects of temperature and irradiance variations (Sommer et al., 1986; Winder & Sommer, 2012).

In particular, at Urbino site the highest contribution to bloom occurrence in spring was due to *Pseudo-nitzschia* spp., which already showed positive correlation of its growth

rate with irradiance (Husson et al., 2016; Terseleer et al., 2013; Thorel et al., 2014) and this taxon showed a significant density increase in autumn. Similarly, both in winter and spring, *Pseudo-nitzschia* spp. abundance significantly increased on the long term at Diana lagoon and showed maximal bloom frequency in both lagoons in winter. Parallel water and air temperature increases were detected for both lagoons in spring. Despite the fact that temperature was not found to be a statistically significant factor in bloom triggering in this study, detected trends are particularly concerning with regard to global climate change in the future, as this taxon is frequently correlated with high temperatures (Bouchouicha Smida et al., 2014; Husson et al., 2016; Delegrange et al., 2018). Although the constant presence of this taxon and its regular exceeding of bloom threshold in the studied lagoon has never been associated to toxin production until now, a persistence in water temperature increase in winter or spring could not only potentially increase *Pseudo-nitzschia* spp. blooms occurrence and intensity, but also their toxicity since high temperatures can boost their Domoic Acid production (Thorel et al., 2014). Climate change implications already discussed above can be even exacerbated in spring season, as nutrient inputs, frequent during spring rainfall, can also influence the toxicity of bloom events (Nezan et al., 2006; Terseleer et al., 2013; Van Meerssche et al., 2018). Moreover, this genus can potentially modify community structure as it was found to induce allelopathic inhibition on many species, notably diatoms and *Skeletonema marinoi* in particular, as well as Cryptophyceae (Van Meerssche et al., 2018).

In a scenario of future temperature increase, water temperature rise in winter could also lead to unbalance in timing, frequency and magnitude of bloom events, especially with lower biomass accumulation during spring blooms, as hypothesized by Trombetta et al. (2019) following the observation in the French Mediterranean Thau lagoon. These authors found indeed that high winter blooms, triggered by mild winter temperature, induced a cascade effect on the following season by provoking blooms of lower intensity during spring. This phenomenon, already known to occur in coastal environment is expected to increase in the future (Martens, 2001; van Beusekom et al., 2009) and can then potentially affect the whole food-web of coastal lagoons at some point (Trombetta et al., 2021). All these events can also affect specifically aquaculture exploitation, both in terms of toxicity and community shifting. Many studies have already reported that a change in phytoplankton size structure or species composition can affect shellfish farming and aquaculture exploitation in the long term (Collos et al., 2003; Ribera d'Alcalà et al., 2004; Derolez et al., 2020b). Shifting in diatom dominance (such as *Skeletonema* sp. and *Chaetoceros* spp.), an important resource for aquaculture (Dupuy et al., 2000; Pernet et al., 2012), in favour to other less interesting species for this

purpose or even potentially toxic, as it has been the case in Thau lagoon (Derolez et al., 2020b), might be particularly detrimental.

In summer, *Chaetoceros* spp. produced blooms of the highest seasonal magnitude and largely contributed to bloom occurrence in both lagoons. This taxon, which is typically encountered in summer blooms thanks to its ability to exploit regenerated production and to rapidly accumulate nutrients in new biomass, even in low NO_3^- concentration, is fundamental in shellfish farming sustain (Collos et al., 2003; Bec et al., 2005; Derolez et al., 2020b).

Punctual proliferations of dinoflagellates were highlighted during the study, especially in autumn. In general, harmful dinoflagellate blooms are commonly occurring during summer season (Fraga et al., 1995; Armi et al., 2010; Reñé et al., 2011); however, some studies report dinoflagellate preference to late-summer/autumn conditions (Carrada et al., 1991; Sarno et al., 1993a; Gilabert, 2001; Carstensen et al., 2015).

Despite the low dinoflagellate contribution in winter, a punctual bloom of Gymnodiniales was detected at extremely high density at Diana lagoon in 2008. Species of this group are generally associated with summer-autumn conditions, characterized by high salinity and temperature (Carrada et al., 1991; Fraga et al., 1995; Reñé et al., 2011). However, lower salinity and temperature associated with high nutrient input can favour harmful dinoflagellate blooms (Bouchouicha Smida et al., 2014) and during winter 2008 a positive rainfall anomaly was found, indicating the possibility of nutrient high load from the watershed. In autumn, two potentially toxic taxa stood out for their intensity in bloom events: Gymnodiniales and *Gyrodinium* spp. Both are known to frequently bloom in coastal and lagoon environment and in the Mediterranean region (Carrada et al., 1991; Fraga et al., 1995; Reñé et al., 2011). Some species of the Gymnodiniales group, like *Gymnodinium catenatum*, can produce Paralytic Shellfish Poisoning toxins, depending on the cellular density reached, suggesting that this may rise concern during bloom events (Carrada et al., 1991; Sarno et al., 1993a). *Gyrodinium* genus comprises some toxic species, notably *G. corsicum*, firstly identified in Diana lagoon and responsible for fish mass mortality and neurotoxin production (da Costa et al., 2005). The observation of blooms of these T.U.s during autumn season is in accordance with their established correlation with high salinity values (Fraga et al., 1995), as for both lagoons maximal salinity values were found at this season. In addition, in Diana lagoon, a significant positive effect of salinity was found for bloom triggering, and Urbino lagoon showed a similar tendency. A potential increase in salinity during this season could enhance bloom frequency, these latter also being known to be positively correlated with salinity in autumn (Armi et al., 2010). Our results show the dominance of dinoflagellates in autumn and a slight increase in abundances of this class in most recent years at all seasons, though not significant, maybe linked to large-scale climatic processes.

Compared to other similar lagoons, another study identified the importance of dinoflagellate blooms in autumn in Thau lagoon, highlighting their emergence in the context of long-term oligotrophication and especially the rise of toxic HAB-forming *Alexandrium catenella* (Collos et al., 2009).

4.3 *Final large-scale considerations*

Diana and Urbino lagoons show an oligotrophic regime and are not subjected to strong artificialization such as increasing urbanization. They may therefore be considered close to a hypothetical reference state for similar Mediterranean lagoons, in particular Urbino, which is clearly dominated by seagrass meadows as primary producers and reflects a quasi-pristine condition. Observations in these environments can thus give an idea of future evolutions in oligotrophication processes, despite the difficulty in their prediction, as well as giving information on shellfish farming-exploited environments. On the whole, the two studied lagoons showed similar trajectories and are evolving over time, despite different exploitation carried out, left aside some dissimilarities linked to specific local environmental conditions. In fact, major differences could be identified.

Urbino lagoon showed slightly wider range in salinity variations and a more variable salinity evolution on the long term as well as higher silicate content and far longer residence time than Diana lagoon. In contrast, turbidity was generally higher and more variable in Diana lagoon. The origin of these phenomena is not known, yet it can be suggested that salinity variations may depend on local differences in exchanges with the sea, watershed inputs or local meteorological factors. Groundwater exchanges with the lagoon can also play an important role in local conditions and may be involved in the differences in silicate content between the two lagoons (Erostate et al., 2020). This, together with high developed seagrass meadows, can also determine lower turbidity in Urbino lagoon, due to sediment trapping. Aquaculture exploitation in Diana lagoon can also provoke higher turbidity through the release of suspended organic matter. Lastly, some local climatic factors not investigated in this study can be involved, like the different exposure to winds relative to surface, as the two lagoons show different shapes and surfaces. These observations could suggest dissimilarities in hydrological functioning and local regulation of the two lagoons and explain different major driving factors acting on phytoplankton dynamics previously discussed: Diana's highest stability in terms of salinity values could imply a stronger response of the community to minor variations, while the same would happen at Urbino site, but regarding turbidity.

Despite the complexity of the systems at local scale, overall seasonal dynamics discovered by this study for Diana and Urbino lagoons are supported by other

observations in similar lagoon environments (Bec et al., 2005; Collos et al., 2009; Leruste et al., 2019; Derolez et al., 2020b). In particular, winter and spring importance of *Skeletonema* sp. (Borkman & Smayda, 2009; Collos et al., 2014; Hernández Fariñas et al., 2015; Derolez et al., 2020b), and general *Chaetoceros* spp. dominance were also found in other oligotrophic lagoons, like Ayrolle lagoon in South of France (Leruste et al., 2019). Even if the studied lagoons are relatively preserved from anthropic pressure and show oligotrophic status, some changes in phytoplankton community structure and trends are already ongoing, indicating that the changes depicted during the study must be related to large-scale processes, such as climate influence.

Despite their relatively preserved conditions, the two studied lagoons showed some worrying trends, like Chl *a* increase over winter and the occurrence of blooms of potentially harmful algae.

In both lagoons, the presence, magnitude, frequency and trends of harmful *Pseudo-nitzschia* spp. blooms seem to be the most alarming point, especially given the fact that their intensity and frequency are already known to be increasing over the Mediterranean basin (Bouchouicha Smida et al., 2014; Husson et al., 2016; Melliti Ben Garali et al., 2020). Other punctual proliferations of potentially toxic groups (like Gymnodiniales) should be considered a potential risk, since similar HAB emergences were already found in other similar lagoon environments at oligotrophic state (Collos et al., 2009). Moreover, potential effects of salinity and temperature variations on these two lagoons were highlighted. Even at regional scale, climate change should then be taken into account for future monitoring and conservation of these environments, since expected future variations in temperature, salinity, precipitations and nutrient loads are likely to play a role in favouring potentially harmful phytoplankton proliferations, changing size structuring and provoking bloom shifts, with all consequent economic, social and sanitary drawbacks (Tatters et al., 2012; Sahraoui et al., 2013).

5. CONCLUSIONS

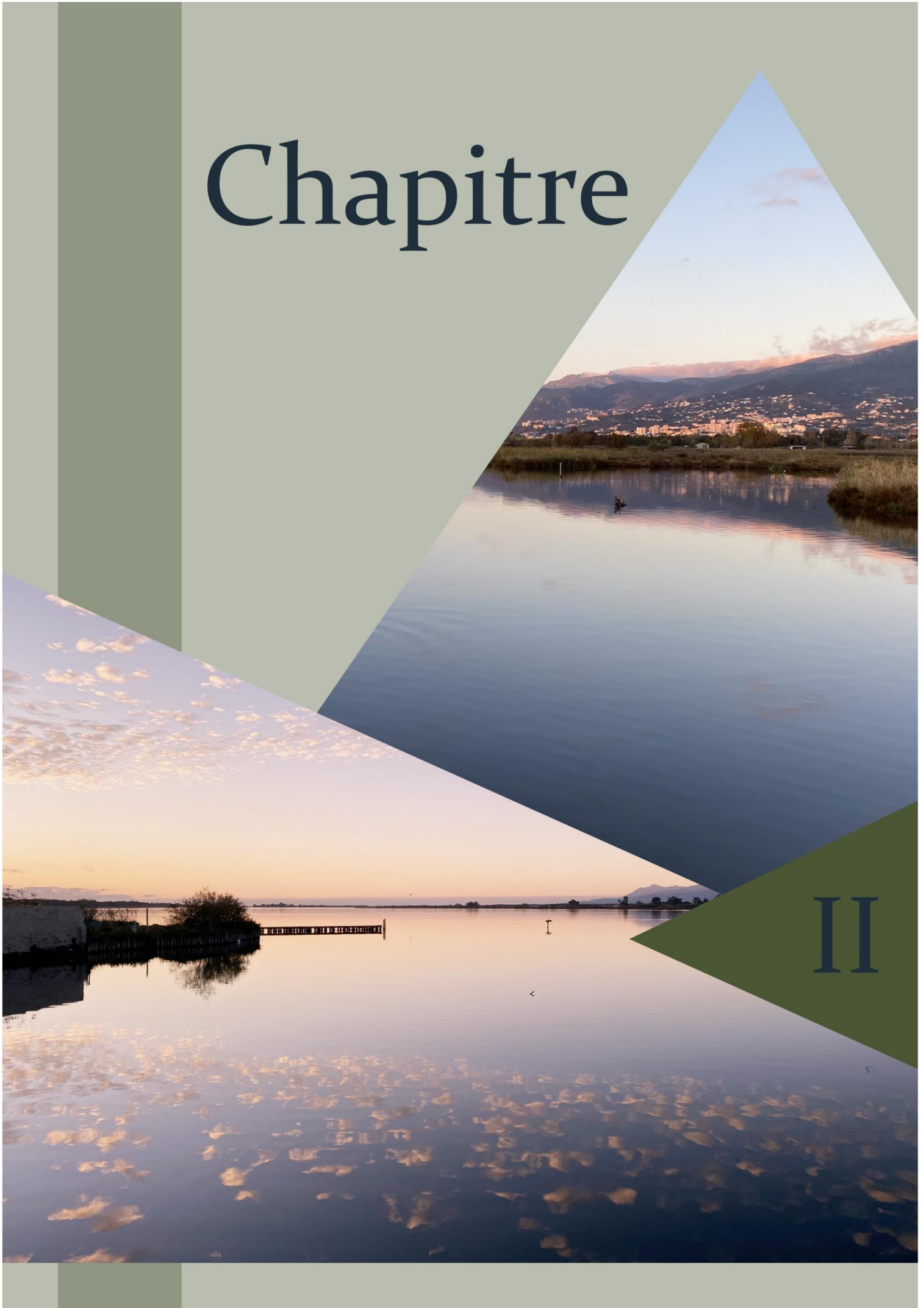
Through our study, we demonstrated that significant changes are ongoing in two oligotrophic Mediterranean coastal lagoons in the Corsica Island. Our study, based on a detailed seasonal characterization over long-term time span, consists in a good starting point for a better understanding of the phytoplankton communities' dynamics within oligotrophic Mediterranean coastal lagoons and suggested key relationships linking HAB events to the ecological functioning of water bodies.

However, we highlighted some limitations: the available environmental data seem insufficient to fully explain phytoplankton dynamics. The high complexity of the

coastal lagoon functioning makes it hard to detect clear relationship between phytoplankton and few environmental variables, as many different factors are involved. For future long-term studies, the lack of seasonal nutrients monitoring should be filled and regular counting and identification of total phytoplankton community should be continued. Also, quantification of smaller phytoplankton size classes should be performed on a seasonal basis, especially with regard to their importance in oligotrophic lagoons and in a climate change perspective (Derolez et al., 2020b). Moreover, top-down control through zooplankton grazing and fish predation was not considered in the study due to lack of long-term information and complexity of the relations in these environments, despite them being important in the regulation of phytoplankton communities (Frisoni, 1984; Bouchouca, 2010). Despite these limitations, the results of this study proved ongoing changes in the phytoplankton community structure and bloom events and worrying evolution of the potentially toxic diatom *Pseudo-nitzschia* spp., linked to salinity and temperature changes, in both lagoons. Hence, this highlights the need of long-term seasonal studies to escort the implementation of prospective management of lagoon environments at regional and Mediterranean scales, taking into account their exploitation and the forecasted climate change scenario.

Chapitre

II



LONG-TERM ECOLOGICAL TRAJECTORIES OF A DISTURBED MEDITERRANEAN COASTAL LAGOON (BIGUGLIA LAGOON): ECOSYSTEM-BASED APPROACH AND CONSIDERING ITS RESILIENCE FOR CONSERVATION?

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CONTEXTE GÉNÉRAL ET RÉSUMÉ

Les lagunes côtières sont soumises à des pressions de plus en plus croissantes, souvent d'origines anthropiques directes ou indirectes. Ces milieux sont sujets donc à une dégradation inexorable qui impacte fortement leur capacité de résilience face aux perturbations.

Dans ce travail, le fonctionnement écologique et l'évolution de l'étang de Biguglia, lagune fortement impactée de la côte orientale de la Corse, ont été analysés à travers une approche écosystémique. Ceci comprend l'analyse de plusieurs compartiments biotiques (macrophytes, phytoplancton, espèces invasives) et indicateurs abiotiques (contexte hydro-climatique, eutrophisation), ainsi que la prise en compte des connexions du système lagunaire à son bassin versant et à la mer. La présence et l'activité humaine (actions de gestion, activités de pêche) sont aussi considérées dans un contexte socio-écosystémique, où l'Homme est partie intégrante du milieu, de ses dynamiques et de son écologie.

L'objectif primaire de ce travail est de fournir une analyse globale de la trajectoire d'évolution écologique du système lagunaire de Biguglia sur le long terme (2000-2021), identifiant les facteurs qui influencent ses capacités de résistance et résilience, et ensuite de suggérer des stratégies de gestion pour supporter sa conservation et sa restauration, afin de préserver les services écosystémiques fournis.

Les résultats ont montré que, malgré avoir présenté une bonne capacité d'absorber les bouleversements dans le passé, la lagune a récemment montré des changements considérables au niveau de la composition de sa communauté phytoplanctonique, ainsi que le développement d'une susceptibilité à l'invasion biologique et la diminution des stocks de poissons d'intérêt commercial. En particulier, les résultats plus marquants au niveau des communautés phytoplanctoniques sont une augmentation des *blooms*, la diminution de la diversité des communautés, une tendance au *shift* progressif vers une dominance de dinoflagellés et la parution et persistance d'espèces potentiellement toxiques, comme le dinoflagellé *Prorocentrum cordatum*. Parallèlement, une perte d'herbiers de phanérogames et un changement dans la distribution spatiale des espèces présentes ont été observés, ainsi que l'installation récente et la prolifération massive de plusieurs espèces non-natives, comme le cténophore *Mnemiopsis leidyi* et le crabe bleu *Callinectes sapidus*.

Les variations des paramètres environnementaux, en particulier la salinité, se sont révélées des symptômes d'un fonctionnement déséquilibré et altéré du système, notamment en relation avec la problématique de la gestion du grau et la sécheresse liée au changement climatique en progression. Ces observations ont permis de mettre en

évidence la complexité du fonctionnement hydro-écologique de la lagune et l'importance de maintenir la continuité hydrologique du système bassin versant-lagune-mer. Dans le futur, surtout à la lumière du changement climatique, la lagune pourrait perdre la capacité de résister et reconstituer son équilibre après un bouleversement, même face à une perturbation de faible intensité. Dans ce cas, la lagune pourrait dépasser un point de rupture et faire basculer l'équilibre du système vers un état dégradé et/ou non-désiré, potentiellement très stable ou même irréversible.

L'étude a révélé que la dégradation amène à l'aggravation de la sensibilité du système lagunaire aux perturbations et que les actions de gestion peuvent parfois avoir des effets secondaires indésirés, en raison de la complexité du milieu et de ses interactions. Pour une application à large échelle sur des systèmes lagunaires similaires dans le monde, l'approche écosystémique rétrospective appliquée pendant ce travail s'est révélée une stratégie essentielle pour pouvoir produire une image holistique du système. Cette étape est nécessaire pour améliorer et guider une gestion intégrée de ces écosystèmes de façon efficace : malgré la nature apparemment très descriptive de l'approche utilisée, ceci englobe l'investigation scientifique, mais aussi la perception et l'expertise des acteurs en jeu. Cette vision globale est essentielle pour identifier les facteurs agissant sur la capacité de résilience du système et offre donc une base pour le dialogue et une aide vers la coopération et l'établissement d'un spectre d'états désirés vers lesquels faire converger le système. Sur la base de ces raisonnements, l'investissement des énergies dans une gestion intégrée, visant à protéger et préserver la résilience naturelle de l'écosystème, est primordial pour conserver les services écosystémiques fournis, dans un contexte de changements globaux en progression.



MOTS CLÉS

Lagunes côtières méditerranéennes · Résilience · Gestion · Approche écosystémique (EBA) · Invasion biologique · Dinoflagellés · HABs

1. INTRODUCTION

Coastal systems are particularly fragile, as the development of human activities and climate change are increasingly causing a “coastal squeeze” phenomenon, meaning the subtraction or loss of available space for the natural functioning of these systems (Chacón Abarca et al., 2021), aquatic ecosystem degradation (Perrow & Davy, 2002; Lloret et al., 2008), reduction of biodiversity, and consequent loss of ecosystem services (Elmqvist et al., 2003; Nyström et al., 2012) with, ultimately, reduced resilience and resistance to climate change and other pressures (Defeo et al., 2021). Coastal lagoons are transitional systems, strictly dependent on their connection to adjacent systems (Tagliapietra et al., 2009). They are characterized by complex spatio-temporal diversity compared to other transitional systems, and this makes it difficult to distinguish human-driven impact from natural stress (Pérez-Ruzafa et al., 2019b). Moreover, coastal lagoons are particularly subjected to more human-induced pressures than many other ecosystems (Elliott & Whitfield, 2011). Efficient management has become increasingly vital in order to sustain lagoons’ ecosystem services and avoid their loss (Jennerjahn & Mitchell, 2013).

Constant long-lasting (e.g., urbanization, exploitation, and temperature rise) or punctual (e.g., extreme events) disturbances bring about degradation in coastal lagoons, sometimes resulting in the shift of these systems into alternative stable states, different from the initial state, in which they can be locked due to higher stability of degraded states (Scheffer et al., 2001; Carpenter et al., 2012; Nyström et al., 2012; Pérez-Ruzafa et al., 2018). The capacity of a natural system to experience disturbance without losing its essential function, structure, and identity is referred to as “resilience” (Walker et al., 2006). At first limited to the capacity of the system to return to equilibrium after disturbance, resilience is a concept that recently expanded to a human–environmental framework, since “human systems are a component of, and in turn shape, ecological ones” (Cote & Nightingale, 2012). Anthropogenic presence and growth impose a necessity for the sustainability of ecosystems, meaning the optimization of resource use and maintenance of ecosystem services provided (Cote & Nightingale, 2012; Pasqualini et al., 2020; Walker, 2020). Resilience is not linked to sustainability in a strict sense; however, a social component is inevitably present since the coexistence of “natural” ecosystem functioning and human activities leads to the aim to converge to a spectrum of “desired states”, in a dynamic context of constant (mostly of anthropogenic origin) change (Elmqvist et al., 2019; Walker, 2020). Resilience concept is hence now represented by a broader dynamic approach: it involves the social–ecological perception of natural environments and also anthropic activities as the ability of humans to maintain development in face of change (e.g., climatic, geopolitical, and anthropic context) and

in a sustainable and durable way; it is tightly linked to management questions (Folke, 2006). That is why recently ecosystems are often considered as “social–ecological systems” constituted by ecological and human components and in which anthropic activities are integrated as part of their ecology. Hence, from a conservation point of view, resilience re-joins the idea of a “desired state” through the “resilience thinking” notion, which revolves around three main concepts: resilience, as persistence; adaptability, as the capacity of actors in a system to influence its resilience; and transformability, as the ability to transform the stable system into a different new one when it is no longer possible to sustain it with the preexisting ecological, economic, or social structures (Folke et al., 2010).

Changes are related to both temporal and spatial scales, as they are linked to local anthropic activities and broader scale processes such as climate change or geopolitical events and the interaction between these multiple factors (Folke et al., 2021). Hence, the present global changing and dynamic context results in the difficulty or even impossibility of the classic approach, based on historic reference state, to the conservation of natural ecosystems, and leads then to a wider approach of multi-disciplinary integrated management (Walker et al., 2006; Hobbs et al., 2009). However, integrated management is deeply intricate, especially in coastal lagoon systems, due to their complexity and natural variability. These environments show wide internal gradients of salinity, going from estuarine to hypersaline characters depending on variable freshwater influence and connection to the sea, exhibit different trophic regimes, and globally evolved in very contrasting anthropogenic contexts (Pérez-Ruzafa et al., 2011c). These different contexts and functioning make it difficult to classify these systems and hence establish general rules or recommendations (Pérez-Ruzafa et al., 2011c; García-Ayllón, 2017). In order to contemplate efficient integrative management, it is essential to understand what controls the resilience capacity of an ecosystem following disturbances and how human activities can alter this capacity, from a social–ecological point of view. This implies deep technical and scientific knowledge of the system’s functioning (Davoudi et al., 2016). To do so, it is particularly important to trace and analyze the trajectories of the system, in order to describe its evolution in marking events and highlighting its connectivity with other systems (Biggs et al., 2015; De Wit et al., 2020; Derolez et al., 2020a; Pasqualini et al., 2020).

The main consequences of ecosystem degradation generally consist of a simplification of the biological community structure, with the loss of specialized species and the success of more generalist species, especially at the primary producers’ level, as these react more rapidly to environmental change (Pasqualini et al., 2017; Le Fur et al., 2019). In particular, different stages of primary producers shift along the degradation

process of lagoon systems, mainly regulated by nutrient content and hydrological functioning, are well described in the literature (Schramm, 1999; Pergent-Martini et al., 2005; Pergent et al., 2006; Bec et al., 2011; De Wit et al., 2017). Basically, in pristine conditions characterized by low turbidity and dissolved inorganic nutrient concentrations, the community is dominated by slow-growing submerged angiosperms, like *Ruppia* and *Zostera* spp., with weak phytoplankton densities (Schramm, 1999; Pergent-Martini et al., 2005; Pergent et al., 2006). As nutrient loading increases, the system goes through successive stages: at first, light limitation occurs due to the development of epiphytes on angiosperms' leaves; hence, angiosperms start decreasing and shift toward opportunistic macroalgae, such as *Gracilaria*, *Ulva*, and *Cladophora* spp., or phytoplankton starts to take place and may eventually flip the ecosystem into a phytoplankton-dominated and turbid state (Schramm, 1999; Bec et al., 2011; De Wit et al., 2017). Recently, phytoplankton biomass, community shifts, and proliferations of harmful species, known as harmful algal blooms (HABs), are increasing worldwide and especially in the Mediterranean region and coastal lagoon environment, linked to anthropogenic pressures ("cultural eutrophication", Malone and Newton, 2020) and global change (Hallegraeff, 2010; Kudela et al., 2015; Fischer et al., 2020; Ligorini et al., 2022a). Lately, shifts toward dinoflagellate dominance were increasingly observed (Xiao et al., 2018; Fischer et al., 2020). This class and especially some potentially toxic species, like *Prorocentrum* spp., can have the upper hand by taking advantage of rising temperatures, increasing eutrophication and nutrient inputs from terrestrial runoff in coastal environments or management actions (Aligizaki et al., 2009 and references herein; Collos et al., 2009; Xiao et al., 2018; Fischer et al., 2020). These events can lead to drawbacks on higher trophic levels, like biotic homogenization, decrease in zooplankton biomass, decrease in fish catch, toxin bioaccumulation, and risks to human health (Smayda, 1997a; Fischer et al., 2020; Zingone et al., 2021).

Another cause of biotic homogenization and disturbance is the introduction (intentional or accidental) of non-native species. Such species may sometimes have the upper hand over native ones, usually by taking advantage of degradation, and successfully install themselves by becoming "invasive" and exacerbating homogenization and degradation, especially in lagoon environments (Boudouresque & Verlaque, 2012; Tordoni et al., 2019). Tracing and understanding biotic invasion are essential to preserve biological diversity and hence enhance the resistance capacity and resilience of ecosystems (Elmqvist et al., 2003). Invasions of the ecosystem engineer polychaete *Ficopomatus enigmaticus* (Fauvel, 1923) are long known in many lagoon environments worldwide (Argentina, Balearic Islands, Italy). This species is known to have negative impacts on macrophytes, fish nets, water and sediment circulation, inducing cascade effects along the trophic network and ecological and economic

damages (Fornós et al., 1997; Bazterrica et al., 2012; Brundu & Magni, 2021). Eurasian carps *Cyprinus carpio* (Linnaeus, 1758) are the most widely introduced species in temperate aquatic systems and are drivers of ecological disruption by destructing seagrass beds and fueling phytoplankton blooms in lakes and reservoirs through their feeding behavior (Fischer et al., 2013; Qiu et al., 2019; Dalu et al., 2022). Other very recent and rapidly wide-spreading invaders in Mediterranean lagoons are the ctenophore *Mnemiopsis leidyi* (Agassiz, 1865) and the blue crab *Callinectes sapidus* (Rathbun, 1896). *M. leidyi* has colonized Mar Menor (Spain), S'Ena Arrubia (Italy), and eight Gulf of Lion French lagoons over the last 20 years, causing direct and indirect negative effects on fishing activities, through physical clogging of fish nets and predation on plankton (Marambio et al., 2013; Diciotti et al., 2016; Marchessaux & Belloni, 2021). *C. sapidus* invasions reported in Mediterranean lagoons are relatively recent and rapidly growing, probably linked to climate change, but they are extremely detrimental to the environment and fishing activities (Cilenti et al., 2015; Fuentes, 2019; Taybi & Mabrouki, 2020). This species colonized 17 out of 23 countries along the Mediterranean coasts and was found to negatively impact native wildlife and fisheries through its voracious behavior (Cilenti et al., 2015; Taybi & Mabrouki, 2020).

Integrative management of lagoon environments is therefore essential, especially with regard to the speeding deterioration of these systems over the last few decades, as highlighted by previous works. For instance, Badosa et al. (2007) demonstrated that some management actions may not have desired effects on the system if applied without taking into account the connectivity of the lagoon to surrounding systems. Nevertheless, this kind of study generally focuses on one or few biological compartments, like primary producers, plankton, or invasive species only, instead of describing the complex context of the ecological network and its connectivity (Badosa et al., 2007; Schallenberg et al., 2010a; Delpy et al., 2012).

In this work, we explored the ecological trajectories of the Biguglia lagoon, which is a relevant example of Mediterranean coastal lagoons and can be considered a social-ecological system in its urbanized setting (Pasqualini et al., 2020). The originality of this work consists of the application of an ecosystem-based approach (EBA) to the lagoon socio-ecosystem over the last 20 years (2000–2021). We integrated multiple abiotic and biological compartments, including human activity, in the ecology of the system and also its connectivity to its watershed and exchanges with the sea. The aim of this study is to provide a large-scale comprehension of the lagoon system functioning through the tracing of long-term ecological evolution trajectories in order to provide support to the conservation or restoration of this environment and the maintaining of ecosystem services it offers, as well as improving useful scientific and methodological knowledge

for future management of other similar environments. Three main questions are asked. What is the global ecological evolution context of the lagoon in the last 20 years (2000–2021; hydro-climatic context, connectivity of the lagoon and eutrophic situation, primary producers (macrophytes and phytoplankton), invasive species, and fishing activity)? In the particular eutrophication context of the Biguglia lagoon, how has the phytoplankton community evolved since 2010 observations? Is the system globally resilient and resistant, and which information can be provided to understand which factors influence these capacities and therefore help future management strategies?

2. MATERIALS AND METHODS

2.1 Study site

The Biguglia lagoon is the largest coastal lagoon on Corsica island, covering a surface of 14.5 km² with a watershed of 180 km² (42°36'N, 09°28'E), at the south of Bastia town (Figure 1). This brackish lagoon is characterized by shallow waters (maximum depth of 1.8 m). Exchanges with the sea take place through a long (1.5 km), narrow, natural sea channel located in the northern part. The sea channel mouth, allowing communication with the marine environment, is known as *grau* (Figure 1). Marine water inputs are estimated to reach ≈ 13 Mm³ per year (Mouillot et al., 2000) and are limited due to the tendency of the *grau* to naturally close through sand accumulation. Artificial opening interventions are frequently required to re-establish the connection with the sea, even though these take place only when necessary under the administration of a service within the Collectivity of Corsica regional institution, without a regular management pattern. Freshwater inputs dominate the water budget (≈ 90 Mm³ per year compared to the total volume of the lagoon, 18 Mm³, Dufresne et al., 2017) and are insured by numerous rivers and streams, pumping stations of the agricultural plain, sewage plants, and direct runoff. Major inputs come from the Bevinco river in the north (Figure 1). Freshwater inputs also take place in the southern part through the artificial channel connecting the Golo river to the lagoon at its southern end (Fossone canal; Figure 1); in particular, when Golo river's discharge is limited by meteorological factors (i.e., low rainfall, winds, and currents) and, hence, its outlet tends to close, freshwater cannot flow completely in the sea and is then deviated to the lagoon through the Fossone canal (Figure 1). The hydrological functioning of the Biguglia lagoon is however more complex than this since exchanges with the sea can take place both in the extreme north of the lagoon, through the natural *grau*, and in the southern part, as when meteorological conditions (i.e. wind direction and velocity, and currents) are favourable sea water can reach the lagoon from the Golo outlet through the Fossone canal (Figure 1). Global historical knowledge of the lagoon report that, in addition to huge seasonal

temperature variations (3°C–28°C), the water basin experienced historically a wide range of salinity conditions (4–37) at various temporal and spatial scales (Garrido et al., 2016), according to its high dependence on sea and freshwater inputs and the major impacts of water flux management performed under the government of the Collectivity of Corsica’s service.

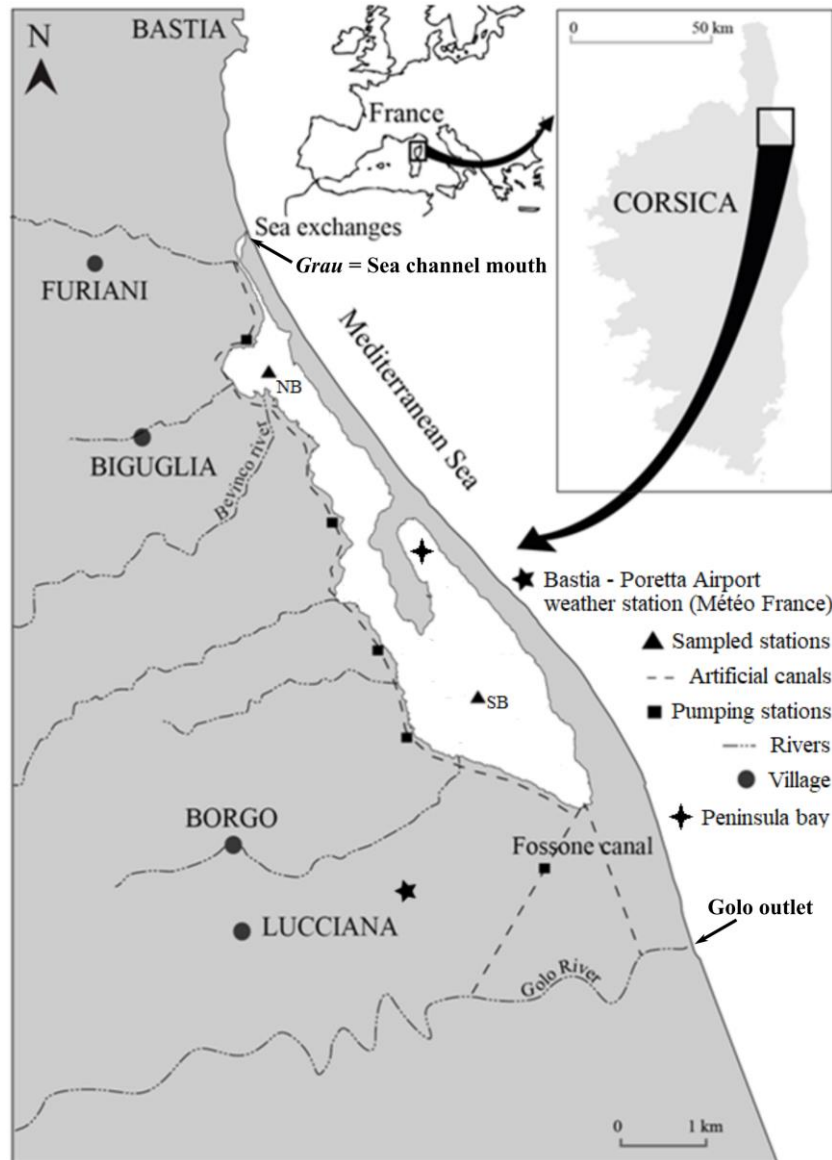


Figure 1 Study site localization: main elements of the Biguglia lagoon watershed, sampled stations, and Bastia-Poretta Airport meteorological station (Météo-France) are represented (figure from Pasqualini et al. (2017) - modified).

Due to its patrimonial biological and ecological interest, the Biguglia lagoon has been recognized as RAMSAR wetland conservation site since 1991 and is a Natural Reserve (Natural Reserve of the Biguglia Lagoon, RNEB) since 1994. It offers numerous ecosystem services of social and economic interest, like fish exploitation and provision of drinking water, as its aquifer (40 Mm³) is the main source of drinking water for the urban area of Bastia (72,000 inhabitants) (Erostate et al., 2022). The lagoon is set in a

highly urbanized context with growing population and increasing artificialization of its watershed and is subjected to regular management efforts under the Water Framework Directive (WFD). Ecological status was classed as “mediocre” in 2018, with phytoplankton, macrophytes, and benthic invertebrates as declassing parameters. The objective of “good status” imposed by the WFD has been postponed twice for the lagoon since 2010 (in 2015 and 2021) and is now set in 2027, indicating a need for the development of new and effective management strategies. The lagoon historically experienced major disturbances and alterations of its natural functioning and even underwent two major dystrophic crises in the past associated with low salinity conditions (in 1991 and 2007; [Cecchi et al., 2016](#); [Garrido et al., 2016](#); [Pasqualini et al., 2017](#); [Erostate et al., 2022](#)). It is currently subjected to ongoing eutrophication, due to increasing urbanization and agricultural exploitation of its watershed, and alterations of its connectivity to the adjacent marine environment ([Pasqualini et al., 2020](#); [Erostate et al., 2022](#)).

2.2 Long-term data collection

To describe the long-term evolution of the lagoon, historical data on different environmental and biological parameters were collected from multiple sources. For meteorological data, daily rainfall and mean air temperature data were collected from Météo-France at the Bastia-Poretta Airport meteorological station (42°32'26" N; 9°29'07"E; [Figure 1](#)). In order to characterize climatic long-term trends, an annual dataset of cumulative rainfall and mean air temperature from 1950 to 2021 was constructed. Potential multiannual monotonic trends were investigated through the Mann–Kendall (MK) trend test (*modifiedmk* package in R, [Hamed & Rao, 1998](#); [Patakamuri & O'Brien, 2020](#)), applied to annual cumulative rainfall and mean air temperature means. The Theil–Sen slope estimator was provided in the case of significant MK (i.e., p-value < 0.05). Then, an analysis that focused on the 2000–2021 period was performed on cumulative annual rainfall and mean annual air temperature to characterize meteorological conditions over the study period. This was compared to the standard reference value over the reference period established for France (1991–2020) according to the World Meteorological Organization guidelines (*WMO-No. 1203* © *World Meteorological Organization, 2017*). Over the same period, a monthly database was also constructed to discriminate and compare the extension of dry periods between different years.

In order to describe the global context of the study site, monthly cumulative water discharge and nutrient (nitrate, NO₃⁻) contents of the two main rivers of the watershed (Bevinco and Golo rivers) were obtained from publicly accessible data

websites (<http://www.naiades.eaufrance.fr/>, <https://www.hydro.eaufrance.fr/>) at several available sampling stations from 2000 to 2021, located at 9 km (Bevinco) and 13 km (Golo) upstream the lagoon. Annual mean values of NO_3^- discharge were then obtained based on monthly available data, by multiplying the nutrient concentration by water discharge. Values obtained were then expressed as tonnes of NO_3^- per year. A monthly database for salinity (PSU), water temperature ($^{\circ}\text{C}$), ammonium (NH_4^+ , μM), nitrate (NO_3^- , μM), nitrite (NO_2^- , μM), phosphates (DIP, μM), silicates (SiOH , μM), and chlorophyll *a* ($\mu\text{g L}^{-1}$) data for the lagoon was constructed based on different sources (Garrido et al., 2013a, 2016; REPHY, 2019 (SEANOE <https://doi.org/10.17882/47248>); RNEB data; this work). This covers the 2000–2020 period, at two main stations, representing distinct basins inside the lagoon: North Basin (NB) and South Basin (SB) stations (Figure 1). When possible, mean values for the entire basin were calculated. Potential relationships between nutrient concentrations in the lagoon, salinity of the lagoon, NO_3^- inputs and flow from main rivers (Bevinco for the northern and Golo for the southern part), and monthly cumulative rainfall were assessed through the non-parametric Spearman's rank-order correlation tests applied on available monthly data. Qualitative information on the opening of the *grau* and the outlet of the Golo river were obtained by visual analysis of available satellite pictures from *Landsat 4/5* (30-m resolution), *Landsat 7* (15-m resolution), and *Sentinel2* (10-m resolution) systems (<https://glovis.usgs.gov/>). Sixteen-day cycle data were available from January 2000 to October 2021. For each image, the outlets were assigned a status of “opened” (1), “closed” (0), or “partially opened” (0.5). To represent dominant trends over the study period, a mean value was then calculated per year. All the years considered within our study presented at least 10 observations seasonally distributed along the year. Furthermore, information on human-mediated openings of the *grau* was collected from the Natural Reserve of the Biguglia Lagoon (RNEB data) and expressed as the declared number of days of artificial openings per year.

In order to analyze biological compartments and evolution over time of different trophic levels, multiple sources were exploited. Data on fish captures (t), fish species evolution, and major invasive species were obtained from professional fishermen, managers of the RNEB, and literature (Bouchoucha, 2010; Etourneau, 2012). Macrophytes (angiosperms and macroalgae) mean percentage coverage over the basin and dominant species information were obtained from the *Observatoire des Lagunes* (OBSLAG) network data (monthly samples during the summer period from 2000 to 2021 at 15 stations in the Biguglia lagoon) and following the method described in Pasqualini et al. (2017). Finally, monthly phytoplankton cellular abundances (cell L^{-1}) and community composition data were collected to analyze relative composition at the class level and identify dominant phytoplankton species and bloom events, defined as cellular

proliferation over 100,000 cell L⁻¹ threshold (Cecchi et al., 2016; Belin & Neaud-Masson, 2017). Data were issued from literature (Cecchi et al., 2016; Garrido et al., 2016; Leruste et al., 2019) and field sampling in 2020. All analyzed data came from optical microscopy identification (inverted microscope CKX31, OLYMPUS) and quantification through the Utermöhl method, applied on samples fixed with formaldehyde solution at 2.5% final concentration (Utermöhl, 1958; AFNOR, 2006). Available monthly data at the two stations covered the years 2010, 2012 (from May to December), 2013, 2014, 2019 (uniquely November), and 2020. Some missing months are due to the impossibility of sample analysis performance or technical problems impeding field sampling (2020). Data were treated for the two main sampling stations separately, NB and SB. For class-level analysis, original data were grouped into five main classes: “Bacillariophyceae” (or diatoms), “Dinophyceae” (or dinoflagellates), “Cyanophyceae”, “Cryptophyceae”, and “Chlorophyta”. All individuals that could not be assigned to one of these five classes were grouped in the class “Others”. To explore the evolution of the two dominant classes, diatoms and dinoflagellates, we calculated their ratio as the abundance of dinoflagellates over the sum of diatoms and dinoflagellates. A finer qualitative analysis of dominant and blooming (cellular density >100,000 cell L⁻¹) taxonomic units was also performed.

3. RESULTS

3.1 Environmental variables

The global meteorological context analyzed over the last 70 years (1950–2021) revealed that mean air temperature and cumulative rainfall were highly variable according to the years (Supplementary – Annexe II – [Figure S1](#)). The MK test highlighted a significant increasing trend in annual mean air temperature over the overall period (1950–2021) (p-value < 0.001, Sen’s slope = 0.025), indicating a temperature rise of more than 1.7°C since 1950. From 2000 to 2021, annual mean air temperature ranged from 15.12°C (2005) to 16.96°C (2019) ([Figure 2A](#)). Until 2010, annual mean air temperatures rarely exceeded the standard reference normal value (16.14°C), except for a peak in 2003 ([Figure 2A](#)). On the contrary, since 2014, they were systematically higher than this value ([Figure 2A](#)). Conversely, cumulative annual rainfall did not show any significant monotonic trend over the period (MK p-value = 0.32). Over the 2000–2021 period, annual cumulative rainfall showed a minimum in 2021 (560.4 mm, [Figure 2A](#)). Until 2010, the standard reference value (816.87 mm) was exceeded five times (2000, 2005, 2007, 2008, and 2010), culminating at 1,375.2 mm in 2008. After 2010, only 2018 resulted in a particularly wet year, reaching a cumulative rainfall of 1,132.4 mm ([Figure 2A](#)). Looking at the monthly scale, high mean air temperatures and low cumulative rainfall tend to last for several consecutive months in recent years, progressively increasing drought

periods, while high cumulative rainfall tends to concentrate in few months, mainly in autumn (Supplementary – Annexe II – [Figure S2](#)).

For characterizing the watershed, the water discharge and NO_3^- load of the two main tributaries (the Bevinco and the Golo rivers) were analyzed. Mean annual fluxes of the Bevinco and the Golo rivers were estimated at 0.66 and 14.2 $\text{m}^3 \text{s}^{-1}$, respectively (data not shown). The average annual NO_3^- load showed mostly parallel trajectories for both rivers and broadly followed the general pattern of rainfall ([Figure 2B](#)), with peaks in 2008, 2013, and 2018. For both rivers, these peaks were mainly due to monthly inputs peaks in January, May, and November in 2008; in March and November 2013; and from February to May and October 2018 (data not shown). The highest mean annual values were found in 2008 at 4.76 and 142.83 t year^{-1} for Bevinco and Golo rivers, respectively ([Figure 2B](#)).

Nutrient concentration data in the lagoon were only available for some months and mostly for the summer season. DIP concentration in the lagoon was low, ranging from 0.02 μM (June 2002) to 0.62 μM (August 2003) (data not shown). Silicate content reached a maximum in September 2009 (322.15 μM), while it dropped to 74.42 μM in August 2017 ([Figure 2C](#)). A gradual decrease was observed during the last 7 years, finally falling to 74.45 μM in November 2020 ([Figure 2C](#)). Nitrogen compounds showed high variability. NO_2^- concentrations ranged from 0.00 to 3.13 μM (June and July 2006) (data not shown). NH_4^+ concentration culminated at 21.42 μM in August 2007 and remained below 5.5 μM from 2010 except for a peak at 8.04 μM in December 2014. NO_3^- concentrations varied during the period, and the highest values were observed in 2013–2014 when the maximum of 61.23 μM was reached in December 2013 ([Figure 2C](#)). Global trend showed rainfall was positively correlated with rivers' flow and NO_3^- inputs from the watershed (Spearman's rank-order correlation coefficients, 0.31 and 0.09, respectively, $p < 0.05$ for both) and negatively with the salinity of the lagoon (Spearman's rank-order correlation coefficient, -0.34 , $p < 0.001$). A significant positive correlation was found between NO_3^- and NO_2^- concentrations in the lagoon with NO_3^- inputs from the watershed (Spearman's rank-order correlation coefficients, 0.31 and 0.28, $p < 0.01$ and 0.001, respectively) and Bevinco and Golo rivers' water discharge (Spearman's rank-order correlation coefficients, 0.47 and 0.42, respectively, $p < 0.001$ for both). All nutrient concentrations within the lagoon were significantly negatively correlated with the salinity of the lagoon (Spearman's rank-order correlation coefficients, -0.50 (NH_4^+), -0.49 (NO_2^-), -0.30 (NO_3^-), and -0.58 (silicates), $p < 0.001$ for all).

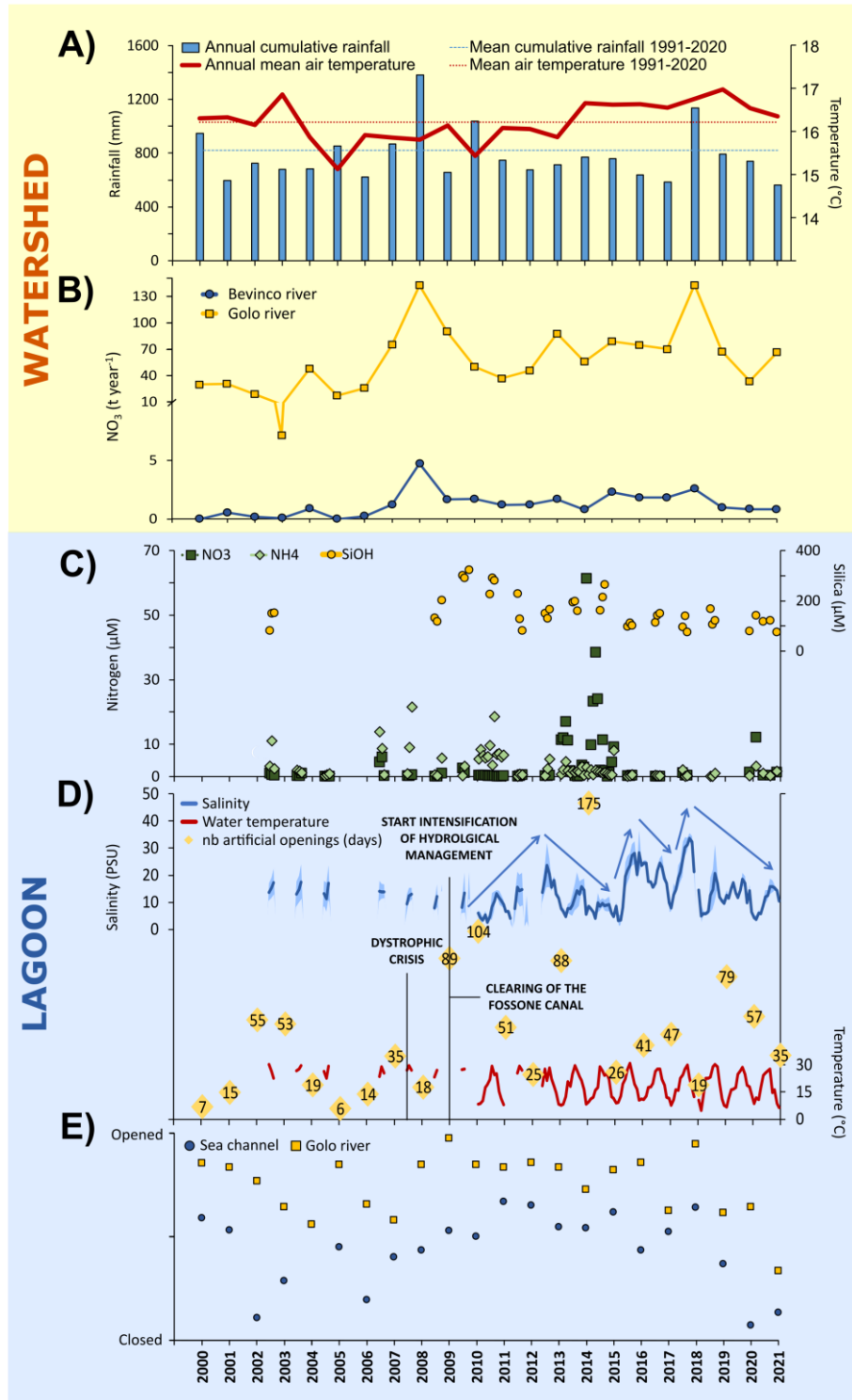


Figure 2 Multi-parameter evolutions over the 2000–2021 period for watershed and lagoon characterization over time. (A) Meteorological context is shown by annual cumulative rainfall (mm) and mean air temperature (°C), together with respective means over the standard reference period (1991–2020; WMO-No. 1203 © World Meteorological Organization, 2017). (B) Annual mean nitrate loads (t year^{-1}) for the Bevinco and Golo rivers. (C) Nutrients monthly mean concentrations (NO_3^- , NH_4^+ , SiOH ; μM) for the water basin. (D) Mean monthly patterns of salinity (PSU), with light blue halo representing standard deviation of sampling stations and water temperature (°C), together with annual management effort on sea channel opening (expressed as days spent on artificial intervention) and major remarkable events. (E) Mean annual open/close status of the seachannel and Golo river outlet.

Mean monthly water temperature followed seasonal variations and did not show any important interannual variability, fluctuating from a minimum of 4.83°C (February 2018) to a maximum of 30.88°C (August 2015) (Figure 2D). Salinity experienced high variability over time, ranging between 2.66 PSU (Mai 2010) to 33.67 PSU (September 2017), and significant trends could be identified. Progressive desalinization was observed until 2010 (Figure 2D). Starting from 2009, an intensification of management efforts to keep the *grau* open (e.g., up to 104 days of artificial intervention in 2010) resulted in gradual salinization until 2012, followed by another desalinization period (Figure 2D). Then, after a steep re-salinization during 2015, wide variations took place, and a gradual decrease went on until 2020, with a marked shoot in 2018 to 4.97 PSU (Figure 2D). Parallel to these variations, some trends could be identified in the status of *grau* and outlet of the Golo river. From 2000 to 2006, both outlets tended to close, except in 2005 (Figure 2E). Then, an opening tendency went on until 2010, followed by a gradual closing trend that is still ongoing these days (Figure 2E).

3.2 Ecological parameters

Ecological trajectories were described through the multiple biotic compartment approach. Mean monthly chlorophyll *a* experienced high variability over the period, with a mean value of 11.57 $\mu\text{g L}^{-1}$ over the whole period and a peak at 272.70 $\mu\text{g L}^{-1}$ in 2007 during a dystrophic crisis (Figure 3A). Other lower peaks were reached in July 2010 (19.48 $\mu\text{g L}^{-1}$), November 2012 (24.45 $\mu\text{g L}^{-1}$), August 2017 (19.17 $\mu\text{g L}^{-1}$), and February 2020 (16.83 $\mu\text{g L}^{-1}$) (Figure 3A).

The macrophyte compartment was dominated by macroalgae for most of the period (Figure 3B). Red macroalgae of the *Gracilaria* genus were usually dominant and systematically present, while green algae dominated sporadically the macroalgal community, notably of the *Ulva* genus (*Ulva intestinalis* (Linnaeus, 1753) in 2009 and *Ulva clathrata* [(Roth) C. Agardh, 1811] in 2021) and *Cladophora vagabunda* [(Linnaeus) Hoek 1963] and *Chaetomorpha aerea* [(Dillwyn) Kützing, 1849] in 2012 and 2017, respectively (Figure 3B). Angiosperm community experienced a decrease in percentage coverage until 2009, then increased until 2014, and finally showed degradation in the last few years (Figure 3B). Remarkable events were the expansion of *Stuckenia pectinata* [(Linnaeus) Börner, 1912], usually confined to the southern basin, to the northern basin from 2017 (Figure 3B). Apparition and important development of the freshwater species *Najas marina* (Linnaeus, 1753) was noticed in 2010 and 2018, and it expanded to the northern basin as well (Figure 3B). This species was then confined to the southern basin; still it was sporadically observed in the peninsula bay (Figure 1) in 2021. A decrease in *Ruppia cirrhosa* [(Petagna) Grande, 1918] was also observed between 2015 and 2017.

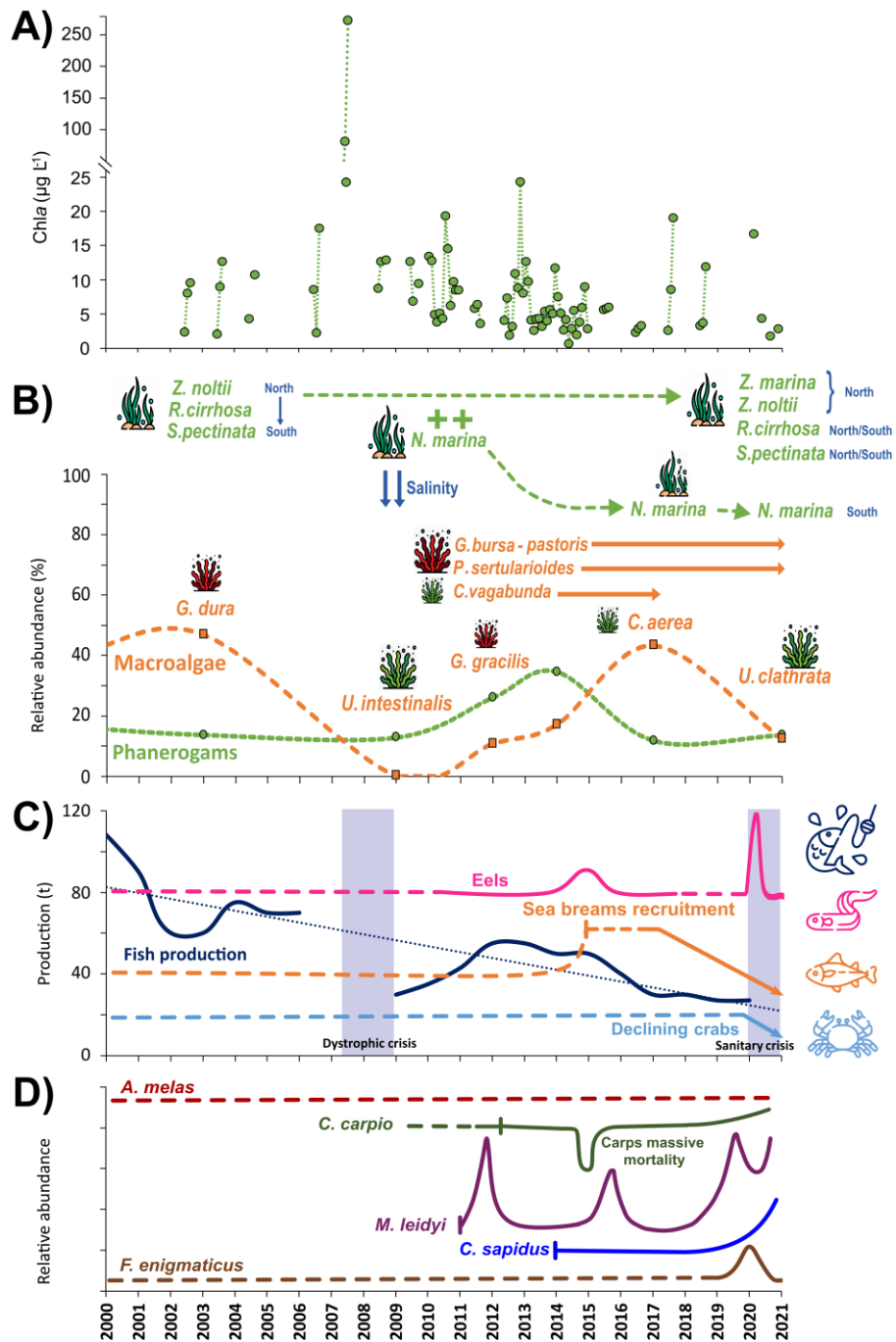


Figure 3 Ecological trajectories description of main biotic variables considered, over the 2000–2021 period. (A) Chlorophyll *a* (Chl *a*, $\mu\text{g L}^{-1}$). (B) Macrophytes (for the genera or species: *C.*: *Cladophora vagabunda*, *Chaetomorpha aerea*; *G.*: *Gracilaria*; *N.*: *Najas*; *P.*: *Polysiphonia*; *R.*: *Ruppia*, *S.*: *Stuckenia*, *U.*: *Ulva*; *Z.*: *Zostera*) main trends in relative abundance and summary description of main dominant species presence and spatial distribution variations. (C) Fish production trends (2007 dystrophic crisis and 2020 COVID-19 sanitary crisis are indicated, as fishing activity was suspended due to these events) and major trajectories for interesting commercial fish based on fishermen interviews. (D) Invasive species major trends based on stakeholders' and managers' interviews and observations, literature, and recent observations during this work. Created with pictograms from <https://www.freepik.com> and [aticon.com/authors/nhor-phai](https://www.aticon.com/authors/nhor-phai).

At a higher trophic level, a global decrease in fish production was observed (Figure 3C). Caught fish are constituted for the most part by mullets, European bass, *Atherina*, and eels. The latter experienced high recruitment in 2015 and an important fishing proportion in 2020 (Figure 3C). Great recruitment through the sea channel of the highly commercially important species *Sparus aurata* (Linnaeus, 1758) took place in 2015; then the fish stock was gradually consumed for the next 5 years (Figure 3C). Eurasian carps (*C. carpio*), introduced for recreational fishing in the surrounding streams around 2013, colonized the lagoon and became invasive (Figure 3D). This species is not commercialized in the area and always presents high abundance in the basin. In 2015, massive mortality of this species was observed following the salinization of the lagoon, with around 5 t of carcasses found in the canals around the lagoon (Figure 3D). Other invasive species are established in the lagoon, notably *Ameiurus melas* (Rafinesque, 1820), a non-commercial catfish species; the polychaete *F. enigmaticus*, which showed a worrying development in 2020 (especially in the northern basin) but then regressed in 2021 (Figure 3D); and the ctenophore *M. leidy* and the crab *C. sapidus*, both introduced very recently (Figure 3D). *M. leidy* was observed for the first time in autumn 2011 and was strongly present since its appearance, with sporadic developments at very high densities (Figure 3D). *C. sapidus* was firstly identified in the lagoon in February 2014. The fast rise observed in the last few years culminated with the capture of egg-bearing females in 2021 (Figure 3D). Parallel to the increase of invasive crab *C. sapidus*, a decrease of native crabs, usually inhabiting the northern part of the lagoon, was observed by fishermen exploiting the lagoon (Figure 3C).

3.3 Phytoplankton community

The phytoplankton community experienced some changes over the past 20 years, and remarkable shifts and blooms could be identified in the 2010–2020 period. Globally, total phytoplankton abundances showed wide interannual and monthly fluctuations, as it was the case for Chl *a* concentration, and without a clear trend (data not shown). In summer 2010, cyanobacteria were dominant at both northern and southern stations, with the genera *Anabaena* sp., *Lyngbya* sp., and *Oscillatoria* sp. (Figure 4A). The third genus also showed high contribution during summer 2012 at SB station, where a bloom of Cyanophyceae was also recorded in April 2014 (Figure 4A and Figure 5). Chlorophyta group dominated only sporadically the community (Figure 4A). They were mostly present during summer 2010 at NB, in December 2014 at SB (Chlorophyceae), from July to December 2014 at SB, and in February 2020 (Trebouxiophyceae) at both stations, associated with very low salinity (mean 3.74 PSU). Globally, diatoms dominated the community between 2010 and 2012, and then dinoflagellate contribution began to increase starting from 2013 (Figure 4A). This is supported by the variations observed in

Dinoflagellates/Diatoms+Dinoflagellates ratio: an increasing trend of the ratio was observed at both stations, meaning dinoflagellates rose to diatom detriment and with steeper slope at NB than SB (Figure 4B). Compared to 2010, annual mean and median values gradually increased, almost reaching the ratio = 1 plateau of total dinoflagellate dominance, especially at NB, and with a parallel decrease in interannual variability, meaning the dominance was more and more homogeneous over the recent years and independent from the season (Figure 4B). The year 2020 was almost completely dominated by dinoflagellates at both stations (Figure 4A, B). The most remarkable fact is that in 2020 the community was nearly systematically dominated by one single dinoflagellate species, producing a monospecific bloom, but not necessarily the same species each time. In the overall period, the majority of dominant and bloom-forming species belonged to the dinoflagellate class (Figure 5). The most frequent blooming species belonged to the *Prorocentrum* sp. genus (Figure 5). In particular, the first record of *Prorocentrum cordatum* ((Ostenfeld) J.D. Dodge, 1976) high bloom was in 2010, reaching a maximum of 5.93×10^5 cell L⁻¹ at SB in November (Figure 5). Since then, this species provoked multiple persistent blooms, especially long-lasting in 2020, when it persisted from January to June with a slight time-lag between the two stations, a minimum density of 2.74×10^5 cell L⁻¹ (May, NB) and a maximum of 5.42×10^6 cell L⁻¹ (February, SB). During the same year, another *Prorocentrum* species (*Prorocentrum micans* (Ehrenberg 1834)) produced persistent blooms at both stations from August to December (Figure 5), touching the lowest and highest densities at SB of 1.18×10^5 cell L⁻¹ (December) and 1.79×10^6 cell L⁻¹ (October), respectively.

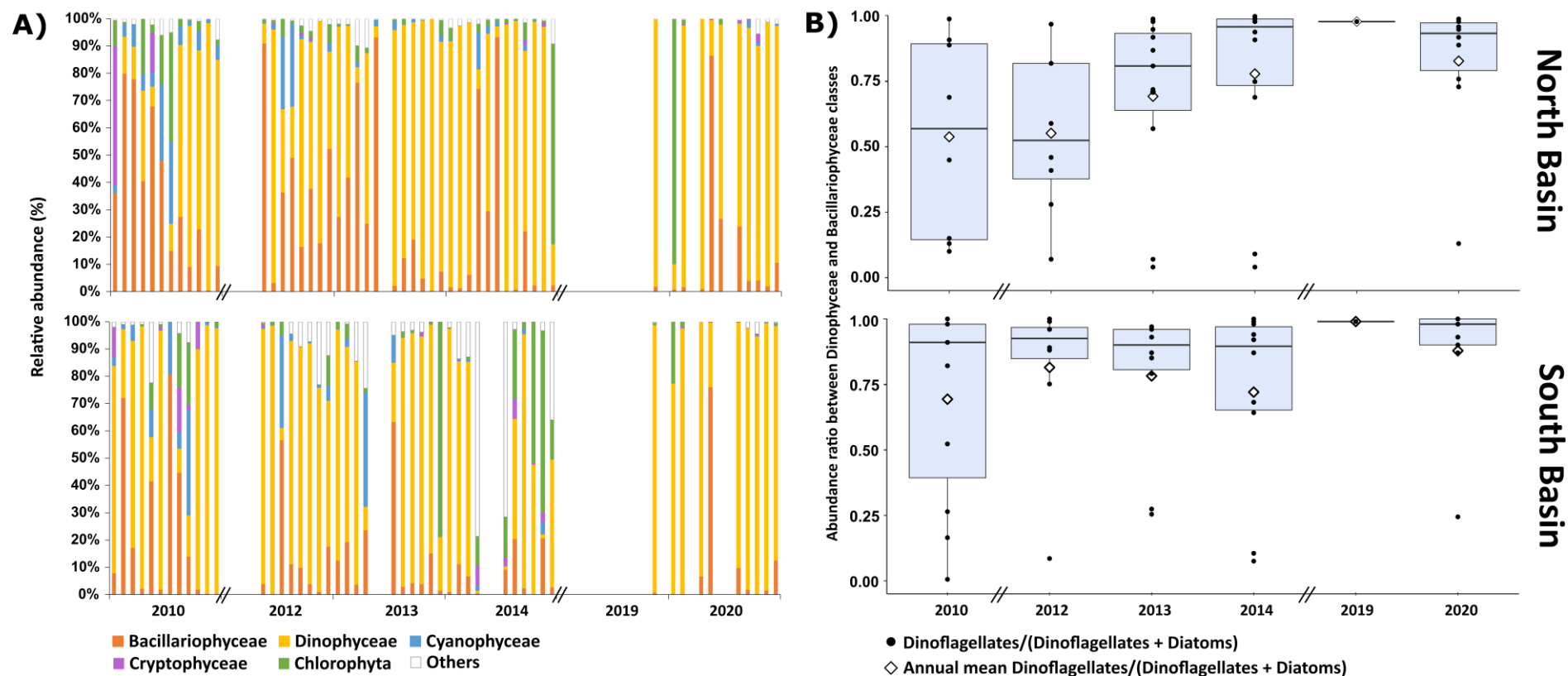


Figure 4 Phytoplankton community description over the study period considered (2010–2020). Class relative percentage composition (A) and Dinoflagellates/Diatoms+Dinoflagellates ratio (B) are represented for the two stations Northern Basin (NB), Southern Basin (SB). (B) Available monthly data on Dinoflagellates/Diatoms+Dinoflagellates ratio are represented by black points, while boxplots represent annual ratios with median (dark horizontal line) and mean (white lozenge) values.

P. cordatum is an invasive potentially toxic species. Blooms of other potentially toxic genera were observed in the lagoon. *Akashiwo sanguinea* ((K. Hirasaka) Gert Hansen & Moestrup 2000) produced a bloom lasting from September to November 2012 (Figure 5), reaching its peak at 4.06×10^5 cell L⁻¹ in October. Blooms of *Gonyaulax* sp. were recorded sporadically in 2012, 2013, and 2014 (Figure 5), with a maximum in November 2013 (3.56×10^5 cell L⁻¹). *Scrippsiella* sp. bloomed occasionally and mainly during the summer season (Figure 5), with a peak at 1.21×10^6 cell L⁻¹ in July 2012. It is worthy to mention that a massive bloom of *Dinophysis* sp. occurred in November 2019 and expanded to the entire basin, with maximum density reached at NB (1.60×10^6 cell L⁻¹) and associated with *P. cordatum* bloom too (maximum cellular density 1.37×10^6 cell L⁻¹, NB) (Figure 5).

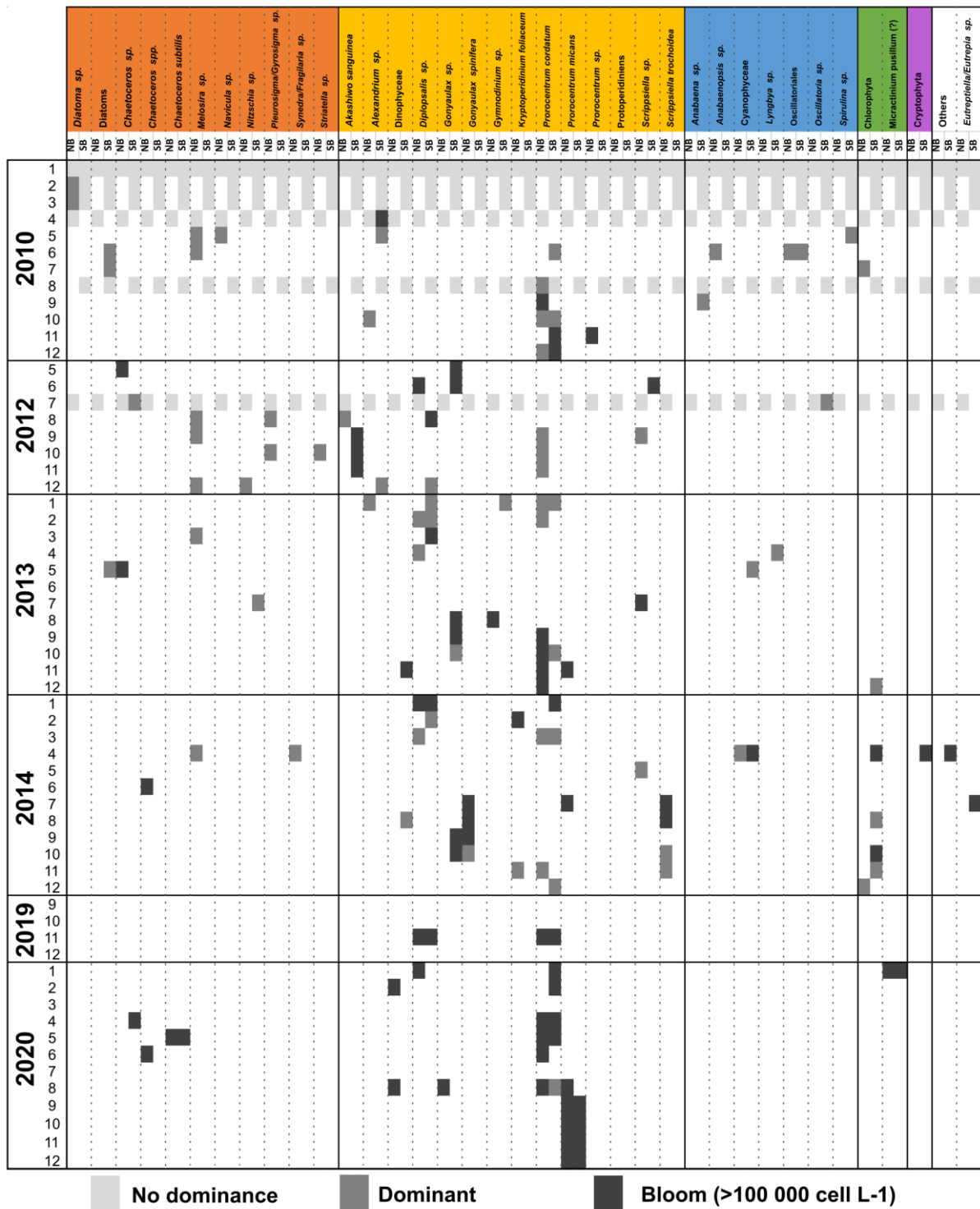


Figure 5 Bloom events and relative phytoplankton species (or taxonomic unit) were recorded in the lagoon over the 2010–2020 period for North Basin (NB) and South Basin (SB) stations. Taxonomic units are color-coded by class (for color legend see [Figure 4A](#)). White cases indicate unavailable samples; lightest colors indicate that samples were available but no dominance was highlighted; dark colors designate the dominance of the corresponding taxonomic unit; darkest colors indicate a bloom (>100,000 cell L⁻¹) of the corresponding taxonomic unit.

4. DISCUSSION

4.1 Global ecological evolution context

In its Mediterranean meteorological context, we demonstrated that the lagoon has been subjected to an increasing trend in mean air temperatures in the last 70 years, in accordance with universally established temperature rise due to climate change (Giorgi & Lionello, 2008). Moreover, during our 20-year study period, the first 10 years was rainier and colder, while the last few years was dryer and hotter, with impacts on the hydrological functioning of the lagoon. Due to its urban setting, the lagoon is exposed to increasing anthropic pressure, as urbanization has increased over five fold during the last century (Pasqualini et al., 2020; Erostate et al., 2022). Historically, the lagoon experienced a wide range of environmental conditions and trophic states (Bec et al., 2011; Cecchi et al., 2016; Garrido et al., 2016; Pasqualini et al., 2017). The main fluctuations documented on the lagoon are linked to modifications of its hydrological regime, which were shaped in relation to human activities and the development of its watershed over time. A steep decrease in salinity was observed from 2000, mostly due to the gradual closing of the natural *grau* and to the Golo outlet's closed status for a longer time. This led to the accumulation of nutrients (from runoff and reduced exchanges with seawater). Parallel to the desalinization, observed until 2010, an increase in nitrates concentration was reported, linked to agricultural activities, and still ongoing, despite management measures taken in the past few years for nitrogen reduction through improved sanitation (Pasqualini et al., 2017; Leruste et al., 2019). This inertial pollution was found to be also due to the accumulation of nitrate in the groundwater (Erostate et al., 2018, 2019; Jaunat et al., 2019).

Until the 1970s, the lagoon showed a good status, characterized by macrophytes dominance; then, it went through multiple statuses and sometimes experienced shifts to phytoplankton and opportunistic macroalgae dominance (Pasqualini et al., 2017; Erostate et al., 2022). The most remarkable event in the ecological history of the lagoon was the dystrophic crisis in 2007. On this occasion, the observed peak in chlorophyll a concentration was due to the proliferation of the potentially toxic cyanobacteria *Anabaenopsis circularis* (Pasqualini et al., 2017), probably favored by salinity decrease (as already mentioned in Cabras Lagoon by Pulina et al., 2011) and loss of connection to the sea, together with an increase in temperature during summer. Management efforts, like the clearing of the Fossone canal and the management of water sewage discharges, were made to ameliorate water circulation in the lagoon and decrease eutrophication. Results seemed to actually improve the situation, as water quality was enhanced and submerged macrophytes started to regain coverage (Pasqualini et al., 2017). However, the operation

resulted in a massive input of freshwater in the system, which was later linked to the appearance and proliferation of the invasive potentially toxic dinoflagellate *P. cordatum* in 2010 (Cecchi et al., 2016; Garrido et al., 2016). Moreover, especially in 2020 and 2021, we assisted in a novel drastic decline in submerged angiosperm coverage, together with the modification of species distribution patterns, like the expansion of freshwater species *S. pectinata* to the northern part of the lagoon (linked to decreased salinity) and the proliferation of opportunistic green macroalgae, like *U. clathrata* and *C. aerea*.

The present and last few years' situations, in fact, present several alarming signs. Notably, the frequent and high proliferation of phytoplankton might be an early sign of a trajectory toward a regime shift, according to Schramm's scheme (Schramm, 1999). We observed a shift toward dinoflagellates to the detriment of diatoms. This phenomenon was already observed in multiple environments after disturbance, as an indication of degradation (Xiao et al., 2018; Fischer et al., 2020). The success of dinoflagellates, and potentially toxic species like *Gonyaulax* spp., *A. sanguinea*, *P. cordatum*, and *Dinophysis* sp., could be linked to decreasing salinity of the basin, increasing nutrient input, especially nitrogen, and increasing temperature (Heil et al., 2005; Dhib et al., 2013; Xiao et al., 2018; Skarlato et al., 2018a; Fischer et al., 2020; Bouquet et al., 2022). These organisms, thanks to their mixotrophic capacity and motility, can take advantage of freshwater inputs and consequent short-term stratification induced so that blooms are easily fueled in these conditions and are expected to increase with forthcoming climate change (Aligizaki et al., 2009; Skarlato et al., 2018b; Fischer et al., 2020). Potentially, the shift toward a dinoflagellate-dominated phytoplankton community and homogenization of the composition, as monospecific dinoflagellate blooms were frequently observed during the study and particularly in 2020, may lead to cascade consequences on higher levels. For instance, these shifts have already been related to a decrease in zooplankton biomass and consequently in commercial fish, a phenomenon that was indeed highlighted during this study (Fischer et al., 2020). Despite the need for further investigations on fish catch decline observed in the Biguglia lagoon during the study, one of its causes might be associated with changes in the phytoplankton community: these can depend on factors linked to the alteration of salinity natural gradients and cause a decrease in fish catch, together with many other factors, such as decreased marine recruitment after the loss of sea connectivity but also the colonization of new species (Pérez-Ruzafa et al., 2018).

One of the main issues of the global disruption of the ecosystems is that it enhances vulnerability to biological invasion, as invasive species show a wide range of growth conditions, making it difficult to link their establishment to one single factor, but can take advantage of disturbed conditions (Boudouresque & Verlaque, 2012; Dalu

et al., 2022; Delpy et al., 2012). This was the case for Berre lagoon's invasion by the ctenophore *M. leidy*, where it was not possible to simply trace back this event to hydrological modification or salinity variations (Delpy et al., 2012). This widely recognized invader is rapidly expanding in multiple different lagoon environments, like French Palavasian complex lagoons and Spanish Mar Menor lagoon (Marambio et al., 2013; Marchessaux & Belloni, 2021), and is also well established in the Biguglia lagoon. However, *M. leidy* is not the only non-native species in the Biguglia lagoon, as its degraded status in the past probably favored the successful establishment of multiple invasive species in the lagoon. The recent first-time capture of egg-bearing females of the non-native crab *C. sapidus* in 2021, since its first official record in 2014, is particularly concerning, as it is an indication of its establishment in the Biguglia lagoon, and this species is well known for being rapidly expanding in the Mediterranean and already becoming invasive in lagoon environments (Cilenti et al., 2015; Fuentes, 2019; Culurgioni, 2020; Kampouris et al., 2020; Taybi & Mabrouki, 2020; Kara & Chaoui, 2021; Mancinelli et al., 2021).

Once established, these invasive species can cause ecological damage. Moreover, the simultaneous degradation of the ecosystem and presence of invasive species can contribute to the self-sustain of the “new system” and also have cascade effects on human activities and economic drawbacks. For instance, the success of the dinoflagellate *P. cordatum*, which is also an invasive species itself, might be at the basis of the establishment and feedback sustaining mechanism of *M. leidy* in the Biguglia lagoon, since it is a fundamental component of larval and post-larval stage diet of this species (Sullivan, 2004).

M. leidy could have played a role in fish stock reduction observed over the study, as it is known to negatively affect fishing activity directly and indirectly in other Mediterranean lagoons (Sullivan, 2004; Marambio et al., 2013; Diciotti et al., 2016). *C. sapidus* constitutes a direct threat to fishing activity, as fish gear damage and attacks on trapped fish have already been attributed to this species (Culurgioni, 2020; Taybi & Mabrouki, 2020). Moreover, a decrease in native crabs revealed during the study may also be linked to the *C. sapidus* invasion, as it was already observed in Italian and Spanish lagoons (Cilenti et al., 2015; Fuentes, 2019). Another concerning point is the presence of the invasive Eurasian carp *C. carpio*. This species is a really disruptive invader, as it can bring about physical, chemical, and biological alterations through its feeding behavior, by increasing turbidity and resuspending sediments. It is well known for boosting phytoplankton blooms and deteriorating seagrass meadows (Fischer et al., 2013; Qiu et al., 2019; Dalu et al., 2022). *F. enigmaticus* and *A. melas* seem to be less concerning in the Biguglia lagoon case, as they were long-established and seem to have reached an equilibrium in the system.

In general, biological invasion tends to lead to native species loss and homogenization. The Biguglia lagoon seems to show early signals of this situation; thus, it is important to control and maintain a good status of its native assemblages and protect biological diversity and redundancy (“response diversity”) (Elmqvist et al., 2003; Biggs et al., 2015). Cascade effects of homogenization can bring about socioeconomic drawbacks, by negatively impacting fishing activities for instance, or even influencing bird behavior and migrations (Bruschetti et al., 2009; Pejchar & Mooney, 2009; Maceda-Veiga et al., 2017). Hence, since the Biguglia lagoon system seems already altered on the ecological level, potential socioeconomic downsides, mainly on fisheries and tourism (avifauna), are not to be neglected for future sustainable development, stressing once again that global ecosystem approach results are essential for this purpose.

4.2 Resilience and future management

The scientific contribution of this work and previous studies led, hence, to the necessity of defining efficient management directions and establishing a “desired state” to which converge. The long-term scheme proposed in this work is intended to provide a holistic image of the Biguglia lagoon socio-ecosystem: we here discuss how based on indicators of “good” ecological status coupled with other parameters both human and environmentally linked, enhancing the resilience of “good functioning” status of the lagoon is the best way to preserve it and guarantee the convergence to this “desired state” previously mentioned. The aim is to avoid falling into non-desired states, which can in turn be very resilient too. The fact that we do not clearly quantify resilience or breakpoint threshold does not prevent coming to these conclusions: first of all, clear information on the reaching of tipping points is rarely provided (Pérez-Ruzafa et al., 2018); secondly, one of the key points of resilience (in the sense of the guiding toward a “desired state” or, even better, a spectrum of “desired states”) is to avoid crossing dangerous thresholds, even still unknown or unpredicted ones, by promoting the functioning of the attributes that confer this resilience to the system, in general (Walker, 2020). In a “future management” set of mind, we here try to explore these attributes, such as response diversity, exposure to disturbance, and ability to quickly react to disturbance, thinking, planning, and managing across scales, through the description of different biotic, abiotic, and anthropic elements’ patterns and trends over ~20 years.

This study highlighted that many disruption signs are simultaneously emerging in the Biguglia lagoon, potentially affecting its resilience capacity. If nothing is done, in the near future, the risk is to let the system fall into a degraded stable state in case of any forthcoming new disturbance (Figure 6). Since now, the system proved itself resilient, meaning despite acting pressures, it was able to absorb disturbances without

shifting definitively toward a new state (Walker et al., 2006; Folke, 2016; Pasqualini et al., 2017). However, the trajectories of degradation we highlighted should be considered alarming. The more the system is degraded, the more it would be easy to reach the breakpoint. If the Biguglia lagoon resilience properties are not protected, it will be gradually eroded, meaning that even a small disturbance might be sufficient to easily trigger a regime shift (Figure 6).

Hence, what can be done to strengthen the system resistance and resilience and prevent further degradation? First, it is important to consider that multiple objectives are desired for the Biguglia lagoon: the alleviation of its eutrophication, the improvement of fishing activity, and the maintenance of other important ecological services (e.g., ornithological interest and tourism) (Figure 6).

This study allowed the identification of some specific needs, applicable to the Biguglia lagoon but also generally applicable to other Mediterranean lagoons in similar cases. Firstly, it is of fundamental importance to understand and monitor lagoon connections and exchanges with adjacent water systems (sea, rivers, watershed, etc.). Globally, correlations highlighted on available samples between lagoon nutrients, and inputs from watersheds, salinity, and rainfall suggest nutrient inputs are mainly driven by water discharge from major freshwater sources and linked to meteorological events. However, we were not able to identify a clear pattern between NO_3^- load from major tributaries and nutrient concentration in the lagoon. This is probably due to different sampling periods available and complex dynamics and multiple factors determining nutrient concentration in the water column. Furthermore, no data on connectivity to groundwater was considered, despite that its importance in the dynamics of the nitrates in the lagoon has already been demonstrated (Erostate et al., 2019). Based on our investigation, we might conclude that the Biguglia lagoon ecological functioning depends on its connection to the sea. The status of the *grau* and especially the Golo river outlet strictly depend on rainfall, as water flows prevent outlets' closing through sediment accumulation. Low flow levels are not sufficient to open the Golo outlet but rather divert freshwater to the South part of the lagoon through the Fossone canal, enhancing desalinization and increasing nutrients and suspended matter inputs. Intensification of this phenomenon is expected with climate change, as decreased rainfall and flash flood events are predicted to increase (Giorgi & Lionello, 2008). In the last few years, the natural *grau* tended to close due to lower or less efficient management owing to stronger sand accumulation and/or insufficient digging depth of the channel. Despite management efforts, energies invested in the artificial openings of the *grau* in terms of days of intervention are often not reflected by significant evolution of the desired effect. The connectivity of the lagoon to the sea is of primary importance (Biggs et al., 2015), although, as suggested by other studies, parallel to hydrologic management,

it is also necessary to proceed with the control and reduction of inputs from the watershed and its monitoring for long-term remediation (Schallenberg et al., 2010a; Jones et al., 2018) (Figure 6). For the Biguglia lagoon, improving exchanges with the sea would mean to reduce confinement, mitigate ongoing desalinization and eutrophication through mixing with seawater, potentially decrease phytoplankton blooms and proliferation of opportunistic and invasive species, hopefully restore angiosperms, and enhance better fish recruitment to boost fisheries activity. Mitigation of desalinization would also allow to reduce intervention in mosquito control, which is currently often carried out since some species developing on the lagoon are vectors for illnesses and constitute a threat to human health. The most common mosquito species, *Culex pipiens* (Linnaeus, 1758) and *Anopheles maculipennis* (Meigen, 1818), are favored by desalinization of the basin; hence, the hydrologic management and salinization can result in a useful tool to prevent or control their development in the basin (Schaffner et al., 2001).

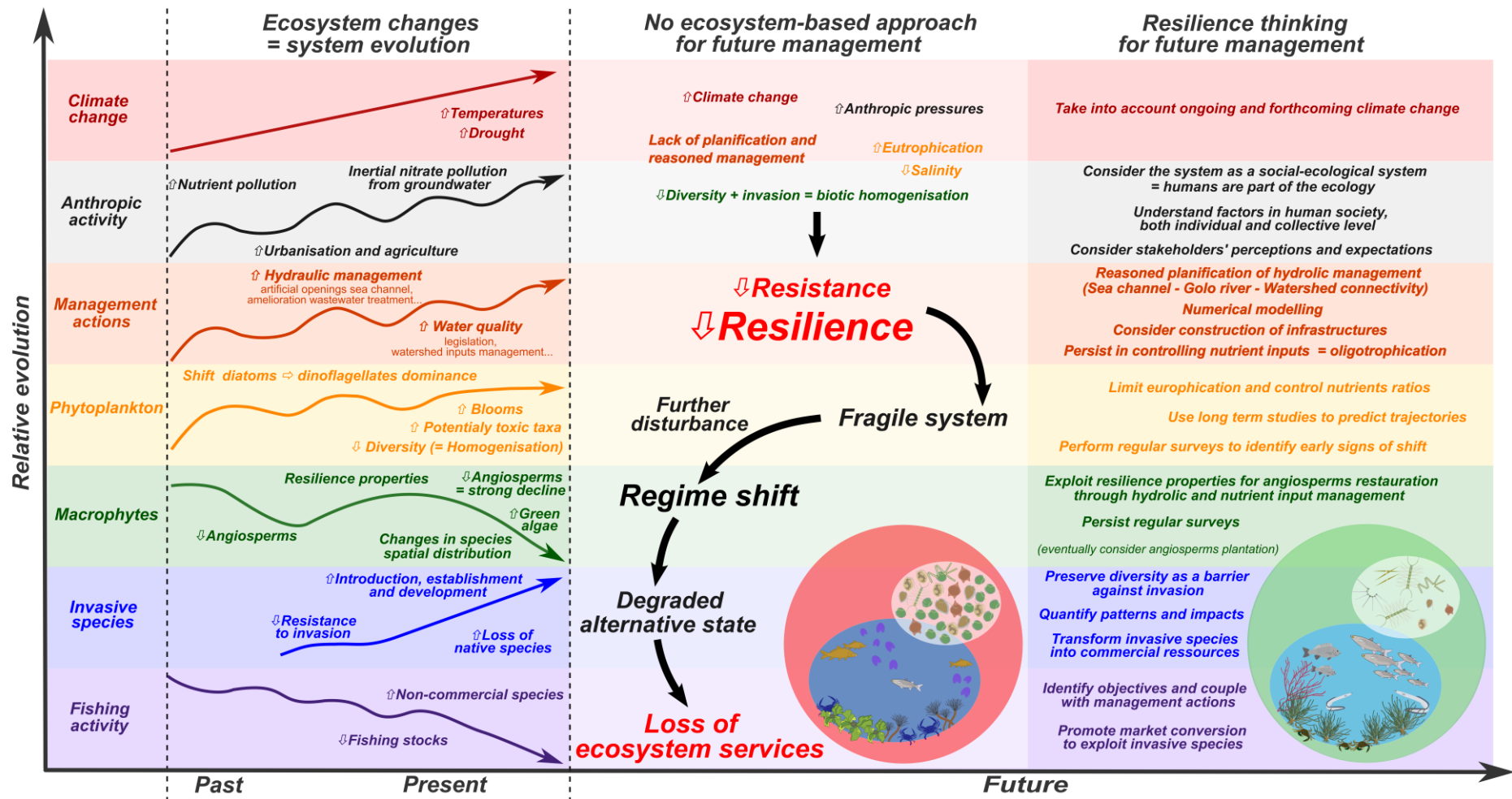


Figure 6 Scheme of functioning dynamics of the Biguglia lagoon: past and present evolutions of main compartment considered in the study, future alternative scenarios, and suggestions in the case of non-application or application of “resilience thinking” concept for future management. Created with pictograms from the Integration and Application Network, University of Maryland Center for Environmental Science (ian.umces.edu/media-library).

Our results suggest that management of the *grau* is required and can be supported by other studies, which demonstrated that artificial openings to the sea may prevent or even revert shifts to phytoplankton-dominated regimes in a lagoon environment (Lloret et al., 2008; Jones et al., 2018). This means that for future management, the openings of the Golo outlet might be also considered or at least regulation of the Golo flow to the lagoon through the Fossone canal should be considered (Figure 6), in parallel with the sea outlet control. Numerical modeling could be in this case a useful tool to build different scenarios and discuss potential management options (Pete et al., 2020). Management of connections should anyway be carefully considered according to local specificities (Tagliapietra et al., 2009; Pérez-Ruzafa et al., 2019b). A further complexity resides in the potential shift into a state of brackish waters at higher salinity: this could potentially impact aquatic plants with freshwater affinity, like rush and *Kosteletzkya pentacarpos* (L. Ledeb., 1842), thus possibly affecting birds' communities, for which Biguglia is also an important migratory site. For instance, one of the most emblematic wintering species on this site, the migratory Anatidae *Aythya ferina* (Linnaeus, 1758), showed a decline in France over the last 20 years according to the Wetlands International waterbirds' survey counting. However, the Biguglia lagoon is at the top of French wintering sites, for this species and populations' fluctuations seemed to follow salinity patterns in the lagoon. Nevertheless, it is difficult to link salinity variation to avifauna trajectories, since multiple factors are involved at both local and larger geographical scales, especially for migratory birds. We suggest that further efforts should be made to understand the complexity of these dynamics and maybe be artificial interventions or even the construction of infrastructures might be considered to control and manage exchanges at the Fossone canal level (Figure 6). Nevertheless, sometimes management actions result in unexpected drawbacks, as we highlighted in the Biguglia lagoon. One of the main reasons could be the scattering of decisional power over the lagoon and its surroundings: multiple institutions are charged with decisions and actions that directly impact the lagoon ecosystem, without the implication of management figures of the Natural Reserve. These institutional problems result in a dispersed and diluted management, where the expertise and global view of Natural Reserve actors are set aside. The fragmentation of management does not allow a coherent approach (De Wit et al., 2021); hence, to ameliorate and make effectively efficient management actions, we believe that stronger concertation between different actors should be foreseen, in order to centralize decisional power and coordinate actions in accordance with the global expected or desired vision of the system that can be provided by manager institution.

A useful tool to improve management is to combine scientific and technical expertise with stakeholders' perception (Figure 6): this would help with political

decisions for the allocation of financial resources and the identification of priorities and “desired state”, as well as help in the development of a roadmap to make the system converge to this state in a process of ecological restoration (De Wit et al., 2020). Ecological restoration raises multiple economic questions on costs and times required, as well as ecological questions on possible consequences of actions or passivity in the face of disturbance or degradation. For these reasons, multi-factorial modeling can be a helpful tool to design potential scenarios and reactions of ecosystems (Pete et al., 2020). These models can then be used to guide exchanges, transfer knowledge from different domains of expertise, and hence help concertation between actors involved in order to ameliorate and converge to adapted and reasoned management plans and decisions (Figure 6). In some cases, the restoration of angiosperms meadows through plantation was proposed to restore degraded environments (Schallenberg et al., 2010a; Rodrigo et al., 2013). However, this operation is expensive, complex, and not necessarily efficient (Rodrigo et al., 2013). We consider that for the Biguglia lagoon, reasoned management of hydrological functioning and inputs from the watershed should be sufficient to restore seagrass meadows at present status (Duarte et al., 2015; Le Fur et al., 2019) (Figure 6).

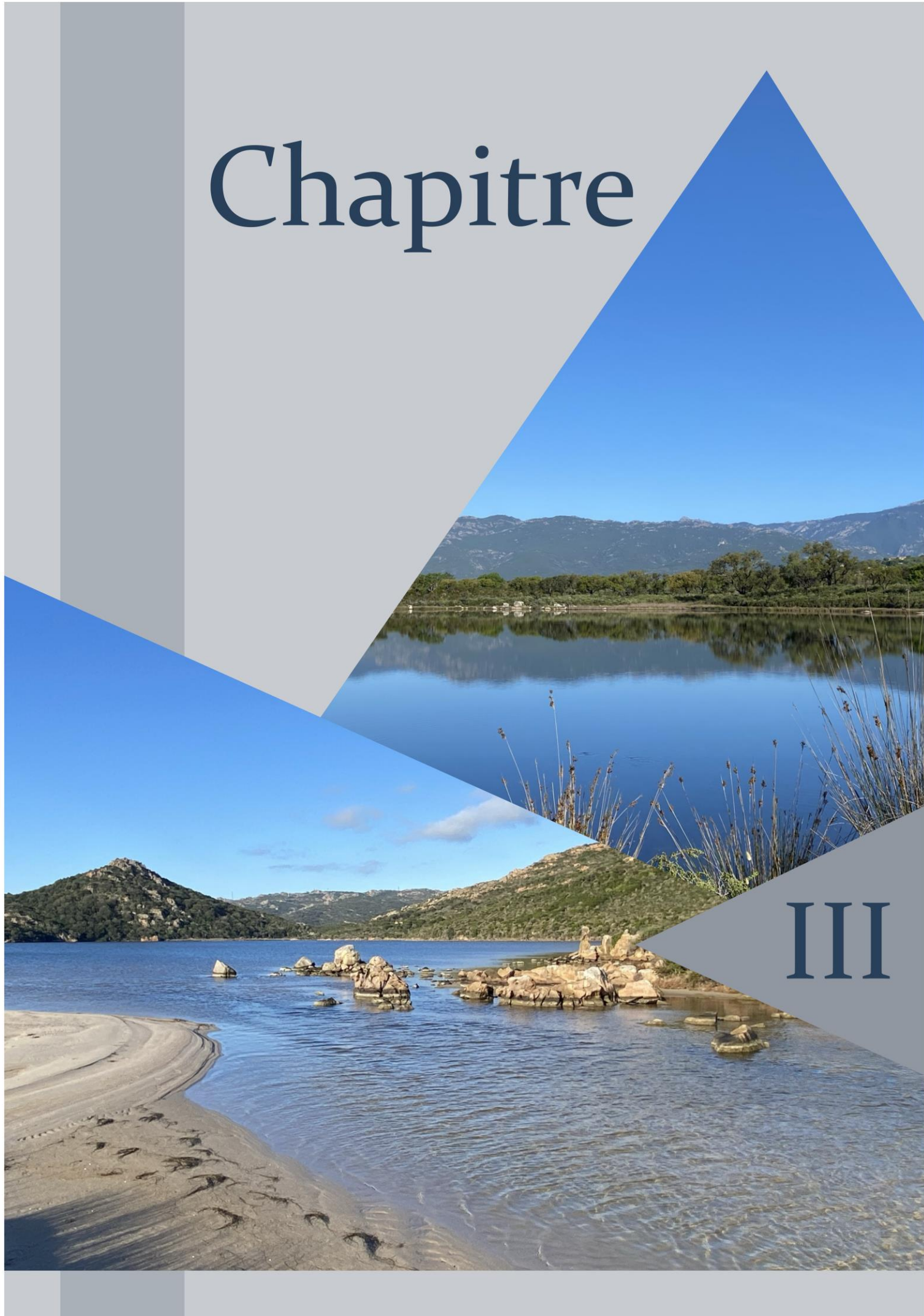
An additional problem that should be addressed is a biological invasion. It is particularly important to better investigate invasive species: quantifying their patterns of introduction, distributions, expansion, individual and population sizes, and life cycle stages is essential to monitor - and partially mitigate - the invasion or prevent new invasion events, especially with regard to climate change (Aligizaki et al., 2009; Skarlato et al., 2018b; Radinger & García-Berthou, 2020) (Figure 6). Also, further knowledge of effective impacts of invasive species on local activities, like fisheries, is capital to decision-making and management (Mancinelli et al., 2017) (Figure 6).

Lastly, we suggest the application of adaptability in the resilience thinking concept (Figure 6). For example, introduced species are now successfully established in the Biguglia lagoon, meaning that they are now part of the “new system”. It has become more and more difficult to remove non- native species from ecosystems, but they can have potential in the “resilience thinking” optic, as they can constitute important elements in novel systems and therefore be essential in providing ecosystem services in the future (Hobbs et al., 2009). This should be carefully handled as often the non-native species can become invasive and contribute to loss in diversity and then potentially affect the resilience capacity of the system (Boudouresque & Verlaque, 2012). However, this could be taken into account as a temporary control measure of invasion, providing economic advantage. Some successful examples of this idea exist: for instance, the invasive species *C. sapidus* was transformed from a threat into a resource in some cases, like the Gargano lagoon (Italy) where a new market was created and the consequent

transformation of fishing activity (Cilenti et al., 2015; Mancinelli et al., 2017). Nevertheless, the commercialization of invasive species as a form of management and control is still strongly debated, due to associated underhand drawbacks at both ecological and economic levels. The dependence of fisheries on invasive species as new food resources can lead to economic problems like overfishing and consequential loss of commercial value (Mancinelli et al., 2017). Hence, the commercialization of invasive species brings about socioeconomic challenges and should be carefully handled, considering all negative potential effects previously mentioned: it should better not be considered as long-term sustainable exploitation but rather be viewed as a temporary solution to decrease and control expansion, foreseeing an exit option afterward (Pasko & Goldberg, 2014).

In conclusion, this study represented a unique opportunity to stress the importance of EBA for shallow Mediterranean coastal lagoons conservation and management. In fact, the Biguglia lagoon is a relevant example of Mediterranean coastal lagoons, as it is a complex system, set in a changing context: it is subjected to increasing anthropic pressure and climate change and exhibits multiple signs of degradation. Our study revealed a degradation pattern and increased sensitivity to disturbance, and we demonstrated how management interventions may not always be beneficial for the entire ecosystem. This work is a good example of why a multiple compartment approach is fundamental in lagoon environments. The evolution scheme proposed, putting together all remarkable events and successions observed over 20 years, constitutes a holistic representation of the social–ecological system’s functioning. If the study can be perceived as very descriptive to a broad audience, it meets the perception and expertise of daily contact with the system of scientific researchers, managers, fishermen, and stakeholders in general, who are very aware of the need to cooperate to converge on a spectrum of “desired states” to promote. A global ecosystem approach is essential for the understanding of the functioning and resistance/resilience properties of the system, the planning, and the decision-making for a sustainable evolution in the lagoon environment. This is the basis for good integrative management of these systems in order to preserve them and maintain or eventually restore the ecosystem services they provide in a changing world, especially in the face of increasing anthropogenic disturbance and climate change. Our study is a good starting point in this direction and lays the first stone for a new way of foreseeing the future and constitutes a good foothold for actors involved in management. We suggest future investigations should integrate other ecological compartments, such as sediments’ analysis, benthic macro-, and meiofauna, entomofauna, and avifauna, in order to provide an even deeper insight into the system’s complex network and functioning.

Chapitre



III

CHAPITRE III

SMALL MEDITERRANEAN COASTAL LAGOONS UNDER THREAT: HYDRO-ECOLOGICAL DISTURBANCES AND LOCAL ANTHROPOGENIC PRESSURES (SIZE MATTERS)

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CONTEXTE GÉNÉRAL ET RÉSUMÉ

Les lagunes côtières méditerranéennes sont affectées par plusieurs menaces (pression démographique, eutrophisation, changement climatique) qui sont attendues augmenter dans le futur et impacter les services écosystémiques fournis. Les normes de conservation et les études scientifiques se focalisent principalement sur des lagunes de grandes tailles ($> 0.5 \text{ km}^2$) en raison de leurs usages et importance économique, alors qu'elles excluent celles de petites surfaces. Ces dernières sont peu connues et peu protégées, malgré leur fréquence et importance dans le monde et dans la région méditerranéenne en particulier. La caractérisation, qualitative et quantitative, de ces lagunes de petites surfaces, en termes de fonctionnement et sensibilité aux changements globaux et locaux, est nécessaire pour développer des stratégies de gestion adaptées à ces milieux. Pour cette raison, l'objectif principal de l'étude est d'attirer l'attention sur ces milieux si peu connus. Premièrement, ce travail fournit le premier inventaire de toutes les lagunes à l'échelle régionale de la Corse. Ensuite, une étude spécifique est portée sur trois d'entre-elles (Arasu, Santa Giulia et Balistra), qui présentent une petite surface, comparable en termes de dimensions ($\sim 0.25 \text{ km}^2$), et qui sont caractérisées par trois différents niveaux d'anthropisation (fortement artificialisée/perturbée, moyennement perturbée et *quasi-pristine*, respectivement). Les principales questions sont : i) est-ce que ces trois lagunes, comparables en taille, mais différentes en termes de cadre d'anthropisation, présentent des différences dans leur fonctionnement physique et écologique ? et ii) quelles sont les implications de ces éventuelles différences dans la vulnérabilité de ces systèmes face au changement climatique et d'autres pressions environnementales.

Les résultats montrent qu'au niveau régional, 91 des 95 lagunes identifiées sont $< 0.5 \text{ km}^2$, ce qui rend la Corse un excellent exemple pour l'étude des lagunes méditerranéennes de petite taille. Les trois études de cas analysées ont montré des différences dans leurs cycles biogéochimiques saisonniers et dans la composition et saisonnalité de leurs communautés phytoplanctoniques (biomasse, diversité, efficacité photosynthétique). L'approche intégrée sur les socio-écosystèmes a montré que les lagunes d'Arasu et Santa Giulia ont subi une augmentation de l'urbanisation de leurs bassins versants (+ 12 % et + 6 % respectivement) dans la dernière trentaine d'années, ainsi que des communautés phytoplanctoniques caractérisées par de biomasses élevées, une faible diversité et la présence de dinoflagellés potentiellement toxiques. Au contraire, l'étang de Balistra a montré un bon état général, avec des communautés phytoplanctoniques riches et diversifiées, mais également des sources de potentielle pollution anthropique majeure sur son bassin versant.

Cette étude démontre l'importance des lagunes de petites surfaces au niveau régional et méditerranéen et fournit des connaissances locales sur les sites étudiés, qui peuvent toutefois trouver une application sur des sites similaires potentiellement présents ailleurs dans le monde. Le résultat principal de l'étude est la mise en évidence d'une forte réactivité de ces milieux, en particulier au niveau de connexion au milieu marin et aux pressions agissantes sur les bassins versants, en raison de leurs petites tailles. Cette réactivité rend ces lagunes de petites surfaces particulièrement vulnérables aux pressions croissantes et susceptibles de disparaître sous un contexte de changement climatique et anthropisation en progression. Parallèlement, la réactivité de ces milieux les rend aussi

des excellents systèmes sentinelles : en raison de leurs réponses rapides aux bouleversements elles peuvent fournir des indications précoces sur les potentielles réponses futures des milieux lagunaires aux futurs changements globaux et locaux. Enfin, l'importance d'une approche intégrée et interdisciplinaire sur les socio-écosystèmes dans leur complexité et interconnexion avec ses systèmes adjacents (bassin versant et mer) est soulignée.



MOTS CLÉS

Lagunes côtières méditerranéennes de petite surface · Menaces · Gestion · Fonctionnement écologique · Hydrogéologie · Phytoplancton

1. INTRODUCTION

Coastal lagoons are water bodies, generally parallel to the coastline, separated from the sea by a barrier but connected at least intermittently to the marine environment through one or more restricted inlets (Kjerfve, 1994). They are very productive ecosystems and biodiversity hotspots, and provide numerous ecosystem services (Loureiro et al., 2006; Niedda & Greppi, 2007; Barbier et al., 2011). Coastal lagoons are subjected to increasing anthropogenic pressures, i.e. urbanisation of the coastal zone that induces increase in water use and habitat loss (MWO, 2018), nutrient inputs from the watershed that lead to eutrophication (Cloern, 2001; Loureiro et al., 2006), and the effects of climate change, notably in the Mediterranean region (MedECC, 2020; Cos et al., 2022). The development of effective management strategies for coastal lagoons is necessary, as they are increasingly subjected to threats which may result in their degradation (Pérez-Ruzafa et al., 2011a; Ferrarin et al., 2014) and are experiencing continuous loss worldwide (Birch et al., 2022 and references therein).

Phytoplankton is considered a relevant indicator of ecological status and ecosystem functioning and it is often a central element in management strategies and norms (E.C., 2000; Birk et al., 2012). In coastal waters phytoplankton responds rapidly to any environmental changes, and alterations in its structure or dynamics have cascade effects on higher trophic levels (Cloern, 1999; Loureiro et al., 2006; Armi et al., 2010; Goberville et al., 2010). Recently, shifts from diatoms to potentially harmful dinoflagellates have been observed in multiple environments and linked to variations in salinity, temperature and nutrient loads (Aligizaki et al., 2009; Collos et al., 2009; Xiao et al., 2018; Trombetta et al., 2019; Fischer et al., 2020). Moreover, changes in timing and increased frequency and magnitude of proliferations of harmful species, known as Harmful Algal Blooms (HABs), have been observed worldwide in recent decades, and especially in the Mediterranean region (Hallegraeff, 2010; Kudela et al., 2015; Trombetta et al., 2019; Ligorini et al., 2022a).

To fully understand the functioning of coastal lagoons, it is necessary to take into account their hydro-climatic context and their connectivity to surrounding water bodies, i.e. exchanges with the sea (Lloret et al., 2008; Biggs et al., 2015; Jones et al., 2018; De Wit et al., 2020), and continental inputs from surface waters and groundwater (Erostate et al., 2018, 2019, 2020; Jaunat et al., 2019). These elements are important to understand past and current pressures, such as watershed urbanisation, through the assessment of nutrient inputs (Erostate et al., 2018), and to be able to plan management strategies and corrective measures. Elevated nitrate (NO_3^-) concentrations in waters are unequivocal markers of anthropogenic pressures, mostly deriving from synthetic

fertilizers and from septic tanks (Re et al., 2017; Vystavna et al., 2017; Erostate et al., 2018). Local hydrological connectivity is deeply influenced by both climatic constraints and human activities through the withdrawal of the initial water resource for any purposes, and the restitution of more-or-less treated water to the hydrographic network. Human interventions (e.g. opening or closure of outlets), local conditions (e.g. winds, currents) and global pressures (sea level rise) may also control the intensity of exchanges with the marine environment.

The main sources of knowledge on European coastal lagoons are the regular scientific surveys carried out in the context of the Water Framework Directive (WFD, European Union (EU), 2000; Loureiro et al., 2006; Renzi et al., 2019). The WFD does not provide a legal definition of coastal lagoons, and national interpretations of the directive often add a surface-size limit set at 0.5 km² for its application to transitional waters (e.g. ISPRA, 2014 for Italy; SDAGE, 2021 for France - Bassin de Corse). Since smaller coastal lagoons are not included in the regulation, they remain neglected, poorly understood and ultimately poorly or even not at all managed. Among Mediterranean coastal countries, at least four (Greece, Italy, Spain, Turkey) have lagoons smaller than 0.5 km² (Cataudella et al., 2015), but quite apart from the WFD and its size-limit, scientific studies usually focus on large lagoons, since they historically sustain economic activities. There have been a few studies on these small systems, but they are mostly very local case studies (Tuncel et al., 2007; Camacho et al., 2012; Mitchell et al., 2017; Doughty et al., 2019). However, small lagoons are extremely valuable and common in various parts of the world, like in the western coasts of Africa and North America, in South eastern American and Australian coasts, and especially in the Mediterranean region (Suzuki et al., 1998; Dye & Barros, 2005; Tuncel et al., 2007; Moreno et al., 2010; Camacho et al., 2012; Mitchell et al., 2017; Doughty et al., 2019). They may also be particularly vulnerable to increasing pressures such as human activities and climate change, in relation with their small size, and hence have less resilience in the face of disturbance (Doughty et al., 2019). The ratio of perimeter to area increases as the size decreases, increasing edge effects and strengthening the coupling between the lagoon and its watershed's land use and hydrology. A better understanding of the structure and function of these highly reactive systems can inform more effective management to mitigate the negative consequences of climate and land use change. Currently, there is no extensive evidence of differences between small and large lagoons, due to lack of knowledge and hence difficulties in comparison. However, it has already been demonstrated that, for continental waters, small lakes host higher biodiversity compared to larger lakes and play an important (and neglected) role in large-scale processes; they are also more active and dynamic than large ones, potentially increasing the threat posed to them by climate change (Downing, 2010). Given all these premises, it is clear that small lagoons deserve

to be considered a priority interest with regard to their conservation. In Europe, apart from the WFD, another norm defines conservation objectives for coastal lagoons, with a different approach: the Habitat Directive (HD, [European Union \(EU\), 1992](#)). This directive does not include a size limit, so the question of small lagoons arises: most of them are not only without any protection status, but they are not even acknowledged, so inventories, quantification and qualification of these systems is needed ([Latron et al., 2022](#)).

An excellent example with regard to this major challenging goal of the conservation of coastal lagoons, especially in the Mediterranean region, is Corsica Island (France), located in the north-western Mediterranean Sea. The island has more than 200 coastal wetlands, mostly brackish coastal lagoons, highly diverse, and is a good example for the study of small-sized coastal lagoon environments ([Ghilardi, 2021](#); [Di Rita et al., 2022](#)). Only the four largest lagoons are well known, since they fit with the WFD criteria and have been the subject of numerous scientific studies and monitoring surveys. In the legislative and social-ecological context previously described, managers are drawing attention to the need to focus on underrated small lagoons. Specifically, research is needed to: (1) improve qualitative and quantitative characterizations of small lagoons, including their hydrology and ecology, (2) predict how climate change will affect small lagoons, and (3) inform management and restoration decisions. In this study, we have sought to answer some of these questions, firstly, by a description of small coastal lagoons at regional level, since their importance is still underestimated, and secondly, by the investigation of three case studies in Corsica Island. The three small lagoons chosen, Arasu, Santa Giulia and Balistra, are of comparable size (e.g. 0.25 km²) but present three different anthropogenic contexts and histories and contrasting current human pressures. We have considered their connection to adjacent systems, in order to better characterise the ecosystems in their hydrogeological and anthropogenic contexts. To do so, anthropogenic tracers from the watersheds of the three case studies were detected to describe sources of human pressure. Then, seasonal samplings over two consecutive years were performed in the lagoons to analyse environmental characteristics and phytoplankton variations, to assess seasonal patterns and to detect relationships between abiotic and biotic factors.

The main aim of the study was to raise awareness of these little known small-surface systems. To do that, firstly, we contextualized the importance of small-sized lagoons at regional and Mediterranean scales. Secondly, for the three case studies two main questions are addressed: i) how do these three small lagoons, of comparable size but with different levels of anthropogenic impact in their watersheds, differ in terms of their physical and ecological functioning? (ii) what implications do these differences have for the lagoons' vulnerability towards climate change and other environmental stressors?

Ultimately, our aim is to provide new knowledge to stimulate the development of management strategies dedicated to small-sized coastal lagoons at regional and global scale.

2. MATERIALS AND METHODS

2.1 Lagoons at Mediterranean and regional scale

A qualitative description of the large-scale distribution of lagoons in the Mediterranean basin was performed on the basis of available data (Cataudella et al., 2015) and used for comparison with coastal lagoons around the Corsican coast. We compiled data from the Environmental Agency of Corsica (OEC; unpublished data) and the Pôle Relais Lagunes Méditerranéennes – Tour du Valat (PRLM/TDV; unpublished data) on the number, surface areas, perimeter, ownership and management of all Corsican lagoons. The water masses considered in this study are classed as "Mediterranean coastal lagoons", according to the definition of the habitat 1150*-2, provided by the European Directive 92/43/CEE (Habitats Directive) applied in France (Barre et al., 2020). Mapping of coastal lagoons (PRLM/TDV; unpublished data) were obtained through the analysis of satellite images from Sentinel-2A and Sentinel-2B (20 m resolution) systems (<https://glovis.usgs.gov/>), over a selected hydrological period (2018-2020) using the ArcGIS 10.3 software.

2.2 Three case studies

2.2.1 Study sites

The three lagoons in the study are located in the south-eastern part of the island (Figure 1a). The contours of the three watersheds were drawn using a digital elevation model (resolution of 5 m) and georeferenced on QGIS software (version 3.22.5 'Białowieża'). Geological maps (1:50000) were retrieved from the Bureau de recherches géologiques et minières (BRGM) website (InfoTerre - BRGM), and simplified by grouping similar geological formations, resulting in three main geological descriptors: sand bar, granitic basement and sedimentary deposits (Figure 1b and Figure 1c).

Arasu lagoon (41°38'34" N, 09°21'55" E, Figure 1b and Figure 1c) covers a 0.26 km² surface area and receives freshwater inputs from a 5 km² watershed (OEC data), which is predominantly constituted of densely fractured and intensively weathered granite (72%). In the southern-lower part of the Arasu lagoon watershed, the geology is characterised by clay-sand deposits, favourable to the presence of a restricted alluvial aquifer, formed by Quaternary sediment deposits and hydraulically connected to the

lagoon in this area. The main freshwater sources are three streams in the western part of the basin, while exchanges with the sea take place in the eastern part only, through a small channel, with a bifurcation (Figure 1c). The lagoon has been considerably altered in the past, as during the 1960s a project for the creation of a marina was initiated. Once abandoned, the project still left certain major alterations, such as the presence of roads on dams crossing the lagoon and dividing its surface into three separate basins (Figure 1c), communicating through small culverts underneath the causeways. Since sediment from the lagoon was dug out, the basins are of different depths, with the middle basin being the deepest (max. depth = 4 m) and a mean depth over the entire basin of 1.5 m. At present, the lagoon is owned by several owners, private and public, including the Conservatoire du Littoral (CdL). It has been designated under the Special Areas of Conservation (SAC) protection status as a Natura 2000 (N2000) site (Habitats Directive) and it is under the management of the Collectivité de Corse (CdC). Major threats for this basin are the growing urbanisation of the north-eastern side and tourism during the summer period (e.g. beach restaurant).

The shallow Santa Giulia lagoon ($41^{\circ}31'32''$ N, $09^{\circ}16'12''$ E; max. depth = 1.5 m, mean depth = 0.3 m; Figure 1b and Figure 1c) extends for 0.23 km² on a north-south axis (OEC data). The geology in the area of Santa Giulia lagoon is very densely fractured (79% granite), with many major clear regional lineaments. The lower watershed is covered by a thick sedimentary layer made of clayey sands that favours the infiltration of water and the rapid saturation of soils as well as the emergence of visibly flowing groundwater springs. The 15.5 km² watershed provides freshwater inputs mainly at the southern end of the basin, near to the outlet of the lagoon, where small temporary creeks flow and are associated with a restricted alluvial aquifer, pumped through several wells and boreholes by local residents for agriculture and gardening purposes. The sea channel is also located in the southern part (Figure 1b and Figure 1c, OEC data). The northern part of the basin does not present a direct exchange with the sea nor strong freshwater inputs (Figure 1c). The lagoon is owned by the CdL and managed by the Environmental Agency of Corsica (OEC) under its protection status (SAC as N2000 site, Habitats Directive). Major threats for this lagoon are the tourism activity around its borders and management difficulties as unauthorised interventions by users of the beach often occur to open the sea channel when obstructed by the accumulation of sand and litter. Small-scale artisanal fishing is carried out by a single fisherman and there is cattle grazing in the south-western area of the watershed (personal observation).

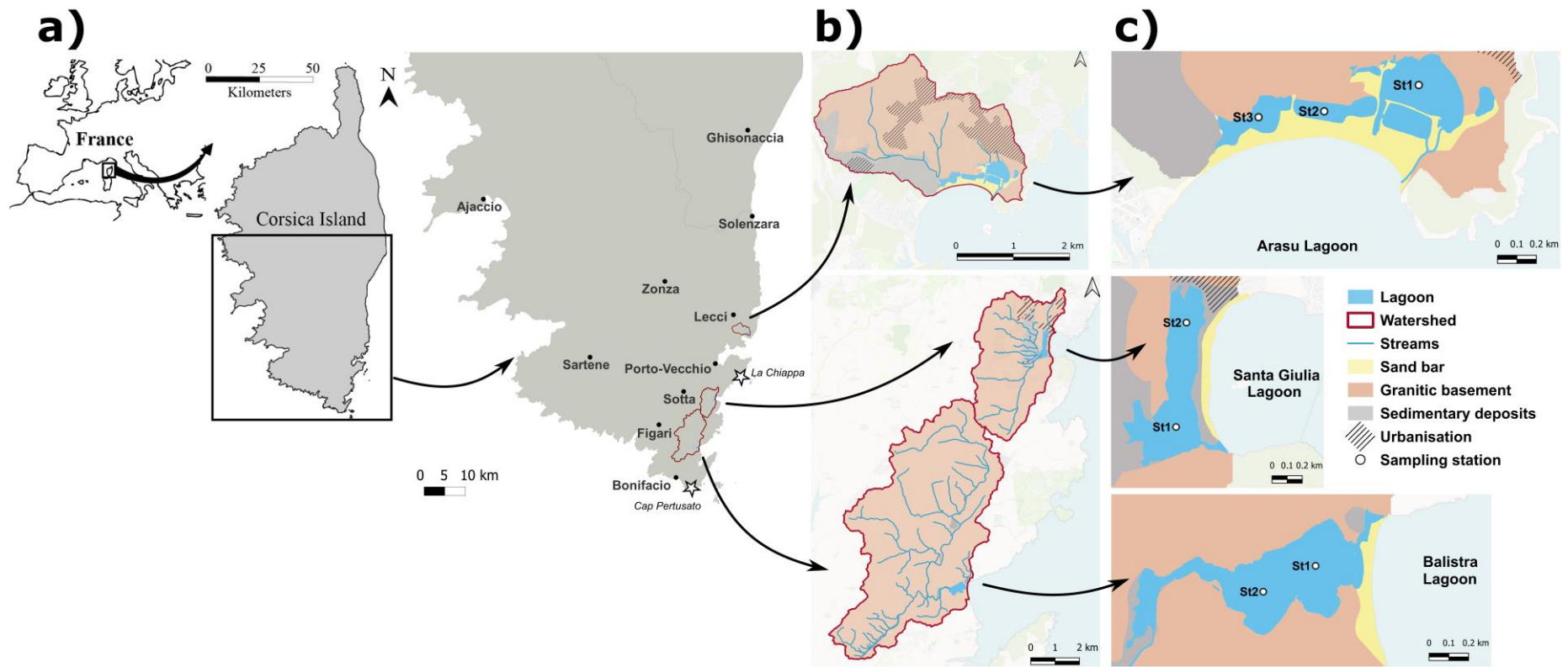


Figure 1 a) Study sites location. Stars on the map correspond to the locations of meteorological stations. b) Main geological elements and urbanisation of the lagoons' watersheds. c) Sampling stations within each coastal lagoon.

The Balistra lagoon (41°26'25" N, 09°13'11" E, [Figure 1b](#) and [Figure 1c](#)) covers 0.27 km² and receives freshwater inputs from the Francolu river in the western part, from a total watershed of 37 km² (OEC data). The Balistra lagoon watershed is mostly granitic (93%) and very densely fractured and weathered, favouring the creation, in the immediate vicinity of the mouth of the Francolu river, of a restricted alluvial aquifer made of coarse sand. This configuration shows a similar hydrogeological structure to that of Santa Giulia, with the emergence of multiple isolated groundwater springs and high porosity, favouring continuous groundwater flow contribution to the rivers and thus to the downstream lagoons.

The depth of Balistra lagoon reaches a maximum of 4.5 m and a mean over the basin of 2 m ([Pergent-Martini et al., 1997](#)). The sea channel is located in the north-eastern part and has a completely natural mode of functioning ([Figure 1](#)). The lagoon is entirely privately owned and is not subject to any management measures at present despite its SAC protection status as a N2000 site (Habitats Directive). The lagoon is located in a barely urbanised area. Nevertheless, some threats do exist, such as a heavy influx of tourists during summer.

On the basis of the little information available, often from non-validated/unpublished scientific reports or non-scientific documents, the three lagoons present a decreasing gradient of current human pressures: Arasu is the most disturbed, Santa Giulia shows a medium status, mostly linked to usages and frequentation, and Balistra could be considered representative of a quasi-pristine condition.

2.2.2 Data collection

To describe the meteorological context both long-term and over the sampling period, daily rainfall and mean air temperature were collected from the Météo-France database. La Chiappa (41°35'41" N, 9°21'47" E) and Cap Pertusato (41°22'29" N, 9°10'42" E) weather stations were chosen (for Arasu and Santa Giulia lagoons and for Balistra lagoon respectively), based on their proximity to the study sites ([Figure 1a](#)). Cumulative monthly rainfall and mean monthly air temperature were calculated to characterise the meteorological context over the period 2019-2021 and for comparison with the standard reference period means established for France (1991-2020) according to the World Meteorological Organisation guidelines (*WMO-No. 1203 © World Meteorological Organization, 2017*).

In order to characterise the progression of urbanisation and touristic pressure over the three watersheds, data on residential homes were collected from the Institut National de la Statistique et des Études Économiques website (©Insee, <https://www.insee.fr>) for various municipalities, depending on the lagoon considered.

The municipalities taken into account are the following: Zonza and Lecci for the surroundings of Arasu lagoon, Porto-Vecchio and Bonifacio for the surroundings of Santa Giulia and Balistra lagoons, respectively. Data on principal and secondary residential homes were available from 1968 to 2018, with a 7-year frequency until 2006 and every 2 years afterwards. The CORINE land-cover map of catchments for 2018 and available previous years (1990, 2000, 2006 and 2012) were then defined ([CORINE Land Cover](#)) using three simplified classes (natural or semi-natural, agricultural and urbanised), based on land cover types automatically defined by the CORINE land-cover program, and compared in order to analyse the urbanisation progression rate over the last 30 years.

Surface water and groundwater were sampled to get an overview of the entire hydrological functioning of the three watersheds, with a focus on the interactions between surface water, groundwater and lagoons. Groundwater was sampled (see [Figure 3](#)) in five springs in the upper part of the watersheds (1 Arasu, 4 Balistra), two hand-dug 1 m depth piezometers close to the lagoons (1 Arasu, 1 Balistra), five wells (around 5 m depth) in the lower part of the watersheds (1 Arasu and 4 Santa Giulia) and three boreholes (40-90 m depth) in the Arasu watershed. Sampling was carried out during autumn 2020 after a dry hydrological year, and NO_3^- concentrations in water samples were determined by Ionic Chromatography (ICS 1100 chromatograph Thermo Dionex, Sunnyvale, CA, U.S.A) at the Hydrogeology Department of the University of Corsica (Corte, France).

Seasonal samplings of lagoons water basins were carried out over the two consecutive years 2020 and 2021 in February (winter), May (spring), August (summer) and November (autumn). Seasonal subsurface (-0.2 m) water samples were hand-collected in the water basins at three sampling stations for Arasu lagoon and at two sampling stations for Santa Giulia and Balistra, between 7:30 and 10:30 a.m. ([Figure 1c](#)). Sampling stations' location and number were chosen to best quantify the spatial variability of the different basins. Triplicate measurements of salinity, temperature, turbidity and dissolved oxygen concentration were performed in situ at each station in subsurface with an YSI ProDSS multiparameter water quality probe. 1 L water samples were pre-filtered on a 200 μm mesh sieve and collected in plastic bottles for further nutrient, phytoplankton pigment and cytometry analyses. Ammonium (NH_4^+) concentrations were determined through the fluorescence method ([Holmes et al., 1999](#)) and nitrite (NO_2^-), nitrate (NO_3^-), dissolved inorganic phosphorus (DIP) and silicates concentrations by the colorimetric method ([Aminot & K  rouel, 2007](#)) after filtration on Whatman GF/F filters (47 mm, porosity 0.7 μm) and water samples storage at -20°C until analyses, at the Mediterranean Institute of Oceanography (MIO) research laboratory (Marseille, France). The use of different methods for the determination of inorganic

nutrients concentrations was imposed by technical reasons and does not compromise comparability, precision and accuracy of the estimates (Burke et al., 1989; Aminot & K erouel, 2007; Alahi & Mukhopadhyay, 2018; Leruste et al., 2019).

Phytoplankton communities were analysed based on their biomass, abundance, diversity and photosynthetic activity. Chlorophyll a (Chl *a*, $\mu\text{g L}^{-1}$) was used as the proxy of phytoplankton biomass. To determine its concentration, water subsamples (250 mL) were filtered on Whatman GF/F filters (25 mm, porosity 0.7 μm) and further stored at -20°C until spectrofluorometric analyses (Neveux & Lantoin e, 1993). To identify microphytoplankton ($> 20 \mu\text{m}$) community composition and quantify abundances, 50 L of surface water were filtered at each station through an Apstein plankton net (20 μm mesh) and 100 mL of concentrated sample were fixed with formaldehyde at 2.5% final concentration. All samples were then examined according to the Uterm ohl method (Uterm ohl, 1958; AFNOR, 2006) with an inverted microscope (Olympus® CKX41). At least 400 cells were counted (estimation error within $\pm 10\%$ limits) (Lund et al., 1958; Uehlinger, 1964). Identification was performed at lowest possible taxonomic level with verification according to several books (Sournia, 1986; Thronsen, 1997; Horner, 2002; Avancini et al., 2006; Hoppenrath et al., 2009; Steidinger & Meave del Castillo, 2018) and databases such as the World Register of Marine Species or AlgaeBase (<http://www.marinespecies.org/>, <https://www.algaebase.org/>, databases available online). In order to characterise community functional diversity, the smallest fraction of phytoplankton communities was also taken into account and analysed through flow cytometry. 1.8 mL of water samples were fixed with glutaraldehyde (0.25% final concentration) and with addition of Pluronic (Poloxamer 188) at a final concentration of 0.01%, as described in Marie et al. (2014). Then, fixed samples were stocked at -80°C and used to perform analyses according to the method detailed in Marie et al. (2014). Different groups could be detected based on their dimension and fluorescence: nanophytoplankton (NANO; $> 2 \mu\text{m}$) and, among the picophytoplankton ($< 2 \mu\text{m}$), autotrophic picoeukaryotes (PEUK), phycocyanin-rich picocyanobacteria (PC-cyan) and phycoerythrin-rich picocyanobacteria (PE-cyan) populations were identified. Photosynthetic activity efficiency was assessed with a Pulse-Amplitude-Modulated fluorimeter (Phyto-PAM Plankton Analyser; Heinz Walz GmbH, Effeltrich, Germany) on samples dark-adapted for at least 30 minutes. Samples were kept in a cooler between 10 and 15°C and analysed between 2 and 6 hours from field collection in order to respect recommended storage conditions for Phyto-PAM fluorimetric analyses (Garrido et al., 2013a). The ratio F_v/F_m , maximum quantum yields of Photosystem II (PSII), was used to assess the health status of the phytoplankton community (Garrido et al., 2013a). It was determined by the equation: $F_v/F_m = (F_m - F_o)/F_m$, where F_m is the maximum fluorescence emitted under a saturating pulse of light ($4000 \mu\text{mol photons m}^{-2} \text{s}^{-1}$) and

F_o is the intrinsic initial fluorescence under non-actinic light when all PSII centres of reaction are opened and potentially available for electron transport (Garrido et al., 2013a). Phyto-PAM analyses were performed in triplicate.

2.2.3 *Statistical analysis*

Data analysis was performed using R statistical software version 4.0.2 (RStudio Team, 2016). Mean seasonal values were calculated for each parameter measured in triplicate: salinity, temperature, turbidity and dissolved oxygen concentration measured in situ, and F_v/F_m measured at laboratory. Abundances by classes of microphytoplankton (Bacillariophyceae or Diatoms, Dinophyceae or Dinoflagellates, Cyanophyceae, Cryptophyceae, Chlorophyta and Others) or groups of pico- and nanophytoplankton (PC-cyan, PE-cyan, PEUK, and NANO) were considered by year and season. Microphytoplankton community was also described through the calculation of diversity indexes (species richness, Shannon's Diversity Index), based on single taxonomic entities identified during counting and considered as taxonomic units. A list of all species or taxonomic units identified can be found in Table S1 (Supplementary Material – Annexe III).

All data were previously $\log_{10}(x+1)$ transformed to normalise data, reduce effects of extreme values and meet ANOVA conditions.

Spatial and seasonal differences within lagoons were assessed through Analysis Of Variance (ANOVA) tests for each variable of interest. When significant ($p < 0.05$), differences were further investigated through post-hoc Tukey's test. For some variables, since normality was not achieved despite transformation, a Kruskal-Wallis (K-W) non-parametric test was applied and eventual significant differences were further tested through Dunn's post-hoc test. Then, a global analysis was performed, with visualisation through Non-metric Multidimensional Scaling (NMDS) of abiotic parameters (water temperature (°C), salinity, turbidity (FNU), dissolved oxygen concentration (%), silicates (μM), DIP (μM), NO_3^- (μM), NO_2^- (μM) and NH_4^+ (μM)), and biotic variables (Chl *a* ($\mu\text{g L}^{-1}$), F_v/F_m, Diatoms (cell L^{-1}), Dinoflagellates (cell L^{-1}), Cyanophyceae (cell L^{-1}), Cryptophyceae (cell L^{-1}), Chlorophyceae (cell L^{-1}), Others (cell L^{-1}), PE-cyan (cell L^{-1}), PC-cyan (cell L^{-1}), PEUK (cell L^{-1}), NANO (cell L^{-1}), species richness, Shannon's Diversity Index) separately. To test potential effects of season, lagoon and stations, datasets were investigated through the Permutational Multivariate Analysis Of Variance (PERMANOVA) test and significant differences ($p < 0.05$) were afterwards detailed through the pairwise post-hoc test.

Finally, relationships between biological and environmental variables were analysed through Spearman's ranks order correlation for each lagoon.

3. RESULTS

3.1 *Small lagoons at Mediterranean and regional scale*

The Mediterranean coastline measures 46 000 km and hosts approximately 400 lagoons, ranging from 0.02 to 780 km² (Cataudella et al., 2015). No clear estimation of coastal wetlands has been established for the Mediterranean region; however, the estimated total lagoon surface area is around 6470 km² according to literature (Pearce & Crivelli, 1994; Cataudella et al., 2015). Apart from knowledge emerging from literature, results from recent studies of the PRLM/TDV, including small-surface lagoons, determined that 95 lagoons can be found in Corsica alone, for a total surface area of 32.81 km² (Figure 2). So, Corsica has 95 lagoons spread over its 1047-km of total coastline, or an average of one lagoon per 11 km, compared to one lagoon per 115 km of coastline for the Mediterranean in general. In Corsica, only 4 lagoons have surface areas greater than 0.5 km², allowing their integration in the WFD, and they cover altogether 28.30 km² (Figure 2).

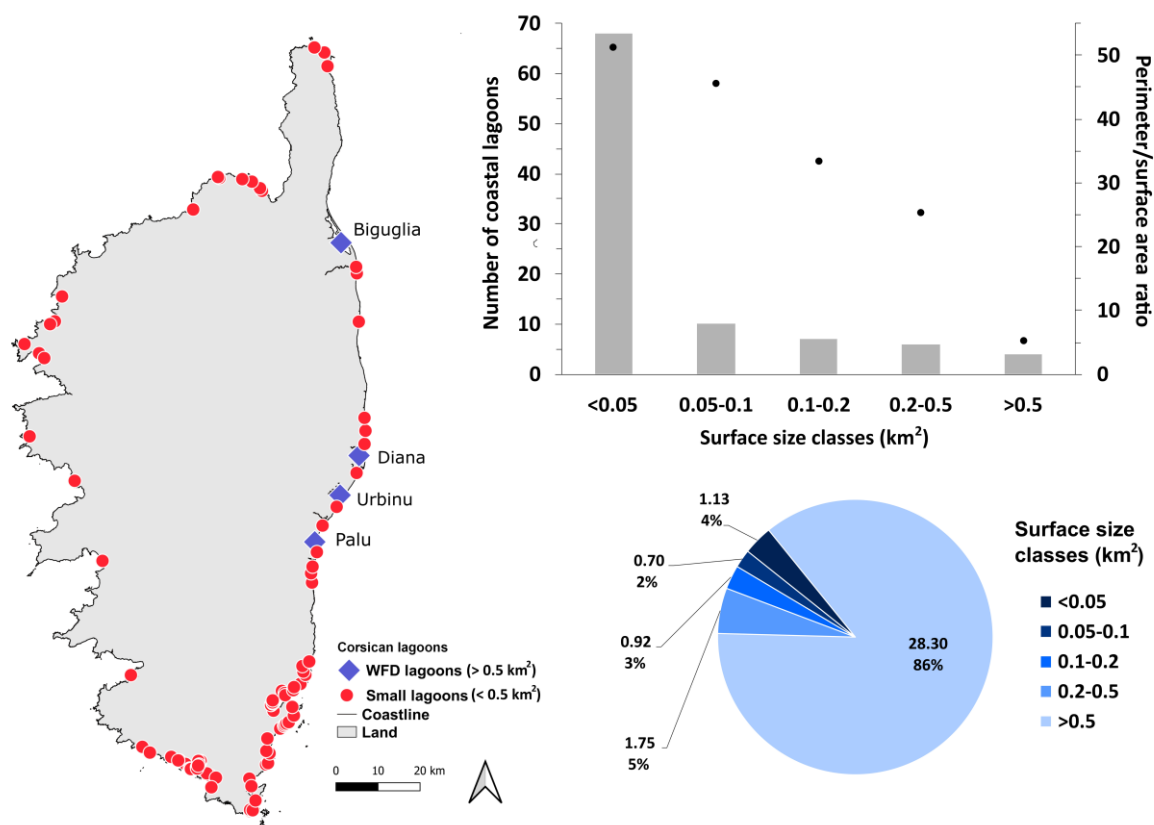


Figure 2 Coastal lagoons in Corsica: locations along the coastline are represented with size-classification according to the WFD limits (left); on the bar chart (top right), number (left scale, bars) and perimeter (km)/surface area (km²) ratios (right scale, points) according to size classes are shown; finally, on the pie chart (bottom right) a representation of surface proportions for each size class is reported (total surface (km²) and percentage for each size class are shown).

The other 91 lagoons, smaller than 0.5 km², represent around 14% (4.51 km²) of the total lagoon surface area on the island, and among them, 68 cover less than 0.05 km² (Figure 2).

Due to their small surface area, small lagoons show a high perimeter/surface ratio, reaching 51.30 for the < 0.05 km² size class, against 5.23 for the four largest lagoons (Figure 2). The total perimeter of small-sized lagoons is even longer than that of the four WFD lagoons, measuring 165.46 vs 148.10 km, respectively.

3.2 *Three case studies*

3.2.1 *Hydro-climatic context and watershed*

Overall, analysis on meteorological conditions highlighted a similar pattern for both meteorological stations over the standard reference period 1991-2020, with a 3-month dry summer season from June to August (Supplementary – Annexe III – Figure S1a). Compared to this period, the overall 2019-2021 period was drier: La Chiappa station in particular was drier than Cap Pertusato station, showing a 5-month dry summer season from May to September, and two winter dry months, February (21 mm mean cumulative rainfall; Supplementary – Annexe III – Figure S1b) and March (22 mm mean cumulative rainfall, Supplementary – Annexe III – Figure S1b). Both meteorological stations showed that rainfall events over 2019-2021 were more concentrated in the autumn season compared to the standard reference period, particularly in November (mean cumulative rainfall over 2019-2021: 128 mm and 150 mm for La Chiappa and Cap Pertusato stations respectively; Supplementary – Annexe III – Figure S1b). The description of the meteorological context over the study period at monthly scale can be found in the Supplementary Material (Annexe III).

As for the quantification of the urbanisation rate of the three watersheds, a dramatic growth of residential homes over the surroundings of all three lagoons emerged from 1968 to 2018 (Figure 3a). Principal residential homes tripled for all municipalities in the three considered areas (Figure 3a). A greater proportional rise was highlighted for secondary residential homes. They increased eight-fold for the vicinity of Balistra lagoon, while they experienced a thirty- and three-hundred-fold increase for the surroundings of Arasu and Santa Giulia lagoons, respectively (Figure 3a). Overall, the highest urbanisation rate over the last 30 years was observed for the Arasu lagoon watershed, which increased from 0.96% in 1990 to 13.2% in 2018 (Figure 3a), while the Santa Giulia lagoon watershed experienced an increase of around 6% in urbanisation over the same period (Figure 3a) and the progression of urbanisation for Balistra lagoon was negligible (Figure 3a). From land use analysis, all three watersheds were

predominantly composed of natural or semi-natural zones, the Balistra lagoon watershed being almost exclusively natural, at 93% land cover (Figure 3b).

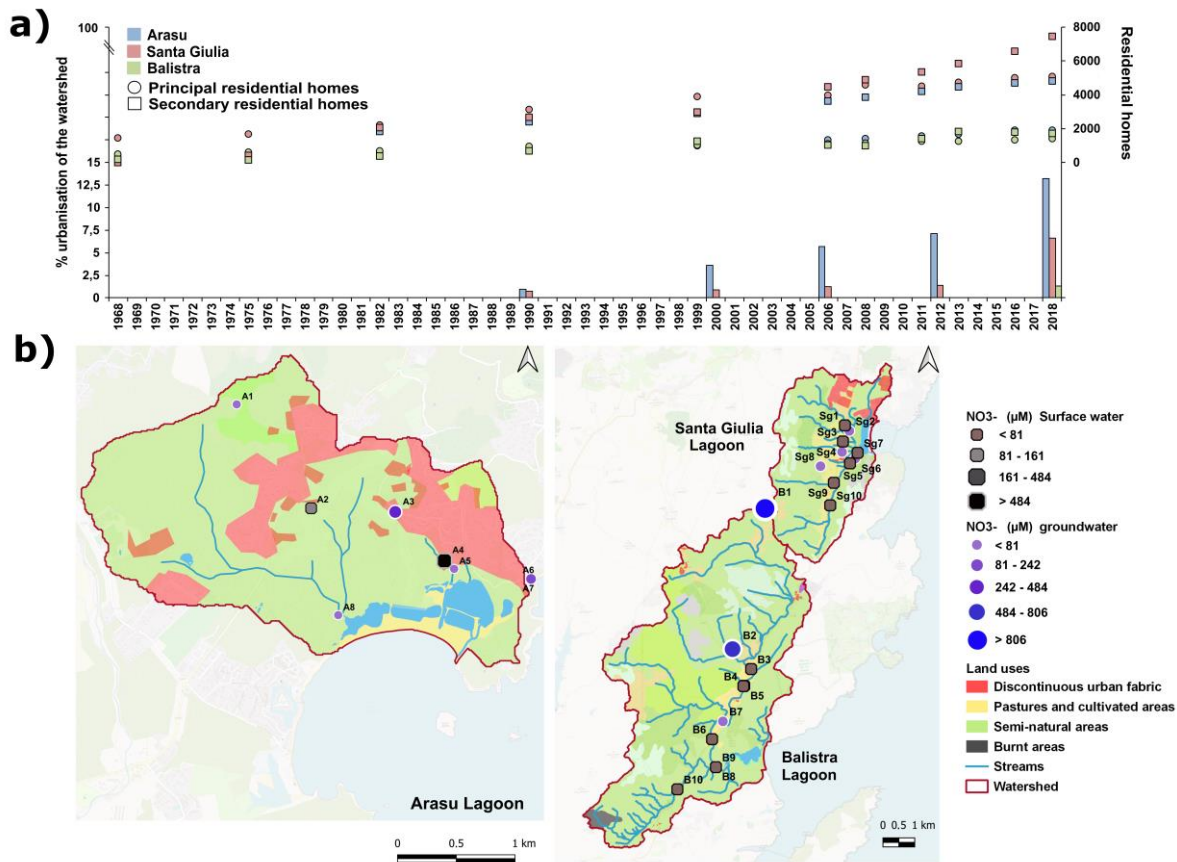


Figure 3 Representation of watershed characteristics: a urbanisation increase is represented as the increase in principle or secondary residential homes over the 1968–2018 period (right scale, points) and as the percentage of the watershed’s urbanised area (left scale, bars); b land uses (2018) are shown, together with sampling points for the nitrates (point size represents concentrations, while point shape indicates weather the sample is from surface water (squares) or groundwater (rounds)).

The Arasu lagoon watershed appears at present as the most urbanised, with 13.2% of urban land cover in 2018, compared to 6.7% and 1.3% at Santa Giulia and Balistra, respectively (Figure 3a and Figure 3b). Rural urbanisation is concentrated in the north and north-eastern part of the basin for Arasu lagoon. Sampling points in the urbanised area of the Arasu lagoon watershed showed NO_3^- concentrations ranging between 164.5 and 487.1 μM for surface waters and between 171.0 and 469.4 μM for groundwater (Figure 3b). All the sampling points, except one, were situated on the flow line of surface and ground waters to the eastern basin of Arasu lagoon (Figure 3b).

The Santa Giulia lagoon watershed presents the most urbanised zone in the north part and upstream of the basin. Also, 19% of the watershed is constituted by agricultural areas, located mainly in the western part (Figure 3b). Highest values of NO_3^- were recorded in stations downstream of the agricultural areas ranging between 83.9 μM in groundwater to 30.7 μM in a temporary river (Figure 3b). Those NO_3^- concentrations are very close to the natural regional baseline level (i.e. < 113 μM). The Balistra lagoon

watershed contains no urbanisation and only very little agricultural development. However, it showed the highest values of NO_3^- in groundwater, with occasional peaks of 837.1 and 1269.4 μM at two sampling sites upstream of the basin, far from the lagoon (3 and 7 km respectively), in hamlets without public sanitation (Figure 3b). These were the only two samples to exceed the World Health Organisation drinking water threshold for nitrate of 50 mg L^{-1} , the equivalent of 806 μM (World Health Organization, 2011).

3.2.2 *Ecological functioning – environmental variables*

During the study, no notable meteorological events preceded sampling days. The only remarkable feature was a general greater exposure to north-easterly winds of Santa Giulia lagoon and sometimes to westerly winds of Balistra lagoon, especially in 2020. For all three lagoons, water temperatures followed the seasonal norms and ANOVA detected a strong effect of season ($p < 0.001$ for all; Arasu: $F_{3,12} = 78.960$, $\omega_p^2 = 0.907$; Santa Giulia: $F_{3,8} = 30.407$, $\omega_p^2 = 0.846$; Balistra: $F_{3,8} = 53.785$, $\omega_p^2 = 0.908$; Supplementary – Annexe III – Figure S2). Oxygen saturation never fell below 88% at Balistra lagoon, while minimum values of 58% and 60% were found at Arasu (summer 2021, St2) and Santa Giulia (summer 2020, St2), respectively (Supplementary – Annexe III – Figure S2). A significant seasonal effect was found from the ANOVA test for Balistra lagoon only ($p = 0.015$; Supplementary – Annexe III – Figure S2). Santa Giulia was overall the most turbid lagoon, with mean turbidity values of 10.6 FNU and reaching a maximum of 42 FNU in summer 2020 at St2, against mean turbidity values of 0.6 and 1.1 FNU for Arasu and Balistra, respectively (Supplementary – Annexe III – Figure S2). This parameter showed significant spatial difference in Arasu lagoon (K-W: $H = 0.191$, $n = 24$, $p = 0.049$; Dunn's test: $\text{St}_1 \neq \text{St}_2 = \text{St}_3$).

Salinity ranged between 2.8 (spring 2020, St3) and 49.9 (summer 2021, St1) in Arasu lagoon with lowest values systematically registered at St2 or St3, except for autumn 2021 (Figure 4). Santa Giulia lagoon showed mean salinity of 40, with a peak at 125.9 in summer 2020 at St2 (Figure 4). Balistra lagoon showed internal spatial homogeneity, with minimum values during the winters of both years considered (min.: 3.2, winter 2021, St2) and mean overall value of 26.1 (Figure 4). An important seasonal effect was detected from the ANOVA test for all three lagoons (Arasu: $F_{3,12} = 5.356$, $\omega_p^2 = 0.353$, $p = 0.014$; Santa Giulia: $F_{3,8} = 9.993$, $\omega_p^2 = 0.628$, $p = 0.004$; Balistra: $F_{3,8} = 72.827$, $\omega_p^2 = 0.931$, $p < 0.001$).

Highest nutrient values were found during winters for all lagoons. Santa Giulia showed highest mean values for NH_4^+ , DIP and silicate concentrations (6.5, 0.2 and 118.3 μM respectively), while highest mean values for NO_2^- and NO_3^- concentrations were registered in Balistra lagoon at 0.2 and 5.6 μM , respectively. At Arasu lagoon, ANOVA detected a moderate effect of the season for NH_4^+ ($F_{3,12} = 4.777$, $\omega_p^2 = 0.321$, $p = 0.020$),

resulting in highest values in winter, compared to other seasons according to the Tukey test. In addition, effects of season and station were found for NO_3^- (K-W: $H = 0.365$, $n = 24$, $p = 0.016$ (season) and $H = 0.236$, $n = 24$, $p = 0.031$ (station)), indicating significant differences of winter from spring and summer seasons and highest values at St1 compared to the other stations (Figure 4).

NO_2^- differed among seasons according to the ANOVA test for all three lagoons (Arasu: $F_{3,12} = 7.427$, $\omega_p^2 = 0.445$, $p = 0.005$; Santa Giulia: $F_{3,8} = 4.916$, $\omega_p^2 = 0.423$, $p = 0.032$; Balistra: $F_{3,8} = 6.772$, $\omega_p^2 = 0.520$, $p = 0.014$). A similar result was found for silicate concentrations, except in Balistra lagoon (ANOVA $F_{3,8} = 4.586$, $\omega_p^2 = 0.402$, $p = 0.038$) where they seemed to follow a seasonal decreasing gradient from winter to summer (Figure 4).

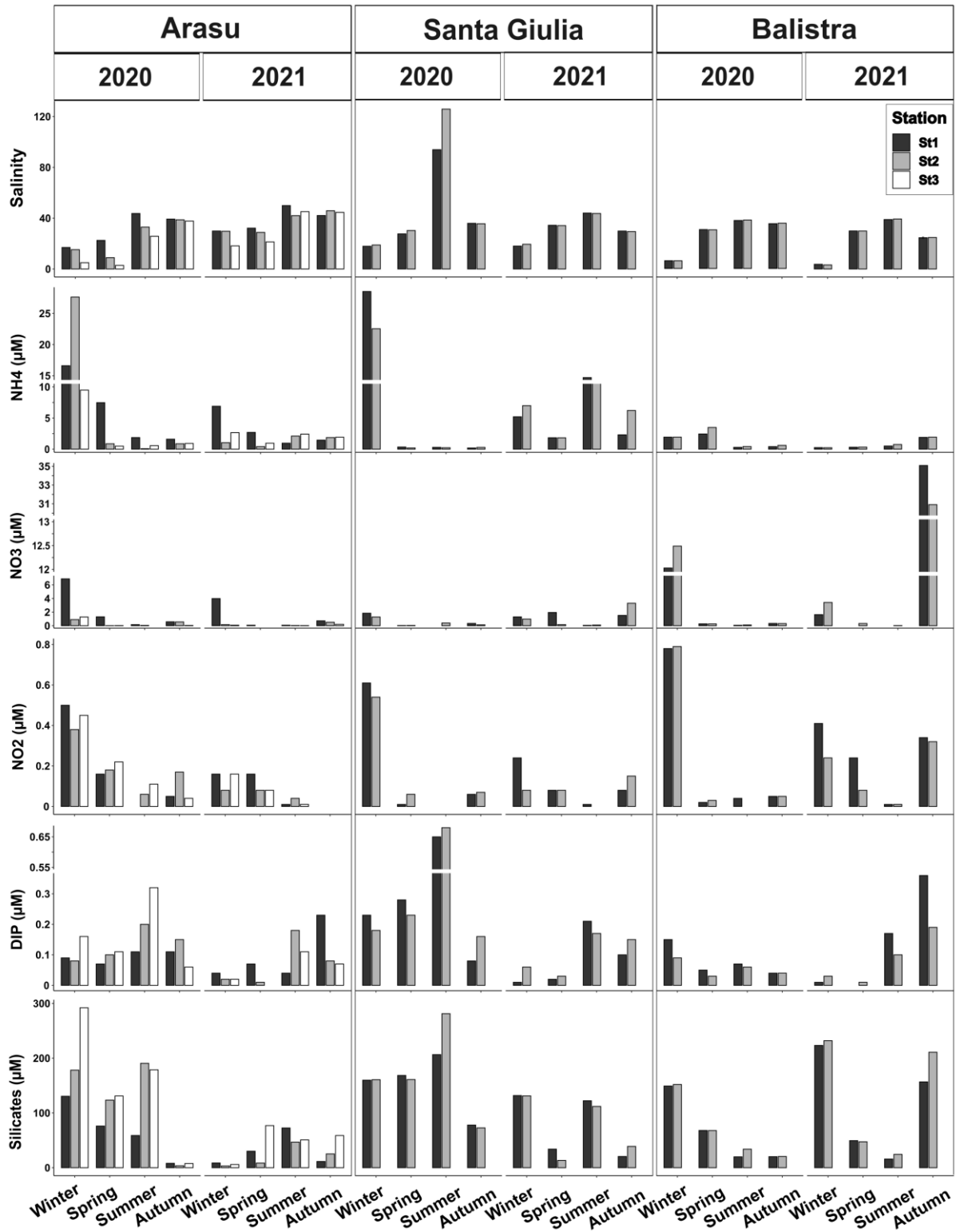


Figure 4 Environmental variables measured for the three lagoons in the two sampling years 2020–2021. Salinity (with error bars representing Standard Error over the three replicates measured in situ) and nutrients concentrations (NH_4^+ , NO_3^- , NO_2^- , DIP, Silicates; μM) for the water basins are shown by sampling stations.

ANOVA tests on the ratio between total Dissolved Inorganic Nitrogen (DIN, calculated as $\text{NH}_4^+ + \text{NO}_2^- + \text{NO}_3^-$) and DIP (DIN/DIP, data not shown) revealed significant differences in N inputs and consequent nutrients imbalance. Results showed an effect of season factor for Arasu and Balistra lagoons (ANOVA $F_{3,11} = 11.475$, $\omega_p^2 = 0.577$, $p = 0.001$ and $F_{3,7} = 12.662$, $\omega_p^2 = 0.700$, $p = 0.003$, respectively), but different trends for the two cases: for Arasu the ratio was higher in winter than other seasons, while for Balistra summer showed a lower value. To characterise the lagoons' trophic status, nutrients ratios were compared to Redfield et al. (1963) and Brzezinski (1985) ratios (Figure 5). Overall, DIP proved to be the most limiting factor, but Santa Giulia lagoon and summer season were sometimes DIN-limited, while silicates limitation was never observed (Figure 5).

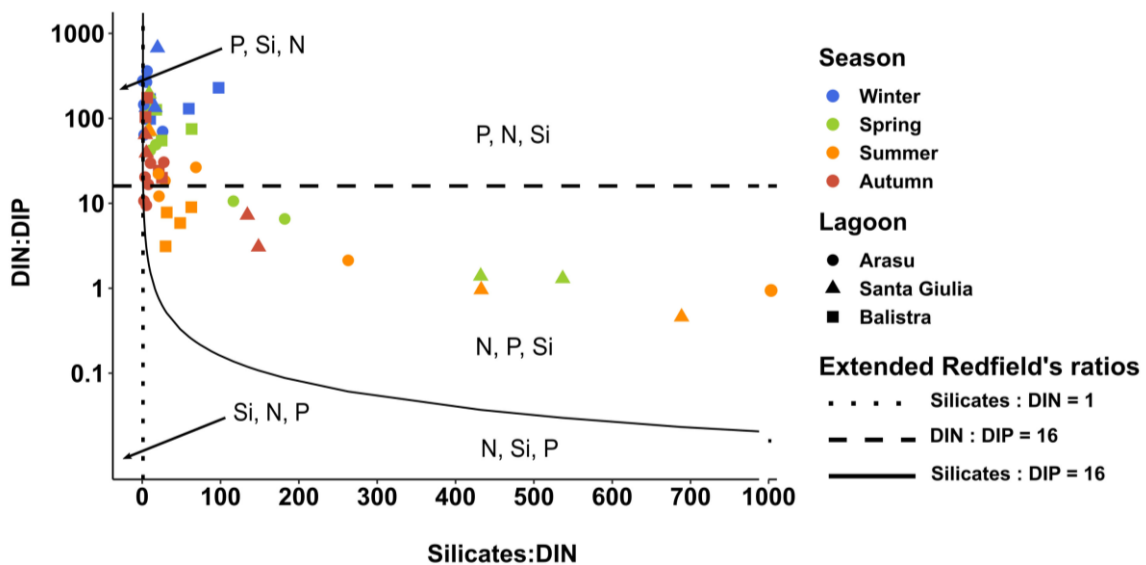


Figure 5 Molar inorganic nutrients ratios measured in the three lagoons at different seasonal samplings. Lines represent molar ratios defined by Redfield et al. (1963) and Brzezinski (1985), with Silicates:DIN = 1, DIN:DIP = 16, and Silicates:DIP = 16, and in the delimited areas nutrients are given in their potential limitation's priority order (Rocha et al., 2002).

In order to obtain an overall characterisation of the three ecosystems, a comprehensive analysis was performed on abiotic parameters datasets to detect potential differences between lagoons and eventually their seasonal and spatial patterns. The analysis highlighted significant effects of both the season and the lagoon factors. From NMDS visualisation, seasons resulted clustered (Figure 6a). Lagoon centroids were clearly separated and station centroids within lagoons only showed high dispersion for Arasu lagoon (Figure 6a). The PERMANOVA test highlighted moderate effects of season ($R^2 = 0.308$, $\omega_p^2 = 0.305$, $p = 0.001$) and lagoon ($R^2 = 0.150$, $\omega_p^2 = 0.169$, $p = 0.001$). All seasons were different from each other according to the pairwise test, while Santa Giulia was different from Arasu ($R^2 = 0.155$, $p = 0.003$) and Balistra ($R^2 = 0.144$, $p = 0.011$) lagoons, which did not differ from each other ($R^2 = 0.057$, $p = 0.099$).

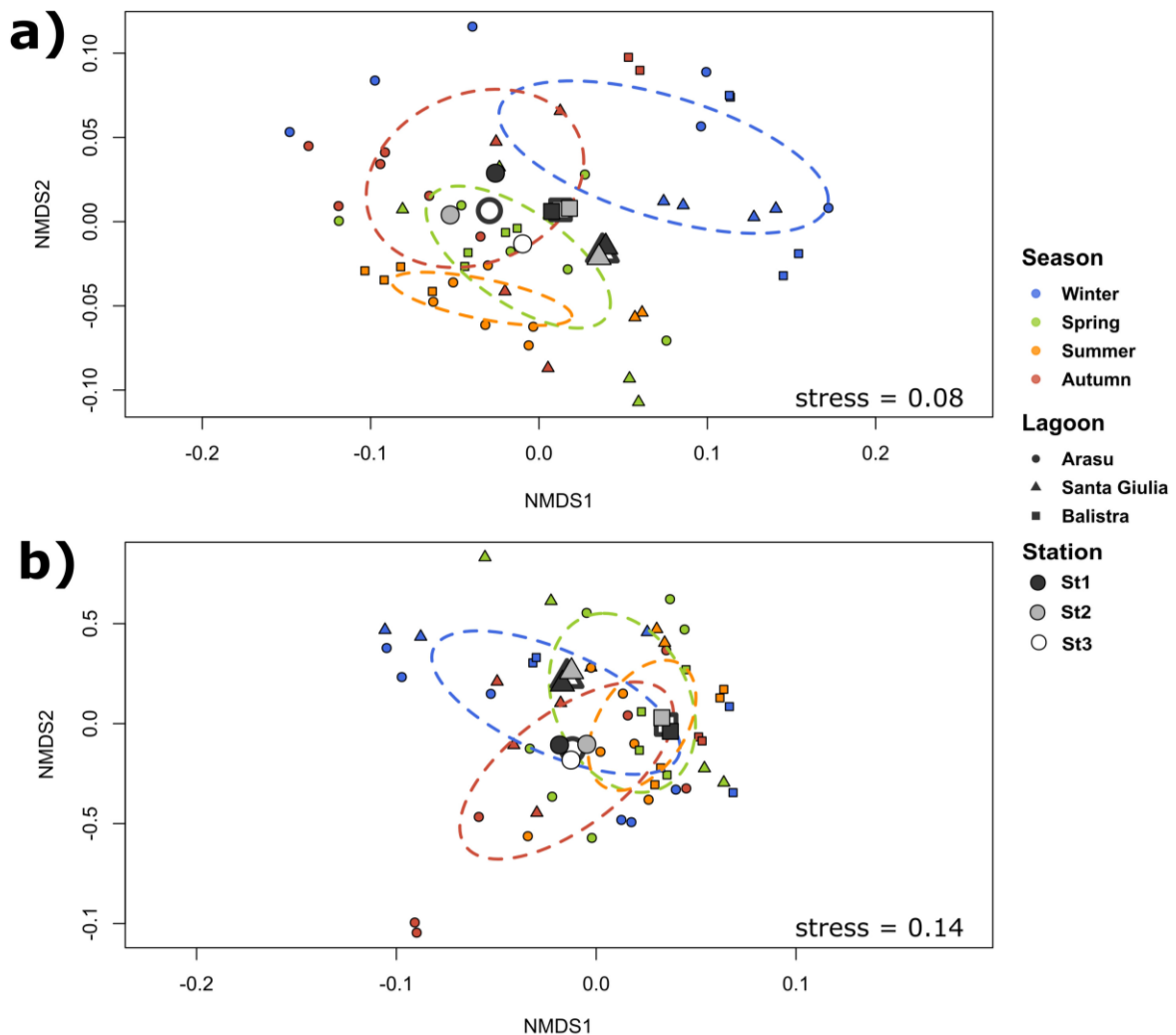


Figure 6 NMDS representation of total dataset for a) abiotic and b) biotic variables. Samples are color-coded for seasons, shapes indicate lagoons and stations. Ellipses are shown to describe seasonal clustering, together with lagoon and station centroids.

3.2.3 *Ecological functioning – biotic variables*

In general, Santa Giulia lagoon stood out for its Chl *a* content, with a mean of 7.1 $\mu\text{g L}^{-1}$ reaching a maximum of 17.2 $\mu\text{g L}^{-1}$ in autumn 2020 at St2 (Figure 7). Arasu lagoon showed Chl *a* values ranging from 0.1 to 7.6 $\mu\text{g L}^{-1}$, usually lower at St1, and mean value of 1.1 $\mu\text{g L}^{-1}$ (Figure 7), while in Balistra lagoon Chl *a* content never exceeded 1.6 $\mu\text{g L}^{-1}$, with a mean of 0.5 $\mu\text{g L}^{-1}$, and did not display marked differences between stations (Figure 7).

Overall, differences between seasons or stations within lagoons were less marked. No significant spatial differences were found for the pico-, nano- and micro-phytoplankton communities' compositions. No marked differences could be seen between stations for communities' percentage compositions: Santa Giulia and Arasu were mostly dominated by PEUK and NANO, except for an almost complete dominance of picocyanobacteria in

Arasu lagoon in spring and summer at all stations and in autumn at St1 in 2020 (Figure 7). NANO contribution in Balistra lagoon was limited, as the community was systematically dominated by picophytoplankton and mostly PE-cyan (Figure 7). Diatoms constituted almost systematically the major component of microphytoplankton assemblages, regardless of season and lagoon, except for St2 and St3 in Arasu lagoon, which were predominantly dominated by Dinoflagellates (Figure 7). Yet no significant effect of station could be highlighted for microphytoplankton composition. A moderate seasonal effect was only found for the Diatoms group in Balistra lagoon (ANOVA $F_{3,8} = 10.446$, $\omega_p^2 = 0.639$, $p = 0.004$), with highest contributions in summer and autumn compared to spring (Figure 7).

Only station effects were detected for Arasu lagoon for Shannon's Diversity Index and Fv/Fm (ANOVA $F_{2,12} = 6.950$, $\omega_p^2 = 0.331$, $p = 0.010$ and $F_{2,12} = 8.917$, $\omega_p^2 = 0.397$, $p = 0.004$ respectively), indicating St1 differed from the others according to the Tukey test. In particular, St1 repeatedly showed higher diversity but lower photosynthetic efficiency of the community (Figure 7). Finally, a moderate effect of season in Santa Giulia lagoon was identified for Fv/Fm (ANOVA $F_{3,8} = 6.499$, $\omega_p^2 = 0.508$, $p = 0.015$), signifying a difference of summer season (lower values, Figure 7) compared to the others, according to the Tukey test.

Overall seasonal and spatial patterns between and within lagoons were investigated through a comprehensive analysis on overall biotic variables. Significant effects of both the season and the lagoon factors were detected. In the NMDS visualisation of biotic variables, season clusters were superposed (Figure 6b). Lagoon centroids were well distinct, with less station dispersion compared to abiotic variables NMDS analysis (Figure 6b). An effect of season ($R^2 = 0.154$, $\omega_p^2 = 0.109$, $p = 0.003$) and lagoon ($R^2 = 0.135$, $\omega_p^2 = 0.106$, $p = 0.001$) emerged from PERMANOVA, and according to the pairwise test all lagoons differed from each other. Conversely, no clear distinction could be highlighted for seasons, except summer, which differed from winter ($R^2 = 0.159$, $p = 0.018$) and autumn ($R^2 = 0.188$, $p = 0.018$) according to the pairwise test.

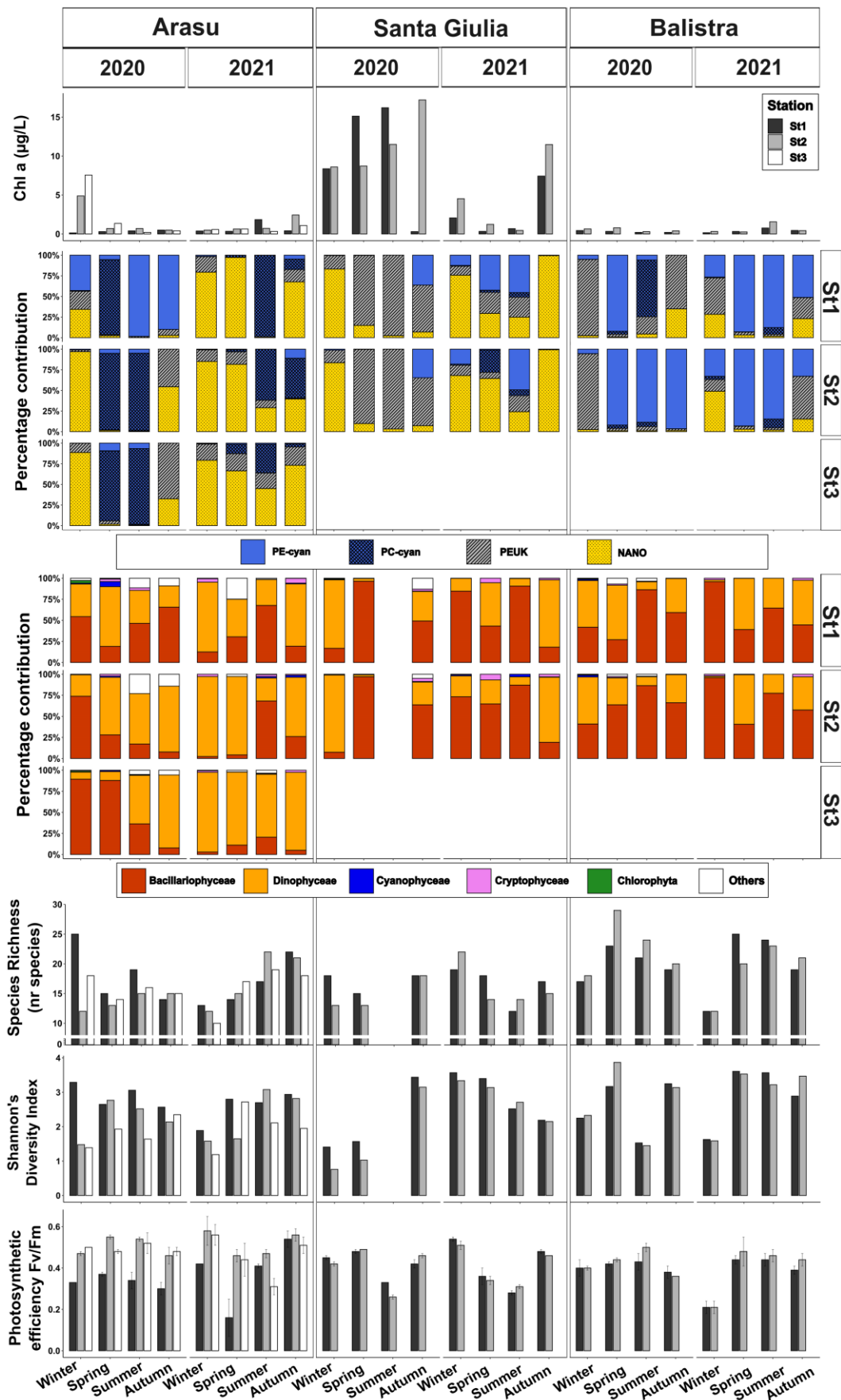


Figure 7 Biotic parameters considered for the three lagoons in the two sampling years 2020–2021: chlorophyll *a*, pico- and nano-phytoplankton, microphytoplankton class composition, species richness, Shannon's Diversity Index and photosynthetic efficiency (Fv/Fm) of the assemblages are represented.

A complete list of microphytoplankton taxonomic units found at each lagoon and season is reported in [Table S1](#) (Supplementary Material – Annexe III). A closer look at the microphytoplankton community structure and composition revealed that total cellular abundance was generally higher at Arasu and Santa Giulia lagoons than Balistra lagoon, almost systematically exceeding 1×10^6 cell L⁻¹ ([Table 1](#)). In Balistra lagoon, these magnitudes were only reached in winter and spring 2020 and in summer of both years ([Table 1](#)). Arasu and Santa Giulia lagoons' communities were frequently dominated by one or a few taxa at high densities, frequently blooming (cellular density > 100 000 cell L⁻¹; [Belin & Neaud-Masson, 2017](#)), as also confirmed by lower species richness and Shannon's Diversity Index ([Table 1, Figure 7](#)). In Balistra lagoon, blooms were rare: the only bloom was recorded during summer in 2020 and was constituted by the diatom *Chaetoceros* spp. ([Table 1](#)). Except this season, Balistra lagoon always showed the highest diversity and species richness amongst the lagoons ([Figure 7](#)). In any case, sometimes dinoflagellates were also present in high densities or even dominant, at times with potentially harmful species, such as *Kryptoperidinium foliaceum*, reaching 72×10^3 cell L⁻¹ in winter 2020 (St2), *Prorocentrum micans* in spring and autumn 2021 (reaching up to 24×10^3 cell L⁻¹ in autumn 2021, St1) and *Protooperidinium* sp. occurring occasionally ([Table 1](#)). In Arasu lagoon, differences between stations could be observed: total abundances were generally higher at St2 and St3 than St1, which also showed lower dinoflagellate contribution compared to the other two stations ([Table 1, Figure 7](#)). The presence or dominance of dinoflagellates was almost systematic and frequent blooms of dinoflagellate species, sometimes potentially toxic, occurred ([Table 1](#)). For instance, *Prorocentrum cordatum* produced an extended bloom over St2 and St3 and was dominant all over the basin in winter 2020 ([Table 1](#)); in addition, *P. micans* bloomed frequently and persisted over the basin and across seasons and years, reaching a peak at 518×10^3 cell L⁻¹ in spring 2021 at St3 ([Table 1](#)). Potentially toxic *Akashiwo sanguinea* was sporadically present and bloomed at 250×10^3 cell L⁻¹ in spring 2021, while dominance of *Chaetoceros* spp. was limited to St3 ([Table 1](#)). In Santa Giulia lagoon the two stations were quite similar: potentially toxic or non-toxic dinoflagellates often dominated the community or bloomed, especially during autumn. For instance, *P. cordatum* reached 68×10^3 cell L⁻¹ in autumn 2020 at St2 and *P. micans* bloomed in autumn 2021 at St1 reaching 102×10^3 cell L⁻¹ ([Table 1](#)). In winter 2020 the lagoon experienced a high bloom of *Diplopsalis* sp., reaching 1×10^7 cell L⁻¹ magnitude at both stations, a scale that was reached again only by *Chaetoceros* spp. in spring 2020, corresponding in both cases to lowest diversity and species richness values ([Table 1, Figure 7](#)).

Table 1 Summary description of dominant microphytoplankton taxa, with percentage proportion in terms of abundance relative to total cellular abundance. Abundance values in bold represent densities over bloom threshold (> 100 000 cell L⁻¹).

		<i>Arasu</i>				<i>Santa Giulia</i>				<i>Balistra</i>						
		St1		St2		St3		St1		St2		St1		St2		
		Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	Dominant Taxon and percentage proportion	Total abundance x10 ³ cell L ⁻¹	
2020	Winter	Undetermined diatom (22%) <i>Prorocentrum cordatum</i> (20%) <i>Amphora</i> sp. (17%)	81	Undetermined diatom (69%) <i>Prorocentrum cordatum</i> (15%) <i>Prorocentrum micans</i> (9%)	1134	Undetermined diatom (79%) <i>Prorocentrum cordatum</i> (5%) <i>Chaetoceros</i> spp. (4%)	3157	<i>Diplopsalis</i> sp. (86%) <i>Navicula</i> spp. (5%) Undetermined diatom (3%)	4097	<i>Diplopsalis</i> sp. (90%)	1116	<i>Kryptoperidinium foliaceum</i> (44%) Fragilariophycideae (33%)	155	<i>Kryptoperidinium foliaceum</i> (45%) Fragilariophycideae (32%)	161	
	Spring	Undetermined dinoflagellate (40%) <i>Prorocentrum micans</i> (26%)	302	<i>Prorocentrum micans</i> (37%) <i>Prorocentrum cordatum</i> (17%)	782	<i>Chaetoceros</i> spp. (62%) Small centric diatoms (17%)	1049	<i>Chaetoceros</i> spp. (73%) Small pennate diatoms (11%) <i>Nitzschia</i> sp. (7%)	6857	<i>Chaetoceros</i> spp. (85%) Small pennate diatoms (5%)	2648	Undetermined dinoflagellate (35%) <i>Scrippsiella trocoidea</i> (21%)	56	Undetermined dinoflagellate (20%) Small pennate diatoms (16%)	101	
	Summer	<i>Amphora</i> sp. (32%) Undetermined dinoflagellate (21%)	225	<i>Prorocentrum micans</i> (41%) Undetermined (23%)	468	Undetermined dinoflagellate (56%) <i>Chaetoceros</i> spp. (34%)	243						<i>Chaetoceros</i> spp. (78%)	162	<i>Chaetoceros</i> spp. (80%)	263
	Autumn	<i>Amphora</i> sp. (45%)	177	<i>Prorocentrum micans</i> (63%)	171	<i>Prorocentrum micans</i> (41%)	282	<i>Prorocentrum cordatum</i> (22%) <i>Navicula</i> spp. (17%)	128	<i>Amphora</i> sp. (33%) <i>Prorocentrum cordatum</i> (19%)	354	<i>Protoperidinium</i> sp. (24%) <i>Cocconeis</i> sp. (17%)	32	<i>Protoperidinium</i> sp. (23%) <i>Cocconeis</i> sp. (23%)	36	
2021	Winter	<i>Protoperidinium</i> sp. (60%) <i>Prorocentrum micans</i> (19%) <i>Amphora</i> sp. (10%)	208	<i>Prorocentrum micans</i> (73%) <i>Protoperidinium</i> sp. (11%) <i>Akashiwo sanguinea</i> (10%)	209	<i>Prorocentrum micans</i> (80%)	194	<i>Navicula</i> spp. (25%) Fragilariophycideae (14%) <i>Cocconeis</i> sp. (14%)	173	<i>Navicula</i> spp. (30%) <i>Alexandrium</i> spp. (15%) Fragilariophycideae (11%)	126	Fragilariophycideae (70%)	42	Fragilariophycideae (70%)	41	
	Spring	<i>Amphora</i> sp. (25%) Others (25%) <i>Prorocentrum micans</i> (18%)	84	<i>Prorocentrum micans</i> (73%)	147	<i>Prorocentrum micans</i> (44%) <i>Akashiwo sanguinea</i> (21%) <i>Kryptoperidinium foliaceum</i> (8%)	1189	<i>Alexandrium</i> spp. (26%) Fragilariophycideae (17%)	53	<i>Nitzschia</i> sp. (21%) Fragilariophycideae (18%)	47	<i>Prorocentrum micans</i> (20%) <i>Protoperidinium</i> sp. (15%)	60	<i>Prorocentrum micans</i> (20%) <i>Protoperidinium</i> sp. (16%)	67	
	Summer	<i>Amphora</i> sp. (36%)	494	<i>Nitzschia</i> sp. (41%) <i>Prorocentrum micans</i> (13%)	124	<i>Prorocentrum micans</i> (65%)	106	<i>Nitzschia</i> sp. (46%) <i>Navicula</i> spp. (13%)	129	<i>Nitzschia</i> sp. (44%) <i>Navicula</i> spp. (15%)	170	<i>Nitzschia</i> sp. (24%) <i>Chaetoceros</i> spp. (16%) <i>Alexandrium</i> spp. (12%)	106	<i>Chaetoceros</i> spp. (29%) <i>Nitzschia</i> sp. (29%)	104	
	Autumn	<i>Prorocentrum micans</i> (47%)	76	<i>Prorocentrum micans</i> (49%)	251	<i>Prorocentrum micans</i> (67%) <i>Akashiwo sanguinea</i> (14%)	166	<i>Prorocentrum micans</i> (60%) Fragilariophycideae (11%) <i>Akashiwo sanguinea</i> (10%)	171	<i>Prorocentrum micans</i> (65%)	99	<i>Prorocentrum micans</i> (40%) Fragilariophycideae (22%)	61	<i>Prorocentrum micans</i> (26%) <i>Chaetoceros</i> spp. (18%)	44	

At lagoon scale, some interesting significant correlations emerged. Overall, Diatoms were not correlated with indexes of richness, diversity or photosynthetic activity, but Dinoflagellates were negatively correlated with Shannon's Diversity Index both in Arasu ($r = -0.41$, $n = 24$, $p = 0.046$) and Santa Giulia ($r = -0.61$, $n = 14$, $p = 0.022$) lagoons. They were also positively correlated with Fv/Fm in Arasu ($r = 0.48$, $n = 24$, $p = 0.017$) and Santa Giulia ($r = 0.62$, $n = 14$, $p = 0.017$), lagoons together with Chl *a* (Arasu: $r = 0.51$, $n = 24$, $p = 0.010$; Santa Giulia: $r = 0.70$, $n = 14$, $p = 0.006$). In Santa Giulia lagoon Shannon's Diversity Index was also negatively correlated with Chl *a* ($r = -0.58$, $n = 14$, $p = 0.030$), while Fv/Fm was negatively correlated with salinity ($r = -0.63$, $n = 14$, $p = 0.015$), water temperature ($r = -0.60$, $n = 14$, $p = 0.025$) and PC-cyan ($r = -0.58$, $n = 14$, $p = 0.029$). Balistra lagoon showed a completely opposite mode of functioning, with a positive correlation between Chl *a* and Shannon's Diversity Index ($r = 0.54$, $n = 14$, $p = 0.045$), and between Fv/Fm and salinity ($r = 0.67$, $n = 14$, $p = 0.009$), water temperature ($r = 0.68$, $n = 14$, $p = 0.007$), PC-cyan ($r = 0.54$, $n = 14$, $p = 0.044$) and PE-cyan ($r = 0.67$, $n = 14$, $p = 0.009$).

4. DISCUSSION

4.1 Ecological functioning of the three small lagoons

Despite some small local differences potentially affecting the three lagoons' hydrological functioning at small scale, we highlighted evidence of climate change such as the extension of the dry period, the occurrence of drought outside the summer season and the intensification of the rainy period over shorter periods. Such impacts are exemplified by the small size of the studied sites that function as temporary coastal lagoons *sensu* Latron *et al.* (2022). We also established that our case study lagoons have been subjected to increasing rural urbanisation over the past few decades and especially seasonal pressure linked to summer tourism. In fact, at regional level, according to available data from the ©Insee (<https://www.insee.fr>), during the 1999-2021 period the resident population increased linearly by a 1.3% annual rate, with the year 2021 reaching an increase of 33% compared to 1999. Furthermore, over the same time span, the number of summer travellers increased by a 0.8% annual rate, with a peak in 2018 at 23% more travellers than the average over the entire period (DREAL Corse). The most directly impacted lagoons appear to be Arasu and Santa Giulia with a 12% and 6% urbanisation rate increase of their watersheds, respectively, within the last 30 years. Regarding our indicator for anthropogenic pollution, the nitrates, the natural baseline concentration for groundwater is estimated at between 5 and 7 mg L⁻¹ maximum (Appelo & Postma, 2005), the equivalent of 81 and 113 µM, hence nitrate concentrations exceeding this threshold can be related to human activities impacting groundwater quality.

For Arasu, a small aquifer is present in the western part of its watershed. Also, in the north-eastern part, there is a permanent stream with its accompanying groundwater. Since the stream is located in the most densely urbanised area of the watershed, it has a potential role in influencing anthropogenic pollution inflow to the lagoon. High NO_3^- concentrations seemed to be attributable to sanitation defects inducing wastewater leakages to the groundwater. Salinity variations were clearly linked to the opening status of the sea channel outlet (Figure 8).

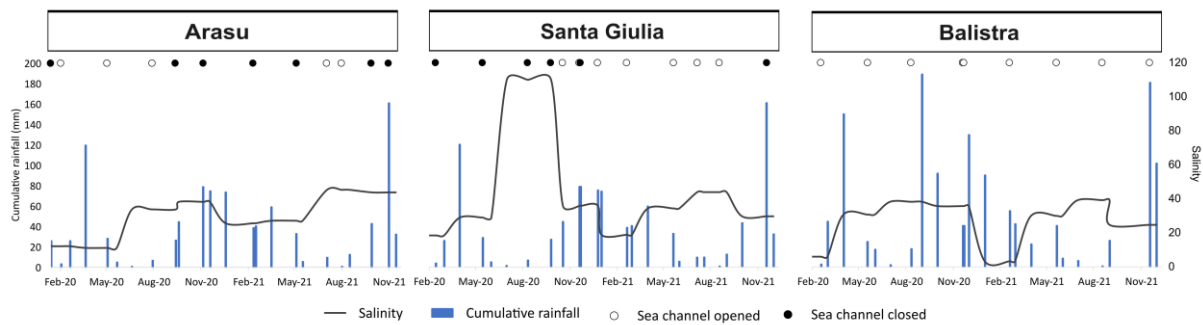


Figure 8 Representation of daily rainfall (mm, scale on the left), mean salinity (scale on the right) over each entire water basin and status (opened as white or closed as black points at the top of the graph) of the sea channel outlet, based on available dates over the study period.

The lagoon functioning is marked by the major anthropogenic alterations to which it was subjected in the past, i.e. the construction of roads on dams dividing the basin into three separate portions. There is a sort of lagged response of salinity to rainfall events and sea channel opening times since freshwater and marine inputs are located at different and physically separate sites. In particular, fluctuations in salinity and nutrient concentrations were markers of the limited water circulation between the three separate basins (Figure 9). The eastern basin was the most impacted by urbanisation and the least productive in terms of phytoplankton biomass, showing signs of degradation, including the complete absence of angiosperm meadows (Figure 9). Lower phytoplankton biomass might be a consequence of greater connection with the sea, where biomass is generally low (Sarno et al., 1993a). Another cause might be anthropogenic impact, which is higher in this area, linked to the exposure to some kind of chemicals or pollution (Lafabrie et al., 2013 and references herein). We hypothesised some sort of current or legacy pollution might be responsible for the degradation. For instance, Lafabrie et al. (2013) demonstrated that sediments can be a sink for contaminants and affect the phytoplankton community by long-term exposure from sediment resuspension. Moreover, absence of angiosperms might be due to eutrophication, pollutants or legacy effects of past sediment rearrangement, as these factors are known to cause a decline in angiosperm coverage in disturbed lagoon systems (Sfriso et al., 2017, 2019, 2021). The high dominance of potentially harmful dinoflagellates, blooms and low species diversity, especially at the St₂ and St₃ basins, indicate degradation of the lagoon, probably due to confinement (Sarno et al., 1993a). *Prorocentrum micans* in particular produced intense

and very long-lasting blooms expanding to all three basins. Potentially toxic *Prorocentrum cordatum* and *Akashiwo sanguinea* also sometimes bloomed. These potentially toxic species are known to produce high density blooms, especially during summer/late autumn, linked to confinement and nutrient inputs (Sarno et al., 1993a; Sahraoui et al., 2013; Bouchouicha Smida et al., 2014).

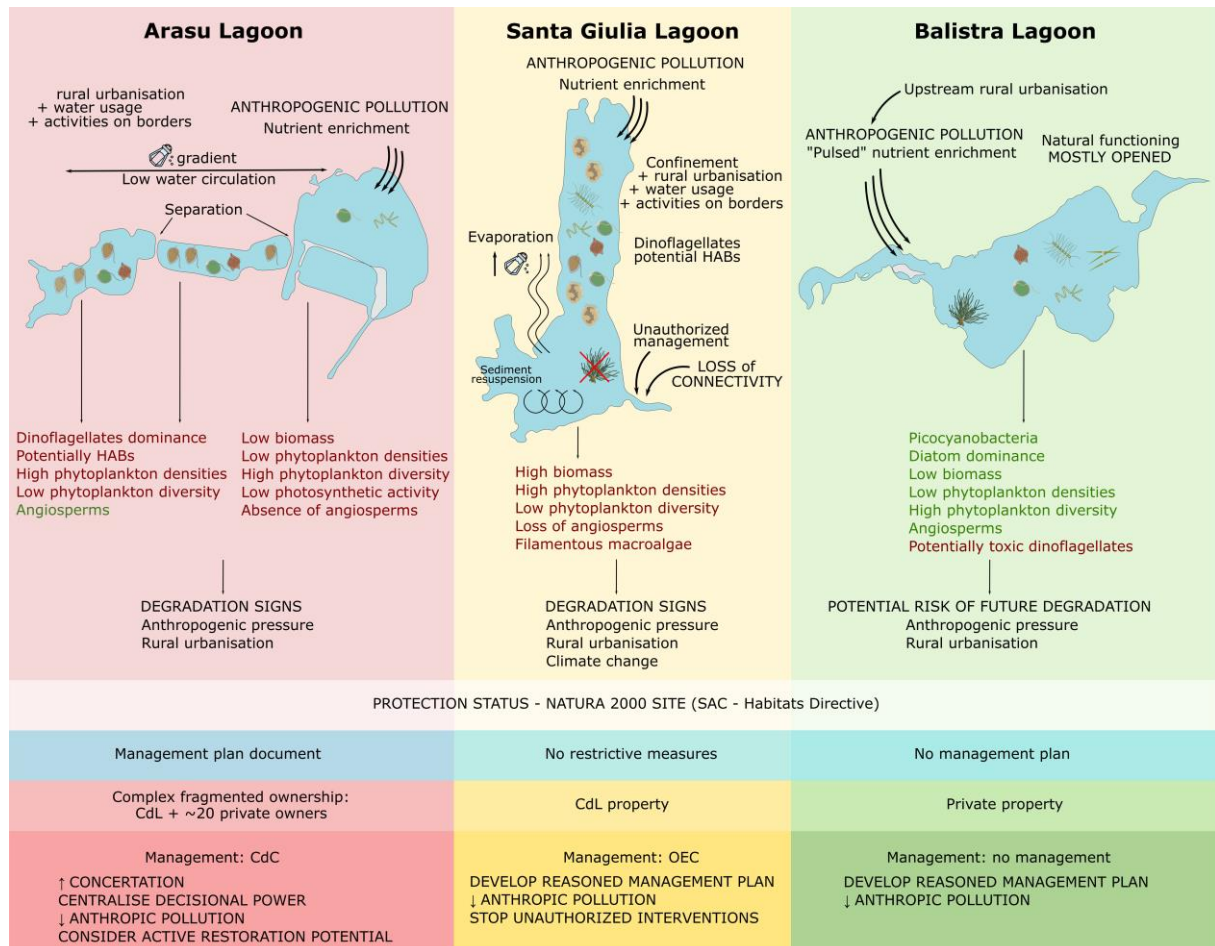


Figure 9 Schematic representation of the main features of the dynamics, functioning, pressures and management of the three lagoons in their current anthropogenic contexts.

The functioning of Santa Giulia lagoon proved to be an excellent example of the impact of human interventions and the importance of the connection with the sea (Figure 9). The sea outlet tends to close naturally due to the accumulation of *Posidonia oceanica* litter. The re-establishment of the connection with the sea seldom takes place naturally. This has already led to some strong evaporation during summer and partial drying of some areas of the basin in the past. At present, most of the time business owners on the adjacent beach privately undertake the artificial opening of the sea channel, without official regulation, in order to maintain good water circulation and prevent unpleasant odours (Figure 9). In 2020, in addition to low rainfall events, tourism activities were negatively impacted due to the Covid-19 health crisis (lockdowns,

restrictions for travel, etc.), with a record loss of 31% of travellers compared to the mean over the 1999-2021 period (DREAL Corse). Artificial openings of the sea outlet were not carried out as often as usual, so that it stayed obstructed by litter most of the time, ultimately leading to the almost complete drying-up of the water basin during summer (Figure 8 and Figure 9). This had catastrophic consequences for aquatic biotic community, by causing fish mortality, phytoplankton biomass development but depletion of photosynthetic efficiency, as well as a complete loss of angiosperm meadows and the development of filamentous macroalgal communities (Figure 9). Loss of connectivity with the sea has already been associated with the increase of eutrophication and phytoplankton biomass in lagoon environment, and our study case confirms the same pattern for small sized lagoons (Pereira Coutinho et al., 2012; Jones et al., 2018). Moreover, high phytoplankton biomass was negatively correlated with diversity, meaning the community was frequently dominated by one or a few taxa and blooms were recurrent. Blooms were alternatively due to diatoms and dinoflagellates, but from autumn 2020 diversity increased, while biomass decreased. This could be a consequence of the drought episode that occurred during summer 2020; in fact, it has already been observed that desiccation can boost phytoplankton diversity (Rojo et al., 2012). Dryness increases eutrophication by releasing nutrients and can structure diversity by favouring the development of stress-tolerant species. In the short term, temporary isolation and the appearance of disconnected sites can promote heterogeneity and consequently enhance species richness (Angeler et al., 2010; Rojo et al., 2012). Extreme situations inducing stress could promote the development of potentially harmful species. For instance, the dinoflagellate *Prorocentrum cordatum*, and *Prorocentrum* spp. in general, is a stress-tolerant potentially harmful taxon and is especially resistant towards high salinity (Sahraoui et al., 2013). This species appeared at Santa Giulia lagoon in autumn, after the summer salinity stress, and *Prorocentrum* sp. was occasionally present at high densities in the lagoon over the sampling period and occasionally blooming. The majority of taxa recorded in Santa Giulia lagoon, such as *Amphora* sp., *Nitzschia* spp. or *Cocconeis* sp., are typically tychoplanktonic, meaning they are generally found attached to substrate and only occasionally in the water column, following some physical process. This is linked to the shallowness of the basin (Carić et al., 2011), which could also explain the high turbidity found at this site (Figure 9): the water body is often exposed to wind so due to its shallowness sediment is easily resuspended, the water column is well mixed and may result in an increase in Chl *a* concentration with the importation of benthic species (Péquin et al., 2017; Trombetta et al., 2021).

Balistra lagoon is an example of the need to consider lagoon functioning together with the watershed influence. Despite its supposedly pristine state, it is in this lagoon

that we found the highest values of NO_3^- and NO_2^- . Upstream from the lagoon, we identified two major anthropogenic pollution sources, probably linked to inefficient sanitation systems of housing (Figure 9). In any case, these high nutrient concentrations do not seem to impact the primary producers compartment, as no particular effects on phytoplankton communities were highlighted and the lagoon is characterised by well-developed *Zostera* sp. and *Ruppia cirrhosa* meadows (Figure 9) (Pergent-Martini et al., 1997; personal observations). Probably, the dynamics of the connection of the lagoon with the sea play an important role in diluting nutrients and suspended matter in the lagoon by enhancing water circulation and hence mitigating their effect on the biotic community (Hyman & Stephens, 2020). This phenomenon was already observed in different Intermittently Closed and Opened Lagoons and Lakes (ICOLLs), where nitrogen decrease was associated with water exchanges with the adjacent marine environment (Schallenberg et al., 2010b). In fact, in Balistra lagoon the sea channel outlet was constantly opened during the study period, indicating a stable connection with the sea (Figure 8). Overall, Balistra lagoon fits well with the characteristics of an oligotrophic lagoon established in the trophic classification of aquatic ecosystems, with low Chl *a* concentration, never exceeding $3.5 \mu\text{g L}^{-1}$ (Smith et al., 1999; Smith, 2003). As is typical for oligotrophic Mediterranean lagoons, in Balistra lagoon the picoplankton contribution, especially that of PE-cyan, is important and primary producers include well-developed angiosperm meadows (Bec et al., 2011). This, together with the overall dominance of diatoms in the microphytoplankton compartment and the good photosynthetic efficiency of the community, indicates a global good status of the lagoon (Smayda, 1997a; Pernet et al., 2012; Garrido et al., 2013b). In general, low microphytoplankton abundances were found but summer blooms of *Chaetoceros* spp. occurred. This chain-forming diatom is fundamental to sustain production and it is often dominant in other oligotrophic lagoons such as the French Ayrolle lagoon (Leruste et al., 2019). Nevertheless, some potentially harmful dinoflagellate taxa were sometimes present or even dominant, such as *Kryptoperidinium foliaceum* and *Prorocentrum micans* (Figure 9). Both these species are highly tolerant and *Kryptoperidinium* sp. in particular can bloom under very different environmental conditions, ranging from almost freshwater to hypersaline, even at the same site (Satta, 2020). Despite the overall good status of the lagoon, potentially harmful species are present and their development can be boosted by nutrient pollution.

Overall, despite their comparable size, the functioning of lagoons thus proved to be different, with some shared trends nevertheless. For all three lagoons, nutrient contexts and molar ratios are consistent with typical Mediterranean lagoon conditions described by Souchu et al. (2010); DIP is consistently the most limiting factor, silicates limitation was never observed and DIN limitation sometimes occurred in summer season. We have

described the current state of the three case studies lagoons, which, to date, seems to be low-impacted. However, if nothing is done, threats highlighted during the study may become cause for concern. Regarding the phytoplankton, diatoms were not correlated to the diversity index, while dinoflagellates showed an inverse relationship with Shannon's Diversity Index, at least for Arasu and Santa Giulia lagoon. Hence, the dominance of dinoflagellates tends to homogenise the community, with high abundances or blooms of one or a few species. Since dinoflagellates and especially potentially harmful species have often been associated with anthropogenic pollution and temperature rise linked to climate change (Xiao et al., 2018; Trombetta et al., 2019), we could expect a potential degradation of these small lagoons in the future (Smayda, 1997a; Fischer et al., 2020; Zingone et al., 2021). Finally, based on the lagoons' functioning descriptions provided by this study, Arasu and Santa Giulia lagoons are prone to be more susceptible to local (urbanisation) and global (climate change) changes.

4.2 Small lagoons in the larger-scale context and management perspectives

Through the realisation of a first inventory and analysis of the regional coastal lagoons, we demonstrated the importance of Corsica Island as an example of coastal lagoons and especially those of small surface area. In the Mediterranean basin, only 50 lagoons have been the focus of scientific publications and many are exploited for human activities (Pérez-Ruzafa et al., 2011a). However, information on small-sized lagoons at Mediterranean scale is lacking, despite the increasing demand from managers for knowledge. Small coastal lagoons not only provide numerous essential ecosystems services, but can also be considered sentinels for change, climate change or human interventions, due to their rapid response to disturbance. Yet this reactivity makes them more vulnerable to growing pressures and prone to more rapid disappearance, hence arising the need for proper management and conservation of these ecosystems (Doughty et al., 2019).

The case studies presented in this work demonstrate that local details are hugely important. This diversity is also an advantage: small lagoons constitute a mosaic of habitats, which promotes biodiversity and potentially constitutes a protection against global change by ensuring a variety of responses of these systems (Downing, 2010). The local diversity, however, makes it difficult to deduce larger-scale processes for these small lagoons. Nevertheless, the great advantage is that the chosen study sites represent different conditions both in terms of hydrogeomorphology and past and current anthropogenic impact. This makes them very good examples to define similarities or dissimilarities in their functioning under different scenarios. This diversity can then

reflect ecological conditions potentially present elsewhere. So, through the three different cases proposed in our study, we were able to identify general elements that are essential for the conservation and management of these small systems, in the wide range of ecological conditions that they can offer.

First, we have demonstrated that investigations on the watershed constitute a vital approach for the study of overall system dynamics of small lagoons and the interactions with adjacent systems. Surface and groundwater samples and land use analyses for the characterisation of the watershed are not systematically carried out for lagoon studies (e.g. Tuncel et al., 2007; Camacho et al., 2012). However, in order to plan an integrative management, these elements cannot be set aside and investigations on water basins and watersheds should proceed in a parallel way, especially for these poorly-understood and reactive small lagoons. Fluxes, exchanges and dependence with groundwater and different markers of anthropogenic pressures should be investigated further. The watershed dynamics are fundamental to understand the functioning of lagoons and to detect potential sources of pollution linked to human exploitation in the surrounding areas (Vystavna et al., 2017; Erostate et al., 2018). Also, a focus on seasonality is important for future studies. In fact, we highlighted high tourism pressure at local scale. This is not surprising since at regional level the population in summer systematically doubles (at least) the resident population since decades: for instance, in 2021 the Island hosted 371 000 tourists, over a population of 346 610 residents (DREAL Corse; ©Insee, <https://www.insee.fr>). This suggests that during summer the lagoons are probably subjected to higher nutrient inputs and hydric stress, due to increased water demand for usages (Orsoni, 2001; Collos et al., 2003). Hence, this justifies the need of attention towards seasonal dynamics for future research.

Secondly, connection with the marine environment is also a crucial point in the small lagoons' functioning and it is essential to take it into account for effective management (Schallenberg et al., 2010b; Biggs et al., 2015; Jones et al., 2018). With the progression of climate change, since rainfall events are expected to become less frequent and more intense, these reactive small shallow lagoons may then increasingly experience confinement or isolation. In turn, this can lead to frequent episodes of drought due to evaporation and have cascade effects at different trophic levels, such as changes in the phytoplankton community and the emergence of potentially harmful stress-tolerant taxa, loss of angiosperms and fish mortality (Angeler et al., 2010; Rojo et al., 2012).

Thirdly, our study focused on a few biotic and abiotic parameters and especially phytoplankton communities for the biotic component. Despite phytoplankton being an excellent indicator of the ecosystem's status, we suggest that an ecosystem-based

approach should be taken into account for future studies, especially considering lagoons' connection to adjacent systems (Ligorini et al., 2022b). This ecosystem-based approach is becoming more and more widely applied, especially in unstable transitional ecosystems, and it would enable a better understanding of ecosystem functioning at multiple levels and help with management decisions (Walker et al., 2006; Hobbs et al., 2009; Biggs et al., 2015; García-Ayllón, 2017; De Wit et al., 2020). Figure 9 offers a preface to this approach, which is essential to answer managers' question regarding the status and functioning of these poorly-known small lagoons.

Additionally, these small systems should be considered as socio-ecosystems; one of the first stages to consider when planning management strategies is the assessment of ecosystem services provided by the ecosystem and their prioritisation, combining scientific and technical expertise with stakeholders' perceptions and demands in order to help with political decisions (De Wit et al., 2020). Ecological issues cannot be completely independent of social-economic ones: the prior establishment of a “desired state” can allow the centralisation of decisional power and the allocation of financial resources in an adapted management roadmap (De Wit et al., 2020). For example, Arasu and Santa Giulia lagoons are set in a high value context in terms of tourism, some business activities have developed on their borders, and they are thus subjected to a political demand for the preservation of these activities, which should therefore be taken into account in management decisions. An important issue then arises: is the good ecological status of lagoons an added value for seaside tourism activities? If so, it is of fundamental importance to create platforms or any kind of exchange tool or space in order to share the scientific knowledge acquired with the multiple actors involved, such as managers and stakeholders, and hence to encourage discussion and consensus towards a commonly established desired state (Maciejewski et al., 2016; De Wit et al., 2020; Pérez-Ruzafa et al., 2020; De Wit et al., 2021).

Moreover, small lagoons are not included in the WFD, so no regular scientific surveys are carried out in this context and no “good status” goal has been established, meaning the acquisition of scientific knowledge is difficult. Unprotected sites are more vulnerable to climate change and other threats (Leberger et al., 2020). All three lagoons in this study are subject to protection status (Natura 2000 sites), but the deployment of actual management plans and actions is still in its initial phase. Despite the accumulation of protection statuses and labels, the application of efficient management can be problematic due to complex property regimes (De Wit et al., 2021; OEC, 2022). The fragmentation of properties and their private status imply dispersed and disconnected management that can therefore prove difficult to implement or ineffective, as is the case notably for Balistra lagoon (Pérez-Ruzafa et al., 2020; De Wit et al., 2021).

Meanwhile, efforts already undertaken by some public institutions, such as the CdL, to acquire Corsican lagoons should be carried on to centralise ownership and management and guarantee the prevention of habitat destruction by the uncontrolled progression of urban and tourism development (De Wit et al., 2021). Arasu lagoon is under mixed ownership by multiple private and public owners. This entails difficulties in terms of management because it requires the coordination and mutual agreement of the numerous actors involved and the satisfaction of different political and ecological demands, making it difficult to prioritise the expertise of managers. In Santa Giulia lagoon, despite its centralised ownership, there are some difficulties, mostly linked to unauthorised management actions carried out independently by stakeholders. These actions are carried out outside the environmental management legal framework and have caused various problems, including the reduction of the surface area of the water basin.

Finally, given all these premises, there is a need for the development of appropriate tools to provide guidance for the management of these small systems. As we highlighted, unauthorised interventions should be prevented, since they can disrupt effective scientific and management programmes by altering the natural behaviour of the system, as it was the case for the small Koggala lagoon (Sri Lanka) (Gunaratne et al., 2011). Nevertheless, human intervention is not to be demonized and is often central for restoration purposes. For example, there is evidence that implementation of active restoration actions and artificial infrastructures can be used to control lagoon functioning, reduce confinement and rehabilitate hydrogeomorphological features in small lagoons (Gunaratne et al., 2011; Camacho et al., 2012). Deeply altered small lagoon, similar to Arasu lagoon, could be potential candidates for active restoration. To consider such interventions, management of sea channel openings or other actions, multi-factorial modelling can be a helpful tool to design potential scenarios and the reactions of ecosystems (e.g. GAMELag, Pete et al., 2020). Our work is hence a valuable contribution for the potential application of this kind of modelling on small-surface lagoons, since this requires a deep knowledge base of the studied systems and of their responses towards local and global change (Gunaratne et al., 2011; Jones et al., 2018; Doughty et al., 2019; Pérez-Ruzafa et al., 2019a; Teixeira & Solari, 2020). These models are an important tool to support discussions between the actors involved and hence achieve consensus on appropriate and well thought-out management plans and decisions.

A major challenge lies ahead for these small-sized lagoons: their importance is acknowledged, but proper management is still lacking and raises many questions. This study is an essential first step towards the understanding of the ecological functioning

of these small-sized lagoon ecosystems (Figure 9). It has provided the first inventory of Corsican lagoons and has enabled us to point out the importance of these systems at regional scale and in the Mediterranean area as a whole. Through the investigation of three case studies, it has provided useful elements for applications elsewhere at larger scale. This work demonstrates how complex, diverse and reactive these small lagoons are, making them not only perfect sentinels of global change, but also highly vulnerable. We have highlighted the need for promoting their conservation through the acquisition of fundamental knowledge in a connected and dynamic context, that will constitute a good tool for offering guidance for management, especially within a challenging perspective of climate change and increasing anthropogenic threats.

Chapitre



IV



CHAPITRE IV

RESPONSE OF PHYTOPLANKTON COMMUNITIES TO VARIATION IN SALINITY IN A SMALL MEDITERRANEAN COASTAL LAGOON: FUTURE MANAGEMENT AND FORESEE CLIMATE CHANGE CONSEQUENCES

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CONTEXTE GÉNÉRAL ET RÉSUMÉ

La région méditerranéenne est soumise à des pressions anthropiques directes croissantes et est considérée comme un *hotspot* de changement climatique.

Les lagunes côtières sont particulièrement vulnérables face à ces pressions et risquent de disparaître. Afin de développer des stratégies adaptées à ces écosystèmes et d'en garantir la persistance dans le futur, il est important d'en évaluer les potentielles réponses aux changements locaux et globaux.

L'importance de la salinité comme facteur structurant les communautés phytoplanctoniques est reconnue, toutefois, son rôle sous le cadre du changement climatique est peu connu.

Ce travail se base sur l'hypothèse selon laquelle des variations de salinité imposées par le changement climatique et/ou des actions de gestion peuvent bouleverser les communautés phytoplanctoniques des lagunes côtières méditerranéennes.

Afin de tester cette hypothèse, deux expérimentations en microcosmes ont été mises en place, pour une durée de cinq jours chacune, sur des communautés phytoplanctoniques naturelles, issues de la lagune de Santa Giulia, une lagune de petite surface située en Corse-du-Sud.

Les deux expérimentations ont eu lieu à deux saisons différentes : l'été et l'automne, avec l'objectif de mimer de différents scénarios plausibles d'évènements extrêmes dans un cadre de changement climatique, i.e. la sécheresse et forte évaporation estivale et un phénomène de *flash flood* automnale.

Pendant ces deux expérimentations, les assemblages ont été soumis à trois niveaux croissants (jusqu'à +69 %) et décroissants (jusqu'à -50 %) de salinité afin de reproduire de différents niveaux d'évaporation et de crue, respectivement.

Les résultats indiquent qu'en condition de sursalure la biomasse était inhibée et la composition de la communauté modifiée, suivant le gradient de salinité croissant. La dessalure, au contraire, a eu un effet moins marqué, limité à une favorisation de l'abondance microphytoplanctonique totale et la diminution de diversité au niveau de désalinisation maximale. Pour les deux expérimentations, et en condition de dessalure en particulier, l'émergence d'espèces initialement rares a été observée. L'augmentation de salinité a provoqué une réduction de l'activité photosynthétique, indiquant une dégradation de l'état de santé de la communauté phytoplanctonique, tandis qu'aucun effet sur ce paramètre a été mis en évidence en condition de dessalure.

1. INTRODUCTION

The Mediterranean region is a hotspot of biodiversity but presents a millennial anthropogenic history. Its coasts host strong and constantly increasing urbanization and are hence subjected to unceasing anthropogenic pressures (Aurelle et al., 2022). Moreover, it is universally considered a hotspot for future climate change in current projections (MedECC, 2020; Cos et al., 2022).

Coastal lagoons are transitional systems characterized by strong physico-chemical gradients and instable nature which make them particularly vulnerable to growing pressures (MWO, 2018; Chacón Abarca et al., 2021). Small lagoons are even more threatened in this changing context since they have low mitigation potential due to their small surfaces and elevated perimeter/area ratio. They are also understudied, as international protection norms and scientific surveys usually focus on larger lagoons, which attract financial interest due to their usages and economic importance. The high reactivity of these small ecosystems makes them fragile towards disturbance but also excellent sentinels for change. Due to their vulnerability, it is essential to understand their functioning and anticipate potential responses of their communities to current and forthcoming disturbances, in order to promote lagoons' conservation and ultimately avoid the loss of ecosystem services they provide.

Phytoplankton communities play a fundamental role in biogeochemical cycles and functioning of lagoon ecosystems, where they are efficient consumers of nutrient inputs and fundamental elements for primary production and energy transfer. In general, phytoplankton communities react rapidly to any environmental changes and disturbances, and any modifications at phytoplankton level can cause cascade effects on higher trophic levels (Cloern, 1999; Loureiro et al., 2006; Armi et al., 2010; Goberville et al., 2010). Hence, phytoplankton is universally considered a relevant indicator for aquatic ecosystems status and functioning (Birk et al., 2012). The structure and dynamics of phytoplankton communities are influenced by multiple factors, mainly temperature, light, salinity, turbulence and nutrients availability. Despite the common recognition of the role of salinity as a primary influence on phytoplankton community structuring, its effects under global change are still poorly understood compared to temperature and nutrients (Dube et al., 2010; Pulina et al., 2012). Some mesocosm or microcosm studies have been already performed to evaluate phytoplankton response to salinity variations, but they mostly regarded marine environment or species (Stefanidou et al., 2018) or brackish systems outside the Mediterranean region (Greenwald & Hurlbert, 1993; Pilkaitytė et al., 2004). More frequently, studies of this kind focus on temperature variations (Pulina et al., 2020) or they have been carried out in indoor laboratories

(Barnes & Wurtsbaugh, 2015). Some studies in different aquatic environments already revealed changes in phytoplankton communities linked to salinity variations: increased salinities often cause a loss in species richness and decrease in biomass or alternatively abundance increase (Schallenberg et al., 2010a; D'ors et al., 2016), while desalinization has been found to mostly impact growth rates and photosynthetic activity (D'ors et al., 2016). Also, the salinity tested remained in the range of usually encountered variation in coastal ecosystems (i.e., 0.2-35). Under growing salinity gradients, changes in community composition seem to converge to the promotion of rare species, resisting to stress and taking the upper hand when dominant ones are inhibited (Flöder et al., 2010). Despite the fact that coastal assemblages and species adapted to transitional environments are considered more resistant to environmental changes and especially strong salinity variations, phytoplankton community changes have already been observed in highly instable transitional environments, like Intermittently Closed and Open Lakes and Lagoons (ICOLLs) (Flöder et al., 2010; Barnes & Wurtsbaugh, 2015). Nevertheless, responses detected are extremely variable, due to the local intrinsic variability of these systems, the salinity values at the beginning of experiments or observations, and of their local specificities in terms of functioning (Schallenberg et al., 2010a; Hernando et al., 2015; Nche-Fambo et al., 2015; Barroso et al., 2018; Hernando et al., 2020).

Salinity gradients and fluctuations in coastal lagoons are driven by connection to the sea through sea outlets and freshwater inputs from their watersheds and rainfall. This implies any artificial interventions, notably management actions on sea outlets and channels, which are commonly carried out in lagoon environment, can influence salinity variations. Furthermore, during summer, high temperatures generate strong evaporation, which results in increased salinity and sometimes drying-up of lagoons, depending on their connection to adjacent hydrosystems. With climate change progression, according to projections for the Mediterranean area, summer temperatures and drought are predicted to increase, thus exacerbating the intensity and frequency of these phenomena (MedECC, 2020; Cos et al., 2022). At the same time, projections also predict an increase in magnitude and frequency of flash flood events, particularly during autumn season (MedECC, 2020). These events provoke sudden massive freshwater inputs into lagoons, thus varying the salinity gradients in an abrupt way, and are already known to impact biotic communities in lagoon environment (Pecqueur et al., 2011). These events can thus become more and more frequent in the near future, hence subjecting lagoons to higher disturbance and frequent sudden salinity variations. Small Mediterranean lagoons are important in terms of number and ecosystem services provided over the Mediterranean basin, but they are also extremely vulnerable towards these local and global changes, in relation to their location and small surface. There is a

general need for proactive management strategies, so, it is particularly important to foresee potential responses of these systems to possible future scenarios, in order to measure impacts on biodiversity and ecosystem functions and to help the development of adapted management strategies in a changing context (Chapman, 2012; Pérez-Ruzafa et al., 2019b; Taylor et al., 2021).

The main objective of this study is to evaluate experimentally the responses of lagoon phytoplankton communities to sudden salinity variations. For this purpose, we carried out two 5-days experiments, during which natural phytoplankton communities from the small coastal lagoon of Santa Giulia, in the South of Corsica Island (Mediterranean Sea), were exposed to strong sudden salinity variations. The two experiments were performed at different seasons in order to mimic potential future scenarios of global change. During the first experiment, performed in summer, phytoplankton community was exposed to increasing salinity gradient, representing potential drought conditions and salinization due to strong evaporation. During the second experiment, performed in autumn, phytoplankton community was subjected to a decreasing salinity gradient, in order to mimic flash flood event or in general sudden strong freshwater inputs from extreme rainfall. Three questions are addressed: i) will the lagoon phytoplankton community structure and functioning be impacted by the increasing and decreasing salinity stress? ii) Will initial dominant taxa maintain their dominance under increasing salinity stress and what is the importance of compensatory growth of rare species? iii) What are the perspectives about the ecological functioning of these ecosystems under predicted implications of climate change and what recommendations can be made for their future management?

2. MATERIALS AND METHODS

2.1 Study site

The Santa Giulia lagoon is a small shallow lagoon located in the south-eastern coast of Corsica Island (41°31'32" N, 09°16'12" E; max. depth = 1.5 m, mean depth = 0.3 m; Figure 1) and it extends for 23 ha on a North-South axis. Freshwater inputs are provided by a 15.5 km² watershed, from few streams and groundwater from the associated alluvial aquifer, mainly at the southern end of the basin. Exchanges with the sea take place in the south-eastern part, through a small sea channel (Figure 1). The northern part of the basin is more confined, without direct exchange with the sea nor important freshwater inputs (Figure 1). The lagoon is property of the *Conservatoire du Littoral* (CdL) and managed by the Environmental Agency of Corsica (OEC) under its protection status (SAC as N2000 site, Habitats Directive). The lagoon is highly impacted by past and current human

activities, and it is subjected to strong tourism pressure during summer. Recently, its management encountered difficulties, as users of the beach often carry out unauthorized interventions to open the sea channel when obstructed by sand and litter accumulation, in order to prevent unpleasant odors by maintaining water circulation. The isolation from adjacent marine environment also caused a drying-up event in summer 2020 due to strong evaporation, with salinity values up to 125. The lagoon hosts a small artisanal fishing activity and cattle farming takes place in the south-western area of its watershed. The lagoon is subjected to typical Mediterranean climate, generally characterized by a three-month dry and hot summer season, from June to August, and two rainy periods, in spring and autumn. This configuration is evident from analyses of meteorological conditions over the standard reference period 1991-2020 established for France (*WMO-No. 1203 © World Meteorological Organization, 2017*).

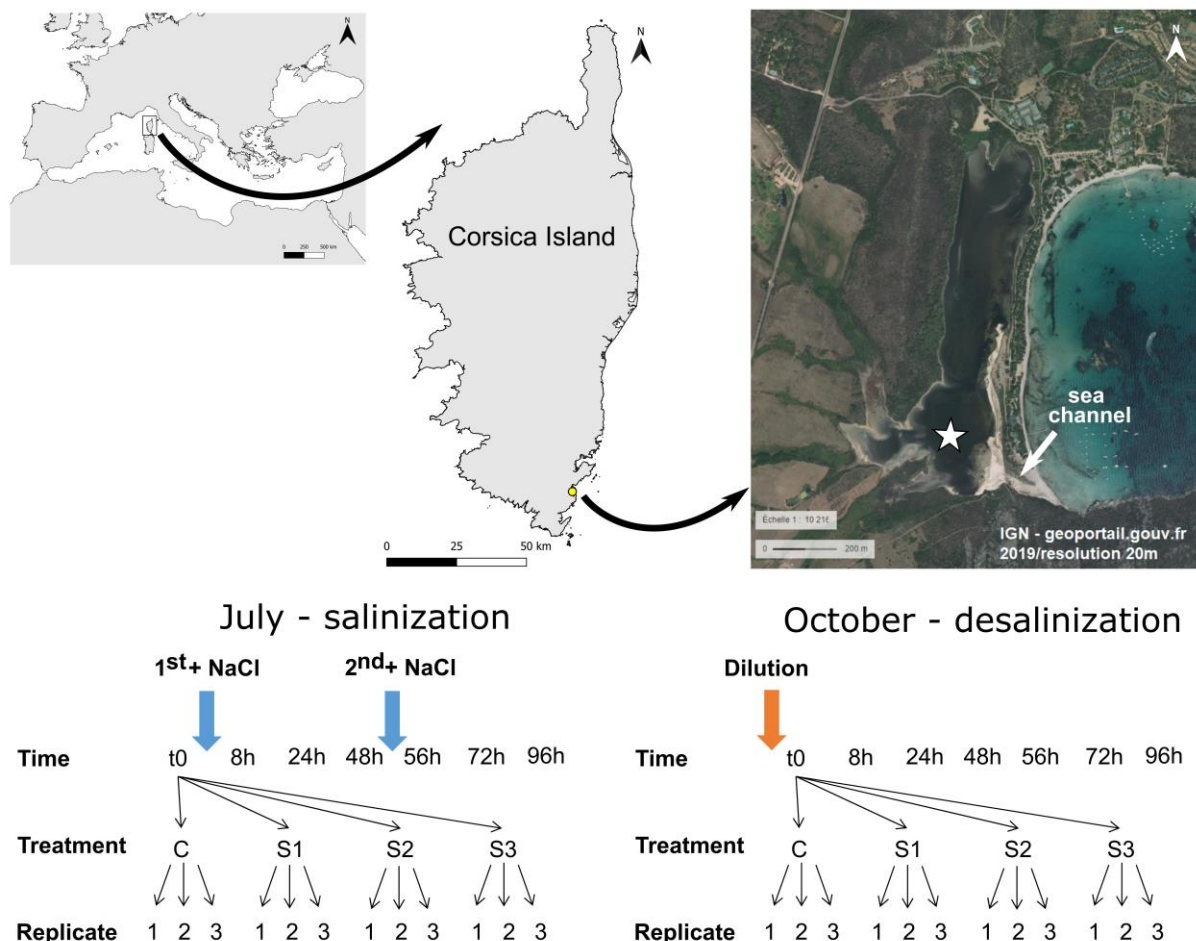


Figure 1 Sampling site location. Exact sampling point is represented by a white star. In the bottom panel, schematic description of experimental design is reported for both experiments.

2.2 *Microcosm experiments*

Two microcosm experiments were carried out in 2021 on phytoplankton communities collected in Santa Giulia lagoon. The first experiment consisted in the exposure of communities to increasing salinity gradient and was conducted in summer, from the 7th to the 11th of July, while the second one consisted in exposure to different desalinization levels and was performed in autumn, from the 10th to the 14th of October. For both experiments, water samples were collected at the sampling station, located in the southern part of the basin (Figure 1). Meteorological conditions on the days preceding sampling were normal for both seasons, with in particular 2 mm cumulative rainfall over the week preceding the October sample and no recent rain during the three days before sampling (14.20 mm cumulative rainfall since the 1st of September until the sampling day; Météo-France data (not shown) - La Chiappa (41°35'41" N, 9°21'47" E) weather station). 40 L of lagoon water were immediately filtered on 200 µm mesh sieve in order to remove debris and mesograzers (Lafabrie et al., 2013; Pulina et al., 2020; Stefanidou et al., 2018), and stocked in a polypropylene container for transport within two hours until the experiment place. At both seasons, the experimental setup was realized in an isolated 600 L plastic tank at the UAR Stella Mare laboratory (42°37'1.5" N, 9°28'48.6" E), installed outdoors in order to provide natural light and temperature fluctuations. Water temperature in the tank was monitored all along of the experiments through hourly measurements by HOBO® temperature probes.

Twelve microcosms were used for each experiment, with three replicates for each level of the treatment (S₁, S₂, S₃) and control (C) (Figure 1). For the salinization experiment, we added salt in two successive steps, in order to minimize osmotic shock and to mimic a gradual evaporation. On the other hand, for the desalinization experiment we applied the dilution in one step, in order to mimic a strong and sudden freshwater input, like in a flash flood event. Each microcosm consisted in a 3.5 L glass Schott-Duran bottle filled at 80% with water lagoon (20% air), in order to maintain the systems closer to natural condition (de la Broise & Palenik, 2007; Lafabrie et al., 2013). For both experiments, microcosms were nutrient-enriched and incubated around 20 cm deep in the tank, in order to mimic sub-surface condition of the lagoon. Samples were collected at the beginning of the experiment (to, just after filling and addition of nutrients) and then at 8h, 24h, 48h, 56h, 72h and 96h from the beginning of incubation (Figure 1). The 8h and 56h intermediate samplings were chosen in order to evaluate potential responses in short-time span (8h) after the application of salinization stress (Lafabrie et al., 2013) and then, the same sampling design was kept for the two experiments. After each sampling, microcosms were randomly redistributed in the tank in order to avoid any bias linked to position. Salinity, temperature and dissolved oxygen were measured at each sampling time. Nutrients analyses were performed before the setup in the collected lagoon water,

considered representative of the initial *in situ* water quality, and in the microcosms at to, 48h and 96h on 60 mL water samples filtered on Whatman GF/F filters (47 mm, 0.7 μm porosity) and further stored at -20°C until analyses. Ammonium (NH_4^+) concentrations were determined through fluorescence method (Holmes et al., 1999) and nitrite (NO_2^-), nitrate (NO_3^-), dissolved inorganic phosphorus (DIP) and silicates concentrations by colorimetric method (Aminot & K erouel, 2007). Dissolved Inorganic Nitrogen (DIN) was calculated as the sum of NH_4^+ , NO_2^- and NO_3^- .

2.2.1 Microcosm setup for salinization experiment

For the summer experiment setup, each microcosm was filled with 2.8 L of filtered lagoon water (200 μm), immediately enriched by adding 1.4 μmol of NH_4Cl . The choice of N form to be added was based on Leruste et al. (2021) and the concentration was calculated in order to double the initial theoretical concentration *in situ*, thus obtaining non-limiting conditions and equivalent starting concentrations for all the microcosms. After to samples, a first salinization was applied, by adding NaCl to treatment microcosms, according to level (Table 1, Figure 1). Then, after 48h, a second salinization was applied again following the same procedure (Table 1, Figure 1). The initial salinity *in situ* was of 43, so the salinization procedure resulted in final salinization of 53 for S₁, 63 for S₂, and 73 for S₃ (Table 1).

Table 1 Description of experimental setup for the salinity levels of the two experiments: salinization, with two consecutive salt adds (after to and after 48h samplings), and desalination, with one unique dilution at the beginning of the experiment.

Treatment	July - Salinization					October - Desalination		
	Initial salinity <i>in situ</i>	First salinization (% of starting salinity)	Salinity after first salinization	Second salinization (% of starting salinity)	Salinity after second salinization (final salinity)	Initial salinity <i>in situ</i>	Desalination (% of starting salinity)	Salinity after desalination (final salinity)
C		+0%	43	+0%	43		-0%	40
S ₁	43	+12%	48	+23%	53	40	-17%	33
S ₂		+23%	53	+46%	63		-33%	26
S ₃		+35%	58	+69%	73		-50%	20

2.2.2 Microcosm setup for desalination experiment

For the autumn experiment, each microcosm was filled with 1.4 L of filtered water lagoon (200 μm) plus a proportion of distilled water and/or lagoon water filtered on 0.2 μm , in order to obtain the right salinity level according to treatment but avoid different dilutions of phytoplankton community and nutrients concentrations between treatments. Final volumes were of 2.8 L. The initial salinity *in situ* was of 40, hence desalination procedure produced final desalination of 33 for S₁, 26 for S₂, and 20 for

S₃ (Table 1). N enrichment was supplied under the forms of NH₄⁺ and NO₃⁻, according to Leruste et al. (2021), and PO₄³⁻ was added too in order to avoid strong N:P ratio unbalance. Nutriments additions were calculated in order to double the initial theoretical concentrations. Assuming a null nutrient input from the addition of distilled water, the final quantity added was calculated related to the initial volume of lagoon water present in each microcosm in order to obtain an equivalent final nutrient concentration between all microcosms at the start of the experiment, regardless of the treatment level.

2.3 *Phytoplankton community*

The concentration of chlorophyll *a* (Chl *a*) was considered a proxy for phytoplankton biomass and measured at to, 48h and 96h. It was determined through spectrofluorometric analyses according to the method detailed in Neveux & Lantoiné (1993), on 100 mL water subsamples filtered on Whatman GF/F filters (25 mm, porosity 0.7 µm) and further stored at -20°C until analyses.

At each sampling time, the community structure was investigated through flow cytometry analyses on 1.8 mL of fixed water samples (mix final concentration 0.25% Glutaraldehyde and 0.01% Pluronic (Poloxamer 188)), further stocked at -80°C until analyses according to the method by Marie et al. (2014). Different ultraphytoplankton groups were discriminated based on their dimension and fluorescence: nanophytoplankton (NANO; > 2 µm) and, among the picophytoplankton (< 2 µm), autotrophic picoeukaryotes (PEUK) and picocyanobacteria (PCYAN), these latter obtained by cumulating *Synechococcus*-like picocyanobacteria (*Synecho*-like) and *Prochlorococcus*-like picocyanobacteria (*Prochloro*-like) populations identified. Lastly, heterotrophic bacteria population was also quantified.

In depth community composition was assessed through pigment analysis performed by High Pigment Liquid Chromatography (HPLC), at to, 48h and 96h, according to the method in Ras et al. (2008). To perform pigment extraction, water subsamples of 250 mL were filtered on Whatman GF/F filters (25 mm, porosity 0.7 µm) which were then stored at -80°C until analyses. To investigate pigment composition, marker pigments were selected to represent major taxonomic groups (Table 2). The composition of phytoplankton communities was also determined at each sampling through a multi-wavelength fluorometer FluoroProbe® (BBE Moldaenke, GmbH). The FluoroProbe® can discriminate four taxonomic groups: Bacillariophyceae/Dinophyceae, Cyanophyceae, Chlorophyta and Cryptophyceae. Measurements were taken on 25 mL of dark-adapted subsamples and values were obtained as the mean of continuous measurement during 60 s. Values were then corrected according to Garrido et al. (2019). To better characterize assemblages' changes, microphytoplankton (> 20 µm) community was investigated and

quantified through counting techniques. At the moment of initial water collection *in situ*, 50 L of surface water in the lagoon were filtered through an Apstein plankton net (20 µm mesh). 100 mL of concentrated sample were fixed with formaldehyde at 2.5% final concentration, in order to determine microphytoplankton community composition and abundances in the original natural environment at the starting point. At the end of the experiments (96h), 1 L water samples were collected from each microcosm and fixed with Lugol solution (4% final concentration) and stored in dark refrigerated chamber until analysis. The use of different fixatives was decided in order to balance advantages and disadvantages of each method, based on the availability of water volume, the conservation time desired and the toxicity of the products. All samples were then examined according to the adapted Utermöhl method (AFNOR, 2006; Utermöhl, 1958) with an inverted microscope (Olympus® CKX41). At least 400 cells were counted (estimation error within ± 10% limits) (Lund et al., 1958; Uehlinger, 1964) and identified at lowest possible taxonomic level with verification according to several books (Avancini et al., 2006; Hoppenrath et al., 2009; Horner, 2002; Sournia, 1986; Steidinger & Meave del Castillo, 2018; Thronsen, 1997) and databases (<http://www.marinespecies.org/>, <https://www.algaebase.org/>, databases available online). The Shannon's Diversity Index was calculated based on taxonomic units identified in the microphytoplankton communities.

Table 2 Marker pigments classification according to information seen in: 1. Claustre (1994); 2. Vidussi et al. (2001); 3. Leruste et al. (2016).

Pigment	Taxonomic group	Reference
Alloxanthin	Cryptophyta	1, 2, 3
Chlorophyll <i>b</i>	Chlorophyta and green flagellates	1, 2, 3
Divinyl Chlorophyll <i>a</i>	Prochlorophyta	2
Fucoxanthin	Bacillariophyceae	1, 2, 3
Lutein	Chlorophyta and Prasinophyta	3
Neoxanthin	Chlorophyta and Prasinophyta	3
Peridinin	Dinophyceae	1, 2, 3
Prasinoxanthin	Prasinophyta	3
Zeaxanthin	Cyanobacteria	1, 2, 3
19'-Butanoyloxyfucoxanthin	Chrysophyta	1
19'-Hexanoyloxyfucoxanthin	Prymnesiophyta	1

Finally, metabolism was evaluated through photosynthetic activity efficiency measurements, performed with a Pulse-Amplitude-Modulated fluorimeter (Phyto-PAM Plankton Analyser; Heinz Walz GmbH, Effeltrich, Germany). 30 mL water subsamples were collected at each sampling time in opaque flasks and dark-adapted for at least 30 minutes before analysis. Samples were kept in a cooler and analyzed within 3 hours from collection in order to respect recommended storage conditions for Phyto-PAM fluorometric analyses (Garrido et al., 2013a). The ratio F_v/F_m , maximum quantum yields

of Photosystem II (PSII), was used as a proxy of phytoplankton community's health (Garrido et al., 2013a) and the effective quantum yield (Φ_{PSII}) was used as a proxy for physiological state of the community and effective photosynthetic performance in the microcosms (Maxwell & Johnson, 2000).

2.4 *Statistical analysis*

All data analyses were performed through the statistical R software (RStudio Team, 2016; version 4.0.2) and same analyses were performed for each experiment separately. Differences between levels of treatment and along time of different variables were investigated through Mixed Analyses of Variance (Mixed ANOVAs). When necessary, data were previously $\log_{10}(x+1)$ or sqrt transformed to meet ANOVA conditions. In the case of failed achievement of normality assumption despite transformation, results were taken with caution and a more constraining level of significance ($p < 0.01$) was applied (Underwood, 1996). When significant effects of treatment, time or interaction were detected ($p < 0.05$ (or $p < 0.01$, if constrained)), pairwise post hoc tests were applied in order to examine differences. Changes in phytoplankton communities' composition were explored through HPLC pigment composition: reference pigments according to literature (Claustre, 1994; Leruste et al., 2016; Vidussi et al., 2001) were kept and evolution over time for Controls were investigated through Mixed ANOVAs. Afterwards, treatments were compared to Controls within each sampling time as percentage variations from respective control. Finally, microphytoplankton variables at 96h were analyzed through One-way ANOVA in order to compare differences in microphytoplankton composition and abundances between treatments at the end of the experiment. Significant effects of treatment ($p < 0.05$) were further investigated through Tukey's post hoc test.

3. RESULTS

3.1 *Physico-chemical parameters*

Salinization experiment: Water temperature in the tank varied from 24.3 to 32.2°C with a mean of 28.2°C. In the microcosms, water temperature stayed in the range between a minimum of 23.6°C and a maximum of 32.3°C (mean water temperature: 26.7°C). No significant differences between treatments were found, however significant time effect was detected (ANOVA $p < 0.001$, $F_{6,48} = 7850.49$, $\omega^2 = 1$). All sampling times differed from each other (pairwise test: $p < 0.001$ for all contrasts). Salinity varied across treatments according to treatment levels imposed by experimental design (Table 1). Dissolved oxygen saturation percentage followed the temperature variations, and a

significant effect of sampling time was detected (ANOVA $p < 0.001$, $F_{6,48} = 53.83$, $\omega^2 = 0.87$). Its values never fell below 83.8% with an overall mean of 96.2%. DIN and DIP concentrations were similar in all microcosms and no significant time or treatment effects were detected (overall mean [DIN] in μM : 7.61 ± 0.59 for C, 9.42 ± 1.55 for S₁, 8.27 ± 0.39 for S₂ and 8.40 ± 0.51 for S₃; overall mean [DIP] in μM : 0.08 ± 0.03 for C, 0.13 ± 0.04 for S₁, 0.10 ± 0.03 for S₂, 0.13 ± 0.04 for S₃). However, DIN/DIP ratio varied over time (ANOVA $p = 0.024$, $F_{2,14} = 6.84$, $\omega^2 = 0.49$) indicating a reduction in the ratio at 96h (pairwise test: to-48h contrast $p = 0.050$; 48h-96h contrast $p = 0.001$). For silicates, again no difference between treatment could be detected (overall mean in μM : 88.62 ± 29.54 for C, 85.82 ± 28.61 for S₁, 85.85 ± 28.62 for S₂ and 84.43 ± 28.14 for S₃) but a significant time-effect was found (ANOVA $p = 0.025$, $F_{2,14} = 6.48$, $\omega^2 = 0.48$), indicating a higher concentration at 96h compared to control (pairwise test: to-96h $p = 0.008$). Overall, a P limitation occurred but the molar nutrient ratios of *in situ* samples also revealed a P-limited situation, so the nutrient balance was not altered compared to that occurring in the natural environment (data not shown).

Desalinization experiment: Water temperature in the tank followed the circadian cycles and was in line with regional autumnal values. It never fell below 15.7°C and averaged at 17.9°C, with a maximum at 19.9°C. In the microcosms, no temperature differences between treatments were detected overall, while significant time-effect was identified (ANOVA $p < 0.001$, $F_{6,48} = 1\,222.25$, $\omega^2 = 0.99$). Salinity values were fixed for the different treatment levels according to the experimental design (Table 1). Oxygen percentage saturation varied with time, following temperature pattern and never falling below 90.6%, with an overall mean at 96.3%. An effect of time factor was detected (ANOVA $p < 0.001$, $F_{6,48} = 92.74$, $\omega^2 = 0.92$). DIN concentration was similar between treatments but significantly varied over time (overall mean in μM : 1.53 ± 0.65 for C, 1.62 ± 0.71 for S₁, 1.75 ± 0.78 for S₂ and 1.79 ± 0.78 for S₃; ANOVA $p < 0.001$, $F_{2,16} = 135.57$, $\omega^2 = 0.94$). DIP concentrations and the ratio DIN/DIP did not show any significant effect for treatment nor for time. However, silicates concentrations (overall mean in μM : 12.73 ± 1.62 for C, 12.60 ± 2.38 for S₁, 10.12 ± 1.28 for S₂ and 9.87 ± 2.05 for S₃), varied significantly among treatments (ANOVA $p = 0.010$, $F_{3,8} = 7.63$, $\omega^2 = 0.74$) and sampling times (ANOVA $p < 0.001$, $F_{2,16} = 49.97$, $\omega^2 = 0.86$). Pairwise post-hoc test indicated highest values at 48h from the beginning of the experiment (pairwise test: to-96h and 48h-96h contrast $p < 0.001$) and lowest concentration at strongest treatment compared to the others (pairwise test: main contrasts C-S₃ $p = 0.012$ and S₁-S₃ $p = 0.033$). From the analysis on nutrients' molar ratios (data not shown), a slight P limitation occurred and a slight N limitation too over time, but the *in situ* samples also revealed a similar situation in field, indicating that natural nutrient balance was not altered.

3.2 *Phytoplankton biomass and small-sized phytoplankton structure*

Salinization experiment: Chl *a* concentrations varied from $0.77 \pm 0.07 \mu\text{g L}^{-1}$ at S₃ at the beginning of the experiment to $1.37 \pm 0.24 \mu\text{g L}^{-1}$ in control at 96h (Figure 2). Significant effects of both treatment (ANOVA $p = 0.003$, $F_{3,8} = 11.47$, $\omega^2 = 0.81$) and time (ANOVA $p = 0.008$, $F_{2,16} = 8.17$, $\omega^2 = 0.51$) were detected. An increase in time was identified (pairwise test: to-96h contrast $p = 0.019$; 48h-96h contrast $p = 0.052$), inversely following the treatment levels, with an overall significant difference between the control and S₃ treatments (pairwise test: C-S₃ contrast $p = 0.003$). As for small-sized phytoplankton structure, PCYAN densities increased only for Control, passing from $12134.2 \pm 492.1 \text{ cell mL}^{-1}$ at the beginning of the experiment to $14619.4 \pm 6353.2 \text{ cell mL}^{-1}$ at 96h, while they decreased slightly for all salinization treatments (Figure 3). PCYAN was entirely constituted by *Synecho*-like group. A significant effect of treatment and time interaction was identified (ANOVA $p < 0.001$, $F_{18,48} = 21.07$, $\omega^2 = 0.89$), with pairwise test confirming a significant decrease for all salinization treatments and a significant difference between Control and S₃ starting from 24h after the beginning of the experiment. PEUK evolution over the experiment showed high variability and no clear pattern (Figure 3). NANO group increased slightly for all treatments, up to $9996.3 \pm 3418.7 \text{ cell mL}^{-1}$ in C at 96h, except S₃, which did not show any temporal evolution (Figure 3). Significant effect of interaction indicated that S₃ showed significantly lower values than other treatments, starting from 48h (ANOVA $p = 0.008$, $F_{18,42} = 4.14$, $\omega^2 = 0.64$). On the other hand, heterotrophic bacteria showed a different trend (Figure 3): an effect of interaction was detected (ANOVA $p = 0.001$, $F_{18,48} = 6.50$, $\omega^2 = 0.71$), indicating that densities significantly decreased in all treatments except S₃, which showed significantly higher values than C starting from 24h from the beginning, according to pairwise test results. Significant differences between S₃ and S₂ were not detected after 24h, while S₁ was significantly lower than S₂ at 56h and 72h.

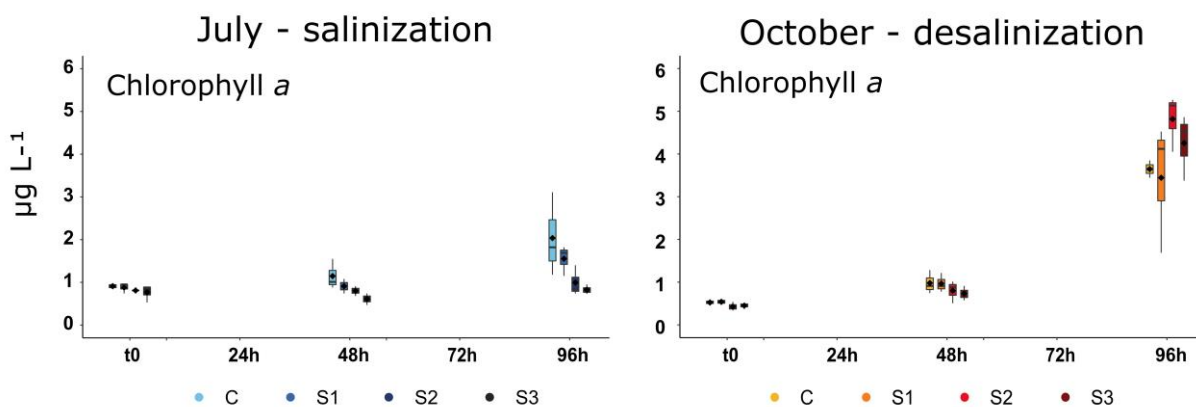


Figure 2 Biomass evolution over the experiments represented by concentrations of Chlorophyll *a* pigment ($\mu\text{g L}^{-1}$).

Desalinization experiment: Chl *a* concentrations significantly increased over time (ANOVA $p < 0.001$, $F_{2,16} = 220.65$, $\omega^2 = 0.97$; pairwise test: $p < 0.001$ for all contrasts), regardless of the treatment. They passed from an overall mean of $0.57 \pm 0.07 \mu\text{g L}^{-1}$ at the beginning of the experiment to a maximum of $4.82 \pm 0.22 \mu\text{g L}^{-1}$ in S2 at 96h (Figure 2). The structure of small-sized community changed over the experiment and showed some differences between treatments. PCYAN group was constituted of *Synecho*-like and *Prochloro*-like populations but dominated by the first one. A general significant loss of PCYAN over time was observed, passing from $27862.9 \pm 291.2 \text{ cell mL}^{-1}$ in the control at the beginning of the experiment to a minimum of $3912.5 \pm 104.0 \text{ cell mL}^{-1}$ in the control at 96h (Figure 3). PEUK group experienced large fluctuations over the experiment. For both PCYAN and PEUK a significant effect of interaction was found (PCYAN: ANOVA $p < 0.001$, $F_{18,48} = 14.54$, $\omega^2 = 0.85$; PEUK: ANOVA $p < 0.001$, $F_{18,48} = 81.89$, $\omega^2 = 0.97$), mainly indicating that C and S1 were significantly lower than S3 towards the end of the experiment, after 72h (Figure 3). NANO group increased slightly from 56h from the start, and globally following the desalinization gradient (Figure 3). A significant effect of interaction was detected (ANOVA $p = 0.004$, $F_{18,48} = 5.25$, $\omega^2 = 0.66$), indicating significantly stronger values in S2 compared to C and S1 at the end of the experiment (pairwise test at 96h: C-S2 contrast $p = 0.035$, S1-S2 contrast $p = 0.034$). Heterotrophic bacteria concentration ranged between $176075.4 \pm 5977.6 \text{ cell mL}^{-1}$ (C at 96h) and $675095.8 \pm 16230.9 \text{ cell mL}^{-1}$ (S2 at 56h) and showed a general slight decrease (Figure 3).

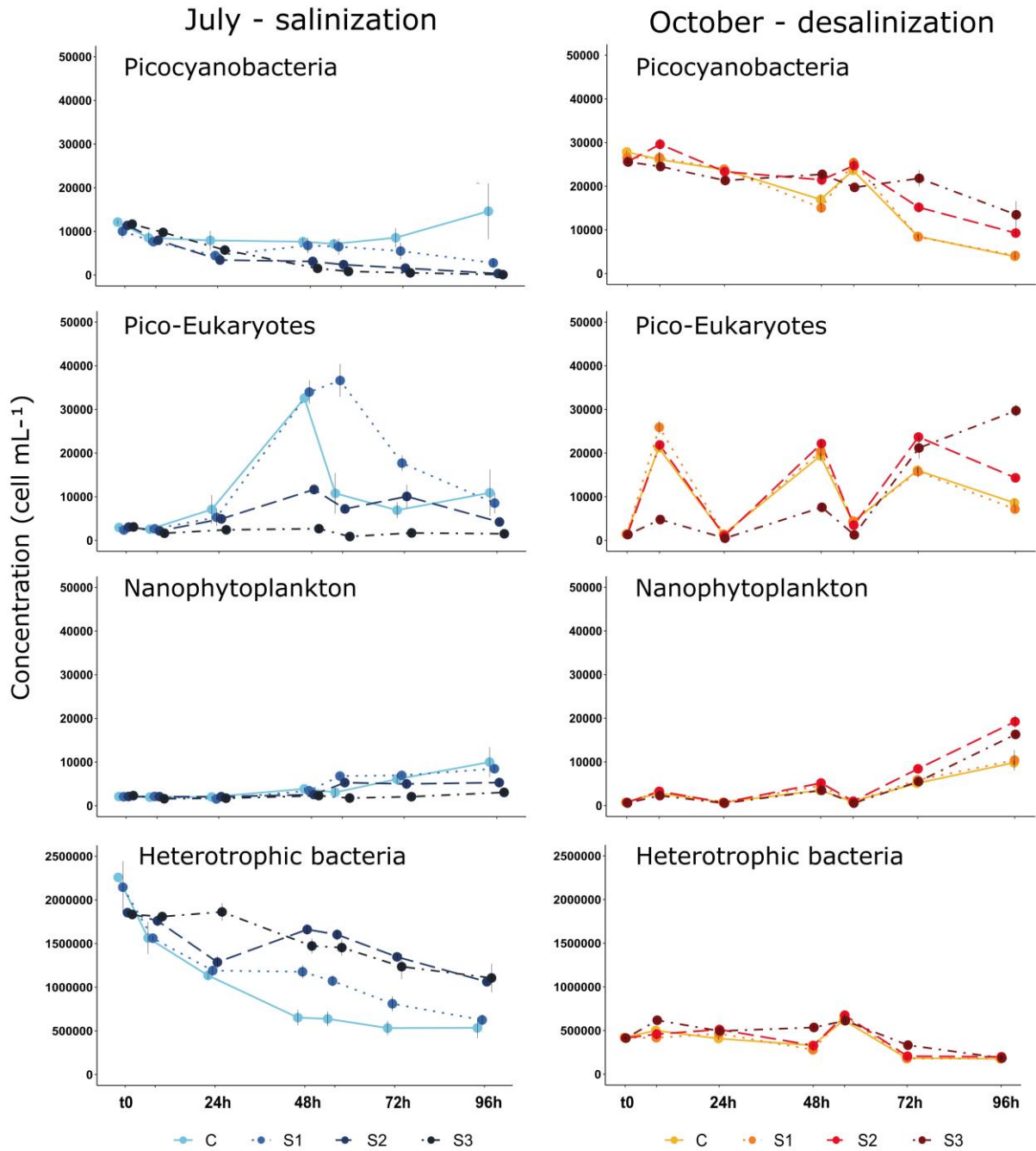


Figure 3 Evolution of ultraphytoplankton and heterotrophic bacteria populations identified over the 1026 two experiments through flow cytometry analyses.

3.3 Phytoplankton communities' composition by pigment analyses, fluorometry and microscopy

Salinization experiment: ANOVAs tests on Controls revealed the pigments concentrations did not vary significantly over time (Figure 4A), except for chlorophyll *b* (ANOVA $p = 0.009$, $F_{2,4} = 43.00$, $\omega^2 = 0.96$), 19'-butanoyloxyfucoxanthin (ANOVA $p = 0.049$, $F_{2,4} = 7.00$, $\omega^2 = 0.78$) and alloxanthin (ANOVA $p = 0.014$, $F_{2,4} = 22.75$, $\omega^2 = 0.92$).

Post-hoc pairwise tests revealed a decreasing trend for chlorophyll *b* and alloxanthin, passing from $0.08 \pm 0.01 \text{ mg m}^{-3}$ and $0.11 \pm 0.01 \text{ mg m}^{-3}$ at to respectively to $0.03 \pm 0.01 \text{ mg m}^{-3}$ and $0.02 \pm 0.00 \text{ mg m}^{-3}$ at 96h respectively, and a slight increase for 19'-butanoyloxyfucoxanthin from below detection limit to $0.01 \pm 0.00 \text{ mg m}^{-3}$ (Figure 4A). From comparison between treatments and corresponding controls, similar composition was confirmed at the beginning of the experiment (Figure 4B). Afterwards, fucoxanthin showed systematically negative percentage deviances of treatments compared to C (S₁: -29%, S₂: -59%, S₃: -66%, at 96h). Fluorometry data confirmed this pattern: Bacillariophyceae/Dinophyceae group ranged between $0.56 \pm 0.03 \text{ eq. } \mu\text{g Chl } a \text{ L}^{-1}$ and $1.26 \pm 0.18 \text{ eq. } \mu\text{g Chl } a \text{ L}^{-1}$ in C at 8h and 96h respectively, and significantly differed among treatments (ANOVA $p < 0.001$, $F_{3,8} = 20.03$, $\omega^2 = 0.88$), with Control values being higher than treatments, following the gradient (Figure 4C). Compared to C, 19'-butanoyloxyfucoxanthin and 19'-hexanoyloxyfucoxanthin were completely lost under salinization treatments, as well as peridinin (Figure 4B). A negative percentage deviation from C was detected for alloxanthin at 48h (S₁: -36%, S₂: -55%, S₃: -64%) and 96h (-29% for S₁, S₂ and S₃) in all treatments, indicating a stronger decrease of Cryptophyta under salinization (Figure 4B). Nevertheless, no Cryptophyceae were detected by fluorometry (Figure 4C). A similar trend could be detected for cyanobacteria, represented by zeaxanthin, which showed negative deviation from C of -35% and -47% in S₂ and S₃ respectively at 96h (Figure 4B). At the end of the experiment, prasinoxanthin percentage deviations were positive for S₁ (+100%) and S₂ (+67%) but negative for S₃ (-67%), as well as neoxanthin (S₁: +100%, S₂: +50%, S₃: -50%) and lutein (S₁: +80%, S₂: +20%, S₃: -40%) (Figure 4B). According to fluorometry data, Chlorophyta group showed an increasing tendency over time, except for S₂ and S₃, but also significantly lower values of S₃ compared to C and S₁ towards the end of the experiment, after 72h (Figure 4C).

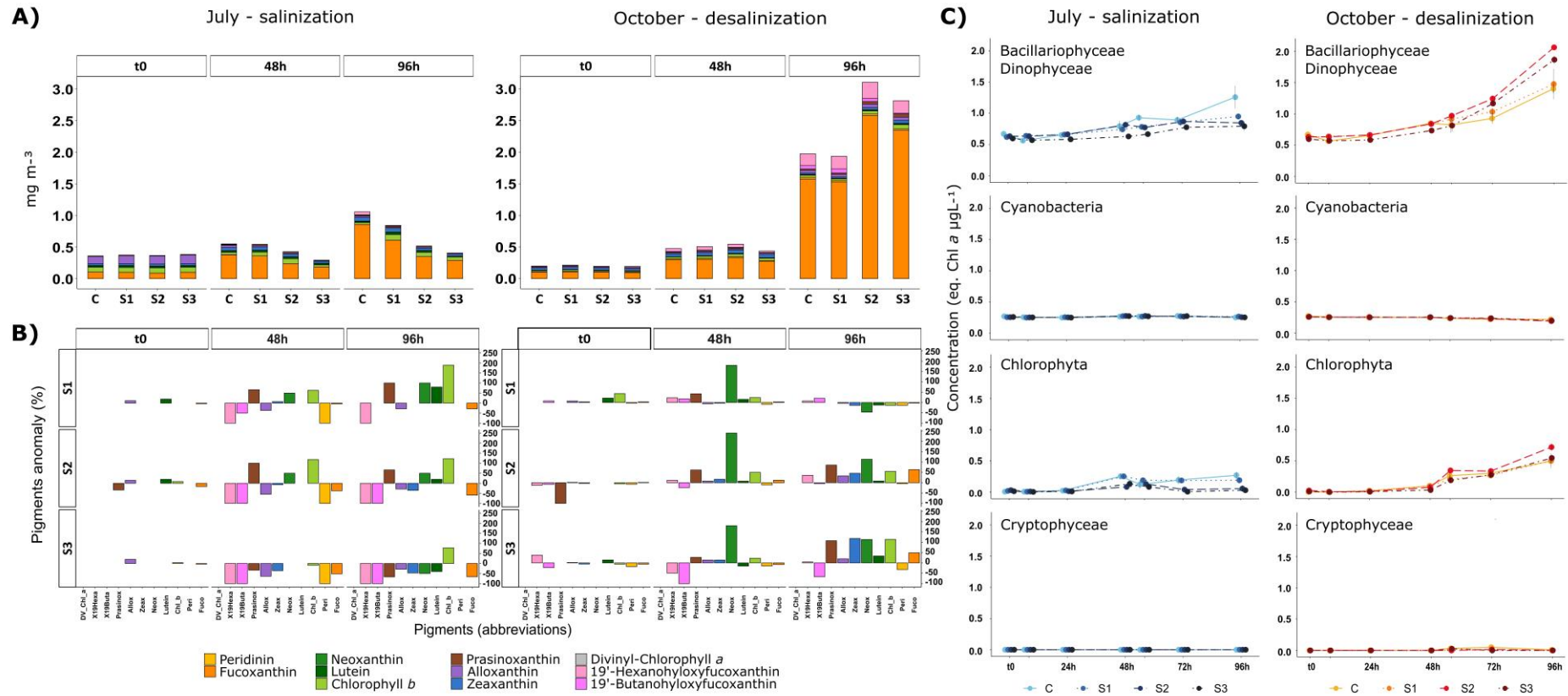


Figure 4 A) Concentration of selected marker pigments quantified through HPLC analyses over the three sampling times; B) evolution of community composition change expressed as percentage deviance of each pigment in each treatment to reference control at the same sampling time; C) evolution of major phytoplankton groups identified by fluorometry for the two experiments.

The *in situ* community resulted dominated by diatoms and dinoflagellates, with *Navicula* sp. being dominant at 31×10^3 cell L⁻¹ (Figure 5; Table 3). Chlorophyta of the genus *Pyramimonas* were also present and reached 18×10^3 cell L⁻¹ (Table 3). At the end of the experiment, total density significantly differed among treatments (ANOVA $p < 0.001$, $F_{3,8} = 28.71$, $\omega^2 = 0.87$), indicating lower abundances following the increasing salinity gradient (Figure 5). This was mainly due to diatoms development, which also differed among treatments according to salinity gradient (Figure 5; ANOVA $p = 0.002$, $F_{3,8} = 13.41$, $\omega^2 = 0.76$), and to the loss of Chlorophyta, which only persisted in Controls (Figure 5; ANOVA $p = 0.001$, $F_{3,8} = 16.85$, $\omega^2 = 0.80$). Small undetermined cells, undetected in field sample, largely developed during the experiment and especially in S₁ and S₂ low- and mid-salinity treatments (Figure 5; ANOVA $p < 0.001$, $F_{3,8} = 30.53$, $\omega^2 = 0.88$). Globally, *Navicula* sp., which was already dominant in field, developed in all treatments, even if reaching lower densities at higher salinities (Table 3). Some species which were rarer at the beginning developed well in the microcosms, like *Nitzschia* sp., still following the salinity gradient (Table 3), but some other species were completely lost, like some Prorocentrales and mostly the Chlorophyta *Pyramimonas* sp., which only persisted in Controls at a mean density of 22×10^3 cell L⁻¹ (Figure 5; Table 3). Overall, Shannon's Diversity Index did not show any significant difference between treatments, however, a tendency could be detected, where the strongest treatment (S₃) showed lower diversity than the others (Figure 5).

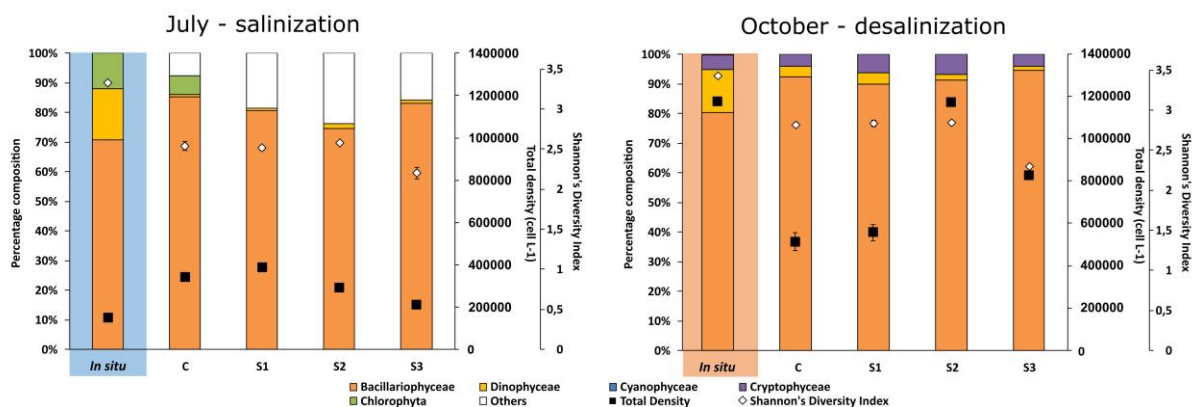


Figure 5 Communities compositions *in situ* (left of each graph) and at 96h obtained from optic microscopy observations. Composition is expressed as percentage contribution of major classes (scale on the left). Total cellular densities \pm SD are also reported and represented by black squares (first scale on the right), as well as Shannon's Diversity Index \pm SD, represented by white lozenges (second scale on the right).

Desalinization experiment: Analyses on phytoplankton composition indicated an evolution of the structure of communities over time and under different treatments (Figure 4A and Figure 4B). ANOVAs tests to detect potential evolutions of the pigments within control level of treatment identified a significant growth over time of the following pigments: peridinin (ANOVA $p = 0.001$, $F_{2,4} = 182.33$, $\omega^2 = 0.99$), fucoxanthin (ANOVA $p = 0.001$, $F_{2,4} = 968.79$, $\omega^2 = 0.99$), 19'-butanohydroxyfucoxanthin (ANOVA $p <$

0.001, $F_{2,4} = 969.53$, $\omega^2 = 0.99$), 19'-hexanohydroxyfucoxanthin (ANOVA $p < 0.001$, $F_{2,4} = 1449.20$, $\omega^2 = 0.99$), alloxanthin (ANOVA $p = 0.017$, $F_{2,4} = 49.07$, $\omega^2 = 0.96$) and prasinoxanthin (ANOVA $p = 0.021$, $F_{2,4} = 30.18$, $\omega^2 = 0.94$). Parallel to that, a significant decrease in zeaxanthin was found (ANOVA $p = 0.010$, $F_{2,4} = 49.19$, $\omega^2 = 0.96$). Diatoms were the group contributing most to growth, since fucoxanthin concentrations passed from $0.10 \pm 0.00 \text{ mg m}^{-3}$ to $1.58 \pm 0.04 \text{ mg m}^{-3}$ at the beginning and after 96h respectively in C, and reached up to $2.58 \pm 0.09 \text{ mg m}^{-3}$ at 96h in S2 (Figure 4A). Fucoxanthin percentage deviation from control at 96h was at + 64% and + 49% for S2 and S3 respectively (Figure 4B). These results were confirmed by fluorometry data, where Bacillariophyceae/Dinophyceae group largely dominated the community, reaching up to $2.06 \pm 0.01 \text{ eq. } \mu\text{g Chl } a \text{ L}^{-1}$ in S2 at 96h, and showed a significant increasing tendency (Figure 4C). The significant effect of interaction (ANOVA $p = 0.007$, $F_{18,48} = 4.58$, $\omega^2 = 0.63$) highlighted a difference among treatments towards the end of the experiment, with C values being lower than those of other treatments starting from 72h, according to pairwise test. The first level of treatment (S1) did not show particular pigments' percentage deviance from C, indicating a similar evolution of communities' compositions over the experiment (Figure 4B). On the other hand, S2 and S3 showed positive deviations from C at 96h for most of the pigments, such as prasinoxanthin (S2: + 85%, S3: + 107%), alloxanthin (S2: + 33%, S3: + 20%), zeaxanthin (S2: + 45%, S3: + 118%), neoxanthin (S2 and S3: + 113%), lutein (S2: + 8%, S3: + 33%) and chlorophyll *b* (S2: + 55%, S3: + 114%) (Figure 4B). Confirming the increase in pigments linked to green algae for S2 and S3, the fluorometry data highlighted significant higher values of Chlorophyta group in S2 compared to other treatments (Treatment: ANOVA $p = 0.034$, $F_{3,8} = 4.80$, $\omega^2 = 0.64$; Figure 4C).

Microphytoplankton communities' quantification revealed some changes in the community composition and diversity from the starting community and among treatments at the end of the experiment (Figure 5). *In situ* community was dominated by diatoms and dinoflagellates, and Cryptophyceae class was also present with $58 \times 10^3 \text{ cell L}^{-1}$ (Figure 5; Table 3). Starting community showed high total density, reaching $1.2 \times 10^6 \text{ cell L}^{-1}$, and high diversity, with Shannon's Diversity Index at 3.42 (Figure 5). The community was mostly dominated by the diatoms *Licmophora* sp., *Navicula* sp. and *Nitzschia* sp. (Table 3). Among the dinoflagellates, *Alexandrium* sp. was dominant, reaching $80 \times 10^3 \text{ cell L}^{-1}$ (Table 3). At 96h, total abundances differed significantly between treatments (Figure 5; ANOVA $p < 0.001$, $F_{3,8} = 33.27$, $\omega^2 = 0.89$), with higher values following the decreasing salinity treatment gradient. This was mainly due to diatoms, which showed the same pattern as total abundances for differences among treatments (Figure 5; ANOVA $p < 0.001$, $F_{3,8} = 28.75$, $\omega^2 = 0.87$). Cryptophyceae developed at significantly higher values in low- and mid-salinity treatments compared to C and S3

(Figure 5; ANOVA $p < 0.001$, $F_{3, 8} = 72.41$, $\omega^2 = 0.95$). Some species did not show much variation from the starting community and between treatments at the end of the experiment, like *Navicula* sp. and *Nitzschia* sp., which stayed dominant and developed well in all treatments (Table 3). Some species initially present *in situ* disappeared or were drastically reduced following the treatment, like most of dinoflagellates (Table 3). Some other species initially extremely rare or not even detected, proliferated during the experiment and were even boosted by desalinization treatment, like for instance *Akashiwo sanguinea* and *Entomoneis* sp., this latter reaching a mean of 325×10^3 cell L^{-1} and 356×10^3 cell L^{-1} in S₂ and S₃ respectively (Table 3). Globally, the strongest desalinization treatment showed a significantly lower diversity compared to all other treatments (Figure 5; Shannon's Diversity Index: ANOVA $p < 0.001$, $F_{3, 8} = 38.02$, $\omega^2 = 0.90$).

Table 3 Microphytoplankton composition of *in situ* and microcosms' communities at the beginning and the end of the two experiments, respectively, expressed as cellular density for each species or taxonomic unit observed during microscopy analyses (mean values over the three replicates). Taxonomic Units are ranged in decreasing order of *in situ* abundance per each class and color gradients represent magnitude of abundance in each column: higher values correspond to darker shades hence to dominant taxa in the sample.

July 2021 - Salinization (cellular abundance, cell L ⁻¹)						October 2021 - Desalinization (cellular abundance, cell L ⁻¹)					
Taxonomic Unit	<i>In situ</i>	C	S ₁	S ₂	S ₃	Taxonomic Unit	<i>In situ</i>	C	S ₁	S ₂	S ₃
Bacillariophyceae						Bacillariophyceae					
<i>Navicula</i> spp.	30828	158689	163999	115443	105124	<i>Licmophora</i> spp.	233609	5078	1327	20352	7669
Fragilariophycideae	23549	8259	5899	5870	2832	<i>Nitzschia</i> spp.	196444	105505	120698	192020	129193
<i>Surirella</i> sp.	12845	0	0	0	0	<i>Navicula</i> spp.	159279	173955	135033	185826	163409
<i>Cocconeis</i> sp.	1132	9144	14158	9494	10088	Fragilariophycideae	132733	8502	6371	8849	0
<i>Ardissonia</i> sp.	9420	0	0	0	0	Small centric	69021	48206	61234	143351	34216
<i>Nitzschia</i> sp.	5994	61057	63712	42618	40882	<i>Petronopsis</i> sp.	47784	0	3451	0	0
<i>Petronopsis</i> sp.	3854	295	0	0	0	<i>Surirella</i> sp.	37165	0	354	0	0
<i>Licmophora</i> sp.	3425	2655	1770	0	0	<i>Chaetoceros</i> sp.	18583	77203	101585	161049	87309
<i>Stauroneis</i> sp.	3425	0	0	0	0	<i>Cocconeis</i> sp.	18583	3853	3274	5309	0
<i>Cylindrotheca closterium</i>	2141	15633	5899	4059	0	<i>Gyrosigma/Pleurosigma</i> sp.	13273	2008	442	0	0
<i>Diploneis</i> sp.	1713	0	0	0	0	<i>Diploneis</i> sp.	7964	340	0	0	0
<i>Entomoneis</i> sp.	0	31856	47194	38765	15397	<i>Amphora</i> sp.	5309	0	0	0	0
<i>Amphora</i> sp.	0	5014	5309	2256	2478	<i>Entomoneis</i> sp.	2655	26315	60084	324752	355723
<i>Chaetoceros</i> sp.	0	2065	6489	239	0	<i>Cerataulina</i> sp.	0	2464	1770	17698	3540
Dinophyceae						Dinophyceae					
Dinophyceae und.	23978	2360	2950	4887	2124	<i>Grammatophora</i> sp.	0	18760	5752	7964	0
<i>Mesoporos</i> sp.	1713	0	0	0	0	Dinophyceae	76985	0	0	0	0
<i>Prorocentrum</i> spp.	856	0	0	0	0	Dinophyceae und.	79640	12402	13539	17698	2360
<i>Dinophysis</i> sp.	0	0	0	239	0	<i>Alexandrium</i> sp.	13273	6643	1681	3540	0
Chlorophyta	0	0	0	0	0	<i>Prorocentrum micans</i>	0	442	4513	2655	9439
<i>Pyramimonas</i> sp.	18411	21827	0	0	0	<i>Akashiwo sanguinea</i>	0	442	4513	2655	9439
Others						Cryptophyceae					
Small flagellates und.	0	20647	29496	26235	8672	Cryptophyceae	58402	20625	34864	79640	33036
Small coccoid und.	0	0	42474	40671	23715	Others	2655	0	0	0	0
Raphidophyceae	0	5899	0	0	0	Dictyochophyceae					
und. 1	0	0	0	2476	1239	<i>Dictyocha</i> sp.	2655	0	0	0	0

3.4 *Phytoplankton communities' metabolism and status*

Salinization experiment: Fv/Fm ranged between 0.19 ± 0.01 in S₃ at 8h from the beginning and 0.51 ± 0.01 in C at 72h (Figure 6), and significantly differed between treatments and sampling times (treatment: ANOVA $p = 0.006$, $F_{3,8} = 9.10$, $\omega^2 = 0.77$; time: ANOVA $p < 0.001$, $F_{6,48} = 141.41$, $\omega^2 = 0.95$), indicating a global increase over time and opposite to the salinity increase, according to pairwise test. Φ PSII variable experienced higher variability and ranged between 0.17 ± 0.01 in S₂ and S₃ at 8h and 0.34 ± 0.00 in C at 56h (Figure 6). A significant effect of the interaction was detected (ANOVA $p = 0.009$, $F_{6,42} = 3.89$, $\omega^2 = 0.63$), and pairwise test confirmed a general tendency to slight increase except for S₃ and significant higher values in C than in other treatments, starting from 24h after the beginning of the experiment.

Desalinization experiment: Fv/Fm ranged between 0.17 ± 0.02 in C at 8h from the beginning and 0.58 ± 0.02 in C and S₂ at 72h, while Φ PSII varied from 0.17 ± 0.04 in S₃ at 8h to 0.36 ± 0.01 in S₃ at 96h (Figure 6). No significant difference between treatments was detected, but a significant effect of sampling time was found for both variables (Fv/Fm: ANOVA $p < 0.001$, $F_{6,48} = 80.24$, $\omega^2 = 0.91$; Φ PSII: ANOVA $p < 0.001$, $F_{6,48} = 57.09$, $\omega^2 = 0.88$), which indicated a global increase over time, according to pairwise comparisons.

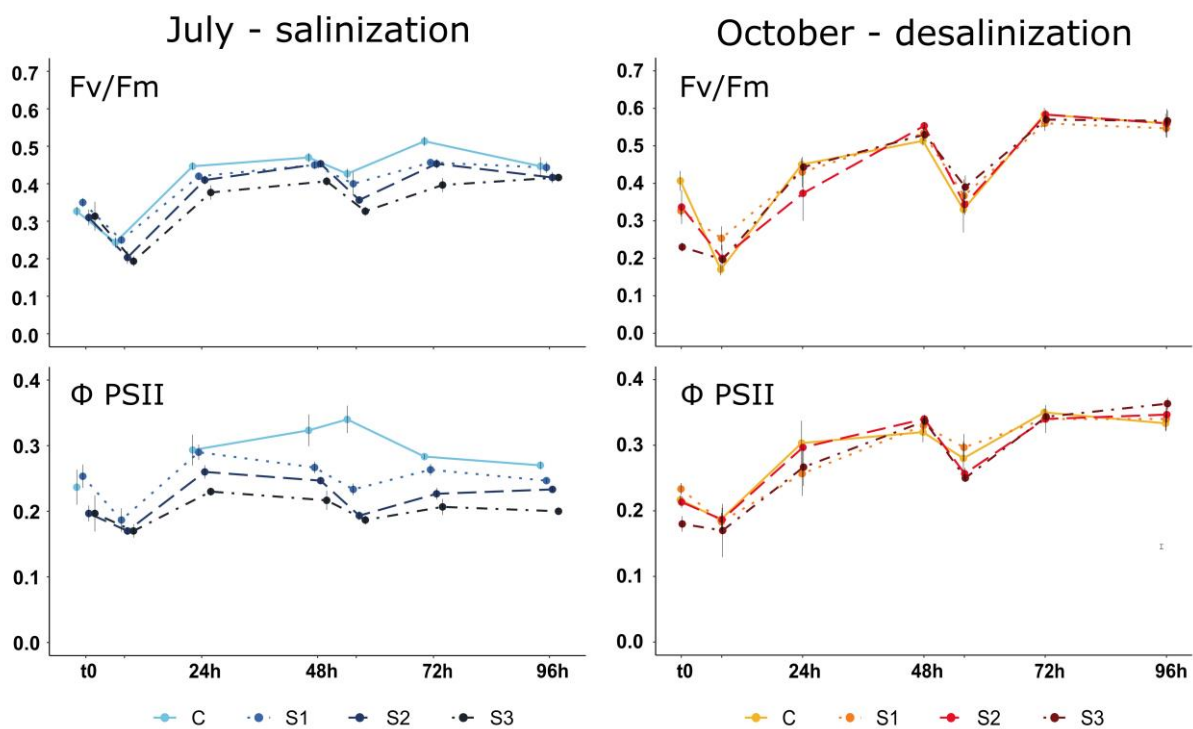


Figure 6 Evolution of photosynthetic activity's proxies Fv/Fm (top) and Φ PSII (bottom) over the two experiments.

4. DISCUSSION

4.1 *Global effects of short-term salinity changes*

Our two experiments clearly revealed that sudden changes in salinity altered the phytoplankton communities of the small Mediterranean coastal lagoon in study. For both the experiments, based on the considerations on the 8h and 56h samples, no significant short-term effect after stress application emerged, except for the photosynthetic efficiency. Nevertheless, as lower photosynthetic efficiency was detected after 8h and 56h from the beginning for both experiments, the depleting effect seems not attributable to salinity stress, but rather to the time of the sampling. In fact, both 8h and 56h samplings were performed in the afternoon, while all the other measures were taken in the early morning, so a reduction of photosynthetic activity might be due to photoinhibition due to strong irradiance in the central hours of the day (Lamont et al., 2022). However, overall, the impact of desalinization was less marked than that of salinization. During the desalinization experiment, the first level of treatment mainly followed the same evolution pattern as the control and strong changes were found at lowest salinities only. On the contrary, for the salinization experiment, despite the choice of increasing salinity progressively through two successive salt adding, effects already started to emerge after the first salinization, 24h after the beginning (8h for photosynthetic activity). This may indicate salinization effects can be more marked than decreased salinity ones, however, the salinity intervals established for the two experiments are not really comparable and must be interpreted keeping in mind the natural conditions. For the desalinization experiment, the maximum salinity gap was of 50% and salinity values changed from around 40 to around 20. This range fits in the most frequent range of salinity found in natural environment (Santa Giulia lagoon) during autumn, so it falls into the natural variability range. Nevertheless, the short-term application resulted in an abrupt decrease, which can explain the observed effects, and mimic in fact a flash flood event, as required by our starting point objective. On the other hand, for the salinization experiment, we applied a larger salinity span, passing from 43 to up to 73, in a very abrupt time interval, thus applying a strong osmotic stress. Such high values are the result of several days-lasting evaporation in the field. In the future, we may expect salinization process through evaporation to be more frequent, long lasting and more rapid, but this abruptness in salinity change, as well as intensity of the gap applied, can explain major impact under our experimental condition. Stefanidou et al. (2018) found an opposite trend, meaning major strong negative impact of decreased salinity than salinization on phytoplankton communities. Discrepancies with our findings might reside in the fact that the authors tested marine communities and small salinity ranges (± 5 PSU): marine environment is a stable system compared to

lagoon one, and marine communities are expected to be less tolerant towards disturbance than brackish ones, which are particularly tolerant towards low salinity conditions and larger salinity ranges (Dube et al., 2010). Moreover, Mediterranean coastal lagoons are usually strongly dependent on watershed inputs and, as mentioned before, salinity ranges applied during desalinization experiment are frequently occurring in the natural environment from which starting communities were collected for this study.

Overall, total biomass inhibition observed under increasing salinity is not universally confirmed by other studies. Some previous works indicated that high salinity boosted biomass and growth of phytoplankton communities (Barnes & Wurtsbaugh, 2015; Barroso et al., 2018; Delaune et al., 2021; Greenwald & Hurlbert, 1993; Nche-Fambo et al., 2015). This was most often due to a decrease in zooplankton grazing pressure and the application of salinity ranges on communities from different freshwater or brackish environments (Barnes & Wurtsbaugh, 2015; Delaune et al., 2021). Some other studies in natural transitional environments actually corroborated our observations, highlighting an inhibition of biomass under increasing salinity (Redden & Rukminasari, 2008; Schallenberg et al., 2010a). A strong difference among treatments was observed in our study, indicating that diatoms, dinoflagellates and chlorophytes were lost or experienced lower growth under increasing salinity stress. Alloxanthin and zeaxanthin variations also indicated a negative effect of increased salinity on cryptophytes and cyanobacteria. Overall, the negative effect of the treatment can be traced back to osmotic stress on the cells, as it was already proposed by different studies on primary producers (Ersoy et al., 2022; Flöder et al., 2010). Microscopy observations at the end of the salinization experiment identified in particular the complete loss of some chlorophytes species and this is in accordance with other studies, like Redden & Rukminasari (2008), who observed a reduction of chlorophytes in a coastal lake (Myall Lakes, NSW, Australia) under salinity increase, even if slight (+4 ppt, from 4 to 8 ppt). Moreover, chlorophytes and cryptophytes are generally associated with freshwater inputs in transitional systems, hence showing a general preference for low salinities (Catherine et al., 2012; Garrido et al., 2019, 2016; Gregor & Maršálek, 2004). For the chlorophytes, there was a contrast in fluorometry, pigment and microscopy analyses, probably linked to weakness of the BBE precision and pigment redundancy (Garrido et al., 2019; Vidussi et al., 2001). As for the loss of cyanobacteria under salinization, this result matched cytometry analysis, identifying a strong loss of picocyanobacteria and particularly *Synechococcus*-like type. Initially dominating the ultraphytoplankton community, at the end of the experiment picocyanobacteria decreased in the favor of picoeukaryotes and nanophytoplankton. *Synechococcus* is the dominant picophytoplankton taxon in rich coastal waters, which can explain the absence or low

Prochlorococcus-like detection over both experiments, also observed in Ghar El Mehl lagoon (Tunisia) (Dhib et al., 2017). *Synechococcus* dynamics are strongly influenced by salinity (Xia et al., 2017). In estuarine context, it has already been proven that community composition of *Synechococcus* populations varies according to salinity, by developing mostly marine, mostly freshwater lineages or mixed populations, allowing a wide salinity range of tolerance (Rajaneesh & Mitbavkar, 2013; Xia et al., 2017; Xiao et al., 2018). The loss of *Synechococcus*-like under salinization might be due to strong sudden osmotic pressure, which could not allow the establishment of a new population's composition, and maybe competition processes (Caroppo, 2015). Competition control is also probably at the base of heterotrophic bacteria's loss: all salinization treatments showed a decrease in bacteria contribution, especially in the control and lowest salinization level, where micro- and nanophytoplankton growth was higher. Top-down control through grazing and bottom-up control through competition of phytoplankton over bacteria populations have already been described in mesocosm experiments (Fouilland et al., 2017).

Parallel to all these modifications, a strong negative effect of increased salinity on photosynthetic activity of the community was detected, indicating a stress induced by salinization, affecting the community health. Supporting in general Fv/Fm values, the Φ PSII values in salinization treatments, always lower than 0.3, indicate a low physiological state of the community (Lafabrie et al., 2013). Salt stress-driven impacts on photosynthetic metabolism were already observed in marine and brackish communities or species, despite some variability in responses (Le Rouzic, 2012; Nikitashina et al., 2022). Le Rouzic (2012) was able to detect Fv/Fm depletion induced by short-term salt stress in microalgal communities from salt marshes, but responses could not be directly linked to this only stressor and strongly varied according to dominant species present. Li et al. (2019) highlighted negative effects of acute stress salinity on estuarine phytoplankton communities, but the effect was short-term lasting (several tens of minutes), while in contrast, in our study we found a strong treatment effect over the entire duration of the experiment, i.e. several days. The same author identified similar responses for decreasing salinity gradient. D'ors et al. (2016) demonstrated a strong effect of desalinization on phytoplankton metabolic activities. Conversely, in our study, no negative effect on photosynthetic activity was found under decreasing salinity treatment. For this experiment, only treatment effects were identified for the community structure and composition. Globally, the lowest treatment did not differ much from control, showing lower picoeukaryotes, picocyanobacteria and nanophytoplankton abundances than stronger treatments towards the end of the experiment. In general, diatoms and chlorophytes were favored by desalinization, together with prasinophytes, cyanobacteria and cryptophytes. This is not surprising as chlorophytes and cryptophytes in particular have been strongly associated with

decreased salinization, both in experimental conditions and in field, linked to freshwater inputs from watershed and flash flood events (Garrido et al., 2019, 2016; Pecqueur et al., 2011). Total microphytoplankton abundances increase with decreased salinity is in contrast with similar studies, which generally identify a loss in biomass linked to lower salinity (Barroso et al., 2018; Hernando et al., 2020, 2015).

Most of dinoflagellates disappeared under desalinization treatments. This is not surprising as most of dinoflagellates, like *Prorocentrum micans*, are generally associated with salinity increase (Dhib et al., 2013). However, the observed loss of *Alexandrium* sp. is more unexpected, as this taxon has already been linked to decreasing salinity processes in coastal environment (Bravo et al., 2010). This might be due to the emergence of an initially rare species, *Akashiwo sanguinea*, which probably took advantage of the low salinity conditions, which are in its growth optimum (Islabão & Odebrecht, 2015; Yang et al., 2012), and took the upper hand on other taxa. The initially rare diatom *Entomoneis* sp. also developed massively under desalinization treatment, becoming from initially rare to dominant at the end of the experiment, to the detriment of other taxa. This genus is generally brackish and low-salinity tolerant (Clavero et al., 2000; Le Rouzic, 2012; Varona-Cordero et al., 2010). Its development contributed to another important effect induced by desalinization, i.e. the loss of diversity in the community. A similar tendency was also found for the strongest salinization treatment despite not being significant. In both cases, these observations are compliant with other studies, indicating a loss of diversity at short term under increased or decreased desalinization stress on phytoplankton communities from various environments (Astorg et al., 2022; Flöder et al., 2010; Stefanidou et al., 2018). For instance, Flöder et al. (2010) found that increased salinity on tidally influenced lake (New Zealand) community induced depletion of dominant phytoplankton species, which were replaced by compensatory growth of initially rare ones. Barnes & Wurtsbaugh (2015) highlighted a loss of diversity even at higher trophic level under increased salinity in a saline lake, thus indicating a biodiversity loss under this kind of disturbance.

Overall, our results highlight changes in phytoplankton community structure and functioning which are compliant with other observations, even though there are sometimes contrasts with previous studies (Barnes & Wurtsbaugh, 2015; Barroso et al., 2018; Flöder et al., 2010; Greenwald & Hurlbert, 1993; Hernando et al., 2015; Nche-Fambo et al., 2015; Stefanidou et al., 2018). This could be due to differences in starting communities and/or environments chosen (Barroso et al., 2018; Hernando et al., 2020; Nche-Fambo et al., 2015). Our results highlighted also strong impacts on the biomass, structure and metabolism of the phytoplankton communities, despite the short duration of the experiments and for both increased and decreased salinity. These short-term changes are indicating that potential transition processes towards completely new

communities' configurations could occur on the middle-long term under salinity perturbation in the future.

4.2 Perspectives and implications on future management of small Mediterranean lagoons

Numerous studies have proven that salinity changes in various environments, like coastal marine waters, saline or tidal lakes, estuaries and lagoons outside the Mediterranean region, can induce modifications in biotic communities in terms of biomass, species composition and richness, diversity and resource use efficiency (Barnes & Wurtsbaugh, 2015; Flöder et al., 2010; Greenwald & Hurlbert, 1993; Hernando et al., 2020; Pilkaitytė et al., 2004; Stefanidou et al., 2018). We demonstrated that such responses took place in Mediterranean coastal lagoon environment too.

Projections for climate change identify Mediterranean coastal lagoons as climate change hotspots. Predicted changes in these systems are expected to be amplified compared to perturbations in the open sea (Ferrarin et al., 2014). In particular, water temperatures are predicted to increase 15% more than in the sea, parallel to salinity increases over forty times stronger than sea (Ferrarin et al., 2014). These effects are predicted to be especially evident in shallow lagoons, with low connection to the sea, since they are more reactive and present a lower mitigation potential towards disturbances, making them excellent sentinels for global change (Ferrarin et al., 2014; Robert & Mazzilli, 2007). Our study is hence a first fundamental step towards the anticipation and understanding of the destiny of these systems under future disturbances. We already highlighted that salinity variations can influence the relationship between phyto- and bacterioplankton dynamics. We suggest that future studies should focus on the testing of more complex biotic communities, including zooplankton and benthic invertebrates. For instance, Barnes & Wurtsbaugh (2015) performed an experiment on salinity variations effects on complex communities from the Great Salt Lake (Utah, USA), which displays a wide salinity range. This made possible to detect and describe complex trophic relationships and combined effects of the environmental variations together with grazing and competition under salinity stress, thus giving a simulation of potential effects of disturbance on communities as close as possible to natural conditions (Barnes & Wurtsbaugh, 2015).

Similarly, it would be interesting to perform further investigations on effects of salinity variations together with other factors or stressors. For instance, the potential of synergic effects of salinity and nutrients' variations on biotic communities has already been established (Fouilland et al., 2017; Ganguly et al., 2013). In natural environment, together with freshwater input, nutrients inputs from the watershed are also usually associated

to rainfall events (Fouilland et al., 2017; Pereira Coutinho et al., 2012). Moreover, together with water, new communities of freshwater affinity are added during these events; it has been proven that these phenomena will take place during flash floods too, hence they will become more frequent under progressing climate change (Fouilland et al., 2017; Pecqueur et al., 2011). Since we already highlighted alterations in communities under decreased salinity, it would be interesting to further investigate on responses coupled to reaction to new communities' composition. For instance, Fouilland et al. (2017) described the increase of Chlorophyceae, picoeukaryotes and bacterioplankton from river water inputs and consequent effects on the phytoplankton community dynamics, alongside responses linked to salinity variations.

Furthermore, an increase in temperature is also predicted under climate change progression. Other studies highlighted synergistic effects of salinity variations and temperature increase on phytoplankton communities (Hernando et al., 2020; Stefanidou et al., 2018). However, effects were different: Stefanidou et al. (2018) found a cumulative negative effect of heat shock coupled with increased or decreased salinity, while Hernando et al. (2020) pointed out that increased temperature could compensate lipid damage under decreased salinity, thus mitigating its negative effects on biomass loss. Since we found similar responses of phytoplankton communities to changes in salinity as those obtained in these studies, like alterations in community composition, biomass and metabolism, it is likely that the community would react under the simultaneous presence of these two stressors showing synergistic effects.

Of course, responses highly depend on the type of communities considered (marine, brackish, freshwater), which makes it difficult to compare between experimental works, as highlighted by several studies (Barroso et al., 2018; Hernando et al., 2020; Nche-Fambo et al., 2015). Moreover, final composition of the communities strongly depends on the starting ones (Barroso et al., 2018; Hernando et al., 2020; Nche-Fambo et al., 2015). This must be considered to fully understand future responses as they will depend on communities present at the time of perturbation (Hernando et al., 2020). Since future projections identify an increase in potentially harmful species linked to climate change (Collos et al., 2009; Fischer et al., 2020; Pereira Coutinho et al., 2012; Trombetta et al., 2019; Xiao et al., 2018), and since we demonstrated that some potentially harmful species can emerge under salinity variations despite being initially rare, like it was the case for the dinoflagellate *Akashiwo sanguinea* in desalinization experiment, we can expect a potential exacerbation of Harmful Algal Blooms occurrence and intensities in the future. Many harmful and invasive species are highly tolerant to disturbance and display wide salinity tolerance ranges (Carrada et al., 1991; Fraga et al., 1995; Islabão & Odebrecht, 2015; Skarlato et al., 2018a). Since we demonstrated salinity variations can change the community composition through the compensatory growth

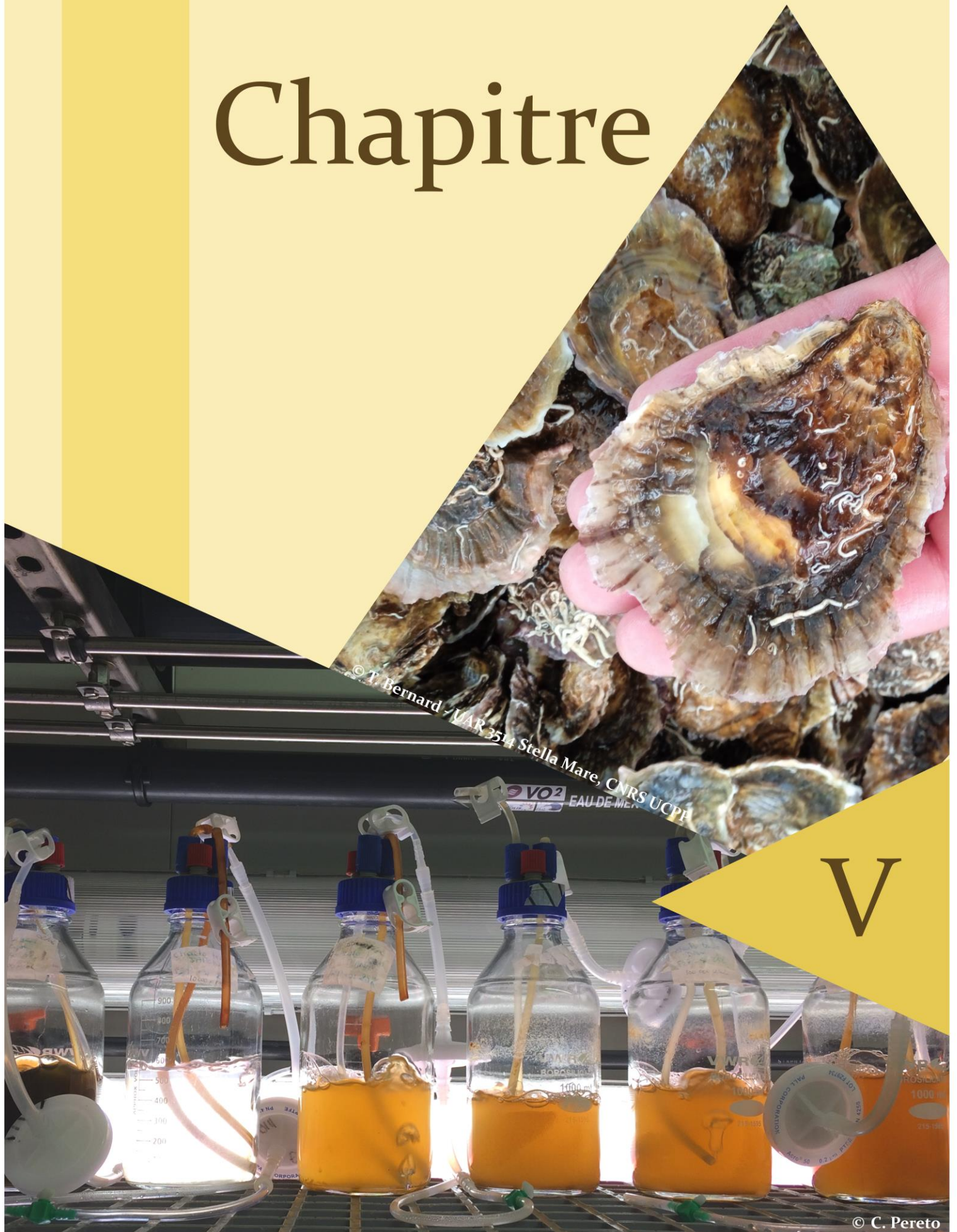
of some tolerant species and the emergence of initially rare ones, we can expect these harmful taxa to appear more frequently and further contribute to biodiversity depletion and ecosystem degradation. Changes in size structure and composition of phytoplankton communities, and especially simplification and loss of biodiversity already demonstrated during our study, can have negative impacts on higher trophic levels, as different phytoplankton groups present different nutritional values, especially regarding lipid content (Astorg et al., 2022). Changes at phytoplankton level may also impact the capacity of higher trophic groups to face disturbance, like for instance reduce the resistance capacity of zooplankton towards salinity stress by insufficient lipid supply from phytoplankton (Astorg et al., 2022). Hence, structural modifications of phytoplankton and diversity loss identified under salinity stress might impact ecosystem functioning, contribute to the degradation of resistance capacity of the system by exacerbating disturbance effects at multiple levels, and ultimately impact ecosystem services provided (Astorg et al., 2022; Ligorini et al., 2022b).

In particular, hypersaline conditions have already been associated to the favoring of stress-tolerant and harmful species (Nche-Fambo et al., 2015). The Santa Giulia lagoon, chosen site for this study, already experienced a drying-up event, reaching salinity values up to 125 associated to long lasting isolation from the sea: it should be avoided to fall into these extreme conditions, which have an increased probability to occur under climate change, in order to limit detrimental effects on biotic communities. In the instable transitional systems known as ICOLs, communication with the sea is essential to regulate salt balance and the system functioning (Coelho et al., 2015; Schallenberg et al., 2010a). Loss of connectivity of lagoons and other transitional systems to marine environment has already been associated to alterations in salinity and biotic communities (Camacho et al., 2012; Jones et al., 2018; Pereira Coutinho et al., 2012). Artificial openings of sea outlets are often used to control water discharges and sea-exchanges in transitional systems (Schallenberg et al., 2010a). With the progression of climate change, natural opening of sea outlets will become more difficult due to the decrease and shortening of rainy periods, normally ensuring outgoing pressure and sediment flushing on sea outlets, and the increase of evaporation (Ligorini et al., 2022b). Moreover, despite climate change being a major driver for long-term environmental change, local environmental management is also strongly involved, as it was demonstrated by Fichez et al. (2017): the authors highlighted strong salinity variations due to freshwater river discharge increase in a tropical coastal lagoon (Laguna de Terminos, Mexico). This was independent of climate change consequences, but rather due to deforestation actions on the watershed to build up space for agricultural fields. Results of this study demonstrated that management actions and decisions, even those involving lagoon surroundings, have power and consequences on the system functioning

and destiny, since they also are drivers, together with climate change, of modifications on long-term scale.

Based on our results on potential responses to salinity variations together with these observations, we suggest future conservation of small Mediterranean lagoons should be subordinated to the application of an integrative management approach (Biggs et al., 2015; De Wit et al., 2020; García-Ayllón, 2017). This should hence focus on the maintaining of hydrological continuum of these small lagoons to adjacent systems, through the management of activities on their watersheds and eventually artificial management of their sea channels, in order to promote a good circulation and avoid confinement. This would hopefully ensure avoidance of falling abruptly into these “extremes” and allow the control or mitigation of salinity variations induced by climate change

Chapitre



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V

CHAPITRE V

ASSESSMENT OF AQUACULTURE POTENTIAL OF A MEDITERRANEAN LAGOON STRAIN OF THE SMALL DIATOM *CHAETOCEROS TENUISSIMUS* BASED ON GROWTH AND LIPID CONTENT

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CONTEXTE GÉNÉRAL ET RÉSUMÉ

Les microalgues constituent une richesse dans le secteur de la bioéconomie, avec des applications très variées dans plusieurs domaines, de la médecine et les cosmétiques jusqu'à la nutrition, humaine et animale, et la bioremédiation environnementale. En particulier, l'utilisation des microalgues est particulièrement appréciée et appliquée dans le domaine de l'aquaculture, à travers l'alimentation de certaines espèces exploitées d'intérêt commercial.

Au sein des réseaux trophiques aquatiques, les diatomées recouvrent un rôle écologique fondamentale en tant que producteurs primaires. Parmi les diatomées, les espèces du genre *Chaetoceros* sont distribuées dans les mers et les océans du monde entier. Au sein de ce genre, l'espèce *C. simplex* var. *calcitrans* est bien connue grâce à son intérêt majeur dans le domaine de l'aquaculture. Au contraire, les souches de *C. tenuissimus* demeurent toujours plutôt méconnues, en particulier au regard de leur potentiel nutritionnel.

Dans ce travail, l'objectif principal est d'évaluer les caractéristiques physiologiques et d'explorer les potentiels d'application aquacole d'une souche de *C. tenuissimus* (CT16ED) issue de l'étang de Diana, dans la plaine orientale de la Corse.

Dans cette optique, des expérimentations ont été mises en place pour étudier les dynamiques de croissance, l'activité photosynthétique et la production pigmentaire et lipidique de cette nouvelle souche de *C. tenuissimus*. Ces caractéristiques ont été étudiées sous deux photopériodes : i) 24 h de lumière vs 00 h d'obscurité, qui correspond à la photopériode la plus utilisée en aquaculture ; et ii) 12 h de lumière vs 12 h d'obscurité, qui est une photopériode similaire à celle du milieu naturel. En outre, les caractéristiques de la nouvelle souche de *C. tenuissimus* ont été comparées avec celles de *C. simplex* var. *calcitrans*, une espèce de collection, communément utilisée en aquaculture, afin de mieux évaluer le potentiel d'application de la nouvelle souche ciblée dans ce domaine.

Les résultats obtenus pour les cultures de *C. simplex* var. *calcitrans* sont corroborés par les connaissances disponibles dans la littérature et montrent une efficacité de croissance remarquable de cette espèce, ainsi que des caractéristiques très propices à l'utilisation dans l'aquaculture, quelle que soit la photopériode. Au contraire, l'effet de la photopériode était marqué sur les dynamiques de croissance, l'activité photosynthétique et le contenu en pigments et lipides de la nouvelle souche de *C. tenuissimus*. Comparé à *C. simplex* var. *calcitrans*, cette nouvelle souche montre quand même des caractéristiques prometteuses pour des applications aquacoles. Principalement, son contenu lipidique, riche en acides gras polyinsaturés essentiels et en particulier une haute proportion en Oméga-3, semble être particulièrement intéressant pour l'alimentation d'espèces d'intérêt pour l'aquaculture, en raison de son

1. INTRODUCTION

In marine ecosystems, diatoms have a fundamental ecological role as primary producers contributing largely to aquatic food webs (e.g. Rines & Hargraves 1988; Armbrust 2009). With more than 200 species, the genus *Chaetoceros* Ehrenberg is highly diverse and is one of the most important genera of diatoms (Shevchenko et al., 2006; Grzebyk et al., 2022). Species of the genus *Chaetoceros* are observed in seas and oceans worldwide (Luca et al., 2019). Many species of the genus *Chaetoceros* have been described, with very different sizes, some of them living as solitary cells and the majority forming colonies (as cell chains or aggregates) (Rines & Hargraves 1988; Lee & Lee 2011). However, many species are still insufficiently documented, particularly small species for which identification remains complex and uncertain. In order to improve the identification of these small species, recent studies have focused on the morphology and genetics of these species, particularly in *Chaetoceros tenuissimus* (e.g. Sar et al. 2002; Grzebyk et al. 2022).

Chaetoceros tenuissimus Meunier (1913) is considered a cosmopolitan species observed in brackish and coastal environments worldwide (e.g. (Tomaru et al., 2018; Grzebyk et al., 2022; Pastorino et al., 2022)). High cell density of *C. tenuissimus* up to 10^7 cell L⁻¹ have been described in natural phytoplankton blooms (e.g. Rines & Hargraves 1988; Tomaru et al. 2018). *C. tenuissimus* shows minute solitary cylindrical cells ranging from 3 to 5 µm in diameter and 3 to 12 µm in length (e.g. Bérard-Therriault et al. 1999; Robert et al. 2004) and is characterized by the presence of long setae which can measure up to ten times the diameter of the cells (Bérard-Therriault et al., 1999). Some of these characteristics (e.g. size, growth rate) are of great interest in the aquaculture industry and some species of the genus *Chaetoceros* are already in use (e.g. Ragg et al. 2010; Miller et al. 2014). For example, *Chaetoceros simplex* var. *calcitrans* Paulsen (1905) is considered as an excellent species for feeding shellfish larval stages in aquaculture due to its little size, its rapid growth and its substantial production of nutrients (e.g. Volkman et al. 1989; Miller et al. 2014). Despite potential interesting characteristics, little is known about the nutritional quality of *C. tenuissimus* especially in terms of carotenoid pigment or lipid content.

For their use in aquaculture, the nutritional quality of microalgae, in particular diatoms, is strongly influenced by the culture conditions, including light intensity (Zhang et al., 2017), temperature (Converti et al., 2009), salinity (Minggat et al., 2021) and inorganic nutrients (Larson & Rees, 1996; Mortensen et al., 1988; Reitan et al., 1994; Roessler, 1990). Light conditions are one of the major factors affecting the physiology of microalgae and their photosynthetic activity (Parmar et al., 2011). Indeed, the

photoperiod is an important parameter which determines the amount of available energy that is required for the photosynthetic process (e.g. Falkowski et al. 1985; Grobbelaar 2009). In order to assess the photosynthetic activity of microalgae, Pulse Amplitude Modulated (PAM) fluorometry is a fast and reliable tool (Schreiber et al., 1995; Garrido et al., 2013a), especially in combination with measurement of chlorophyll pigment content. Moreover, the photoperiod directly influences growth and the production of interesting biochemical compounds such as pigments and lipids (Lim & Zaleha, 2013). Several studies have focused on the effect of photoperiod on the growth and nutrient production capacities of microalgae (e.g. Amini Khoeyi et al. 2012; Lim & Zaleha 2013; Fakhri et al. 2015). In the literature, two photoperiods are particularly used: the 24:00 Light:Dark (L:D) and 12:12 L:D photoperiods. Generally, the 12:12 L:D photoperiod is used in experiments to mimic natural light conditions. Conversely, the 24:00 L:D photoperiod is particularly appreciated in aquaculture. Indeed, several authors have been able to show CO₂ fixation rates, growth rates and maximum biomass production under these conditions. However, some authors have demonstrated a lower production of essential lipids in the 24:00 L:D photoperiod compared to photoperiods including a dark phase (Amini Khoeyi et al., 2012; Lim & Zaleha, 2013). In addition, (Krzemińska et al., 2014) demonstrated that the photoperiod seems to have a species-dependent role on the growth rates of green microalgae.

For aquaculture purposes, microalgae are widely used for their ability to synthesize large amounts of essential nutrients (e.g. Hemaiswarya et al. 2011; Khozin-Goldberg et al. 2011). Among these essential nutrients, microalgae are particularly well known for their production of polyunsaturated fatty acids (PUFAs), especially long-chain Omega-3s (Khozin-Goldberg et al., 2011). These long-chain Omega-3s like EPA (20:5n-3; eicosapentaenoic acid) or DHA (22:6n-3; docosahexaenoic acid) are essential but poorly synthesized by aquaculture marine species (Miller et al., 2014). The supply of microalgae as a direct or indirect source of food is therefore necessary for the proper development of aquaculture marine species. Indeed, it is well established that these Omega-3s play an important role in the functioning of organs such as the brain or the eyes of fish (Tocher, 2003). In addition, these essential lipids allow the proper development of the larval stages of many species (e.g. Brown 2002; Ragg et al. 2010). In aquaculture, diatoms are widely used for their ability to produce large amounts of lipids (Miller et al., 2014). Within diatoms, among the highest contents of EPA have been found in the genus *Chaetoceros*, especially in *C. simplex* var. *calcitrans* (e.g. Volkman et al. 1989; Brown 2002). However, many studies have proven the beneficial effects of mixed cultures of microalgae on the development of aquaculture species (e.g. Gomes et al. 2021). Thus, the study of the biochemical composition of various strains of *Chaetoceros* can be of great interest to improve the diet of aquaculture species. Moreover, the study

of new strains is needed to boost potential for industrial applications (Jusoh et al., 2020). Also, salinity, light and temperature variations often jeopardize the success of cultures for aquaculture purposes, hence, there is a strong interest in the study of strains issued from natural environment, since they can be expected to be more sturdy (Eryalçın et al., 2015; Hotos & Avramidou, 2021). Specifically, lagoon environments are extremely instable and subjected to constant and intense modifications in salinity, temperature, irradiance, nutrient load and pollutants, so that they sustain a high diversity (specific, genetic...) of their biota (Pérez-Ruzafa et al., 2019b). Species found in this harsh systems could potentially show interesting features for aquaculture applications, due to their adaptive capacities to constantly changing environment and hence higher resistance towards variations in the culture medium (Tzovenis et al. 2009; Hotos & Avramidou 2021 and references herein).

Recently, a strain of *C. tenuissimus* (CT16ED) was isolated from a French Mediterranean lagoon (Corsica Island) and subsequently characterized with genetic analyses and a detailed morphological description (Grzebyk et al., 2022). Solitary cells were square to rectangular with a diameter of 3-6 µm and thin setae of 25-30 µm in length. During the exponential growth phase in culture, they observed the formation of a high proportion of cell chains extending from 2 cells to more than 20 cells per chain. However, little is known about the growth characteristics and no information is available regarding the photosynthetic activities or the biochemical composition of this strain. Thus, in this study, we evaluate for the first time the ecophysiological properties of the strain of *Chaetoceros tenuissimus* (CT16ED), before discussing its potential use in aquaculture. For this purpose, we investigated through experimental essays the growth, the photosynthetic activity, the lipid profiles and the pigment composition under two photoperiods (24:00 L:D; 12:12 L:D). Experiments were realized with this new strain CT16ED of natural lagoon origin and for comparative purposes with a common aquaculture strain of *Chaetoceros simplex* var. *calcitrans* (CCAL 1085/3), well documented in physiological characteristics and biochemical composition.

2. MATERIALS AND METHODS

2.1 Strains and culture methods

The strain of *C. tenuissimus* CT16ED (hereafter called CTEN) was isolated from a Mediterranean lagoon (Diana lagoon, Corsica Island, France) during May 2016 (Grzebyk et al., 2022). The *C. simplex* var. *calcitrans* strain 1085/3 (hereafter called CCAL) was obtained from the Culture Collection of Algae and Protozoa (Oban, UK).

Culture medium was made with natural seawater, sterilized with UV at 365 nm (Bio UV TTPE HO lamp), filtered on 0.2 μm and autoclaved at 121°C for 20 min. Then, salinity was adjusted at 25 with distilled water and enriched with Cell-Hi F2P nutrient powder (Varicon Aqua, Worcester, UK) at 0.4 g L⁻¹ and Na₂SiO₃ solution at final Si concentration of 40 mg L⁻¹, corresponding to four times the concentrations of the F/2 medium (Guillard, 1973).

The two strains of *Chaetoceros* were maintained as unialgal stock cultures in 100 mL Erlenmeyer flasks, incubated at 18 ± 1 °C under 40 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (as monitored with a Spherical Micro Quantum Sensor US-SQS/L Walz), and with a 18:06 h Light:Dark (L:D) photoperiod. Cultures were not axenic but bacterial contamination was considered negligible based on inverted optical microscopy observations.

Prior to all experiments, initial stock cultures were used to prepare cultures for the inoculation of experimental bottles, through the following procedure: stock cultures were sequentially increased to a volume of 250 mL and grown in the same conditions as described above for one week, then they were increased to 1 liter and grown for one week in conditions planned for the experiments, as described below.

Each stock culture was volume scaled-up with an initial transfer from 100 mL Erlenmeyer flasks to 250 mL Erlenmeyer flasks (50 mL culture volume) and incubated during one week in the same conditions as maintenance conditions. Growth was monitored through cell counts as described later (section 2.4.1) and each 250 mL Erlenmeyer flask was transferred, at late logarithmic growth phase in one-liter borosilicate Duran bottles (200 mL culture volume; Cell-Hi F2P at 0.4 g L⁻¹; Si at 40 mg L⁻¹; vitamins) and incubated during one week prior to experiments. These one-liter bottles were incubated under a 24:00 h L:D photoperiod (i.e., continuous light) at 18 ± 1°C and used as stock cultures for the inoculation of the experimental bottles.

2.2 Experiment for setting the inoculum concentration

A preliminary work was performed to find an adequate inoculum concentration in order to assess the range of growth response of both CTEN and CCAL strains before further experiments. Cultures were carried out in the growth medium as described above in one-liter borosilicate Duran bottles under a 24:00 L:D photoperiod (i.e., continuous light, at 189 ± 30 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ delivered by white (Cool white F36W/240 Lux Line OSRAM) and pink (F36W/840 T8 pink SYLVANIA) fluorescent lamps in equal proportion) at 18 ± 1°C. For CTEN, inoculum concentrations of 10 × 10³, 50 × 10³, 100 × 10³ and 300 × 10³ cell mL⁻¹ were tested, without replicates. For CCAL, inoculum densities of 10 × 10³, 50 × 10³ and 100 × 10³ cell mL⁻¹ were tested, without replicates. Cultures were monitored during 9 to 15 days in the same conditions as stock culture (e.g. 24:00 L:D;

18±1°C; Cell-Hi F2P at 0.4 g L⁻¹; Si at 40 mg L⁻¹; vitamins). Each culture was sampled daily for monitoring growth by cell count, as described later (section 2.4.1).

2.3 Photoperiod experiments

The cultures were carried out in triplicate per species for two photoperiods, 24:00 h L:D and 12:12 h L:D. These photoperiods were chosen for their frequent use in aquaculture, providing conditions considered more favorable for rapid growth (24:00 L:D) or resembling the natural light cycle (12:12 L:D). The 12 bottles were inoculated at 1.1 ± 0.1 × 10⁵ cell mL⁻¹, incubated at 18 ± 1°C under 189 ± 30 μmol photons m⁻² s⁻¹ delivered by white (Cool white F36W/240 Lux Line – OSRAM) and pink (F36W/840 T8 pink SYLVANIA) fluorescent lamps in equal proportions. CTEN and CCAL cultures were monitored during 9 days for both photoperiod treatments. Cultures were continuously aerated with 1% CO₂ in air. pH was measured each day (7.7 ± 0.7; Hanna Instruments HI 991300). Samples were taken from each bottle: i) every day for growth measurements; ii) every two days for fluorescence measurements and chlorophyll *a* measurements; and iii) only on day 4 for lipid and pigment content.

2.4 Analytical methods

2.4.1 Growth measurements

For growth monitoring during experiments, samples (10 mL) were taken daily for cell counts at the same time of light cycle. Cell counts were performed under an inverted optical microscope with a Nageotte counting cell for samples with low cell concentrations, below 6 × 10⁵ cell mL⁻¹, and with a Malassez counting cell when samples reached higher cell concentrations. A minimum of 400 cells were counted in each sample for an accuracy of ± 10% (Lund et al., 1958). The growth rate (*k*) defined as the number of division per day (div d⁻¹) was calculated according to Guillard's formula (Guillard 1973; equation 1):

$$k = \frac{\log N_2 - \log N_1}{(t_2 - t_1) \times \log 2} \quad (1)$$

where *N*₁ and *N*₂ are the cell concentration on the days of the start (*t*₁) and end (*t*₂) of the considered growth period, respectively.

Chaetoceros cells have a round cylinder shape and because of setae, they usually settle longitudinally. The longitudinal cell section area measurement can be used as an approximation of cell size. To determine cell section area, photographs were taken each day for all cultures (except at day 8 under the 12:12 L:D photoperiod) with an inverted

optical microscope (Leica MC HD 170). Area measurements were made with the image processing freeware (ImageJ, NIH) on a minimum of 15 cells per sample.

2.4.2 *Chlorophyll a in vivo cellular fluorescence measurements*

To measure chlorophyll *a* (chl_a), a 10-mL aliquot of each culture was filtered every two days on a GF/F filter (Whatman, 25 mm diameter, porosity 0.7 μm). Analyses were performed at the Mediterranean Institute of Oceanology (UMR CNRS 7294 MIO, France). A 5-mL volume of 97% methanol (v/v) was added to the filter and left for 12 h in darkness at 4°C to extract pigments. The chl_a concentration of the extracts was measured using a Trilogy Fluorometer 7200-000 (Turner Designs, Sunnyvale, USA) according to [Welschmeyer \(1994\)](#).

Photosystem II (PSII) fluorescence was measured every two days using a Phyto-PAM ED fluorometer and its dedicated Phyto-Win software (Heinz Walz GmbH, Effeltrich, Germany; [Schreiber et al. 1986](#)). For each culture, one aliquot (8 mL) was incubated in darkness for 30 min at the growth temperature, for fully reoxidizing the electron acceptors of the PSII ([Bolhar-Nordenkamp et al., 1989](#)), before performing the measurement. The maximum quantum yield of PSII (F_v/F_m) is considered as an indicator of the cell physiological status ([Maxwell & Johnson, 2000](#)) and was calculated after cell excitation with a saturating pulse (4000 μmol photons m⁻²s⁻¹, F_m) over a weak blue light (1 μmol photons m⁻² s⁻¹; [Genty et al. 1989](#); equation 2).

$$F_v/F_m = (F_m - F_0)/F_m \quad (2)$$

where F_v is the variable fluorescence, F₀ and F_m are the minimum and the maximum fluorescence of the dark-adapted sample).

2.4.3 *Pigment and lipid content*

Pigments and lipids quantifications were realized for the two photoperiods and for all cultures on day 4. For pigment analyses, an aliquot of each culture (10 mL) was filtered on a GF/F filter (diameter 25 mm) and stored at -80°C pending analysis. Analyses were performed at the Villefranche Sea Institute (CNRS IMEV, SAPIGH, France). Filters were extracted (2 hours) in 3 mL of 100% methanol, disrupted by sonication and clarified by filtration (GF/F Whatman). Analysis of pigment composition was performed by HPLC as described by [Ras et al. \(2008\)](#).

For lipid analyses, a 100 mL aliquot of algal culture was filtered on a 47-mm diameter GF/F filter (Whatman), followed immediately by passing 10 mL of boiling distilled water through the filter in order to inhibit lipase activity and prevent lipid degradation

(González-Fernández et al., 2020). Filters were then placed in 6 mL of CHCl₃/MeOH mix (2:1, v:v) under N₂ flux for storage until processing lipid analyses. Analyses were performed at the Lipidocean facility (UMR CNRS 6539 LEMAR, France). Fractionation of neutral and polar lipids was made by solid phase extraction, and quantification of both fractions was realized by GC-FID/MS as described by González-Fernández et al. (2020). Total lipid content was calculated as the sum of polar and neutral lipid fractions. For both lipid fractions, three groups of fatty acids can be formed: i) saturated fatty acids (SFAs); ii) monounsaturated fatty acids (MUFAs); and iii) polyunsaturated fatty acids (PUFAs). In addition, the sum of some PUFAs in the total content was calculated focusing on two essential PUFA subgroups: Omega-3 (i.e. C₁₈:4n-3; C₂₀:4n-3; C₂₀:5n-3; C₂₂:5n-3; C₂₂:6n-3) and Omega-6 (i.e. C₁₈:2n-6; C₁₈:3n-6; C₂₀:3n-6; C₂₀:4n-6; C₂₂:4n-6; C₂₂:5n-6). Two essential Omega-3s have also been focused on because of their high nutritional value: EPA (C₂₀:5n-3) and DHA (C₂₂:6n-3).

2.5 Statistical analyses

All statistical tests were performed under R statistical software (RStudio Team, 2021). Statistical tests for mean comparison were carried out by one factor non-parametric Kruskal-Wallis tests ($\alpha = 0.05$), in order to identify differences between species within photoperiod (growth rate, lipid and pigment content), between photoperiods within species (growth rate, lipid and pigment content), between days within photoperiod and species (cell surface area, *chl a* content, Fv/Fm).

3. RESULTS

3.1 Experiment for setting the inoculum concentration

All cultures of both strains, whatever the inoculum concentration, grew without a lag phase and showed similar growth rates between 1.1 and 1.6 div d⁻¹ during the exponential growth phase (Figure 1A and B; Supplementary – Annexe IV – Table S1). Through days 4-7, the CTEN cultures reached maximum cell concentrations between 4.2 x10⁶ cell mL⁻¹ and 4.6 x10⁶ cell mL⁻¹ (Figure 1A; Supplementary – Annexe IV – Table S1). In contrast, the CCAL cultures grew further until the last day of the experiment (day 14), reaching maximum concentrations around 3 x10⁷ cell mL⁻¹ (Figure 1A; Supplementary – Annexe IV – Table S1).

As a result, the inoculum concentration of 100 x10³ cell mL⁻¹ was chosen as the most suitable to allow observation of the exponential growth phase of the two *Chaetoceros* species over a fairly long period. Indeed, the growth rates observed for these inoculum densities are similar for CTEN (1.3 div d⁻¹) and for CCAL (1.2 div d⁻¹; Figure 1B).

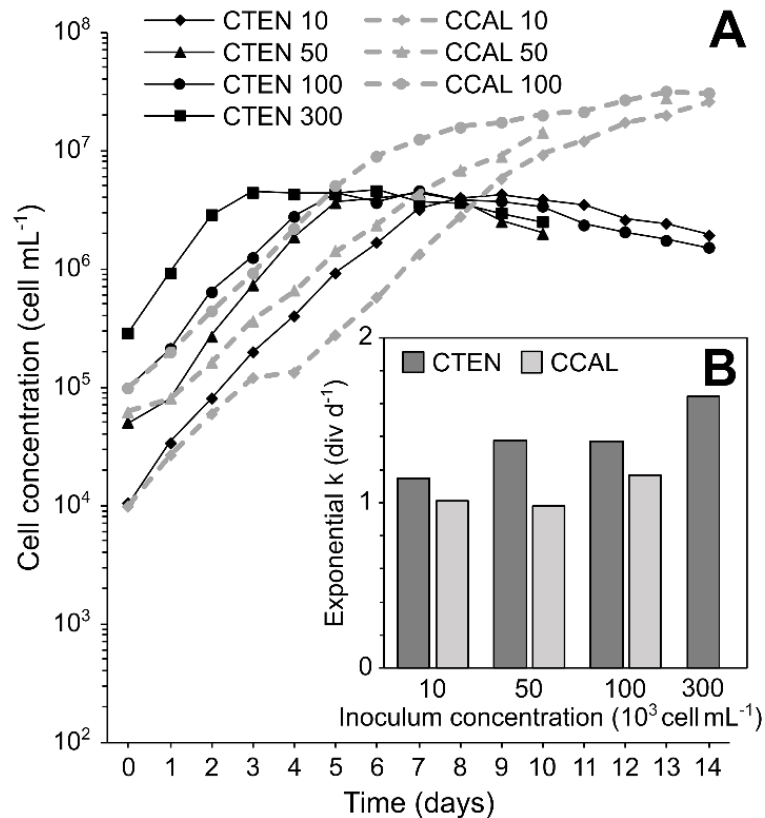


Figure 1 Preliminary experiment for setting the inoculum concentration under a 24:00 L:D photoperiod. A: Growth curves based on cell concentration (cell mL⁻¹) for CTEN strain (full black lines) and CCAL strain (dot grey lines) cultures with inoculum concentrations of 10×10^3 (diamond); 50×10^3 (triangle); 100×10^3 (full circle) and 300×10^3 (square) cell mL⁻¹. B: Exponential growth rate (k ; div d⁻¹) in CTEN (dark grey) and CCAL (light grey) cultures depending on inoculum concentration (10×10^3 to 300×10^3 cell mL⁻¹); the periods considered for calculation are the following: day 0 – day 7 for CTEN 10, day 1 – day 5 for CTEN 50; day 0 – day 4 for CTEN 100; day 0 – day 2 for CTEN 300; day 0 – day 8 for CCAL 10; day 1 – day 6 for CCAL 50 and day 1 – day 5 for CCAL 100.

3.2 Photoperiod experiments

3.2.1 Growth and cell section areas

In photoperiod experiments, after 8 days, the maximum densities obtained for CCAL cultures were between 7 and 8 times higher than those of CTEN cultures, depending on photoperiod treatments. Moreover, CCAL cultures showed systematically higher cell densities than CTEN cultures for both photoperiods (Figure 2A; Supplementary – Annexe IV – Table S2). In the 24:00 L:D treatment, the maximal densities were reached on day 5 for CTEN (3.9×10^6 cell mL⁻¹) and on day 8 for CCAL (33×10^6 cell mL⁻¹). During exponential growth phase in the 24:00 L:D treatment, highest growth rates were similar with $k = 2.1 \pm 0.1$ div d⁻¹ in the CTEN cultures for a short period (from day 1 to day 3) and $k = 2.0 \pm 0.1$ div d⁻¹ in the CCAL cultures between day 0 and day 2 (Figure 2B; Supplementary – Annexe IV – Table S2). The CTEN cultures quickly reached a maximum density plateau on day 4 whereas CCAL continued to grow at a

lower rate till day 8. Under the 12:12 L:D photoperiod, both CTEN and CCAL kept growing until day 8 (i.e. did not reach the stationary phase), reaching 2.6×10^6 cell mL⁻¹ and 19×10^6 cell mL⁻¹, respectively (Figure 2A; Supplementary – Annexe IV – Table S2). Exponential growth rates calculated for this photoperiod were significantly lower (p-value < 0.05) for CTEN (1.0 ± 0.1 div d⁻¹) compared to CCAL (1.6 ± 0.2 div d⁻¹).

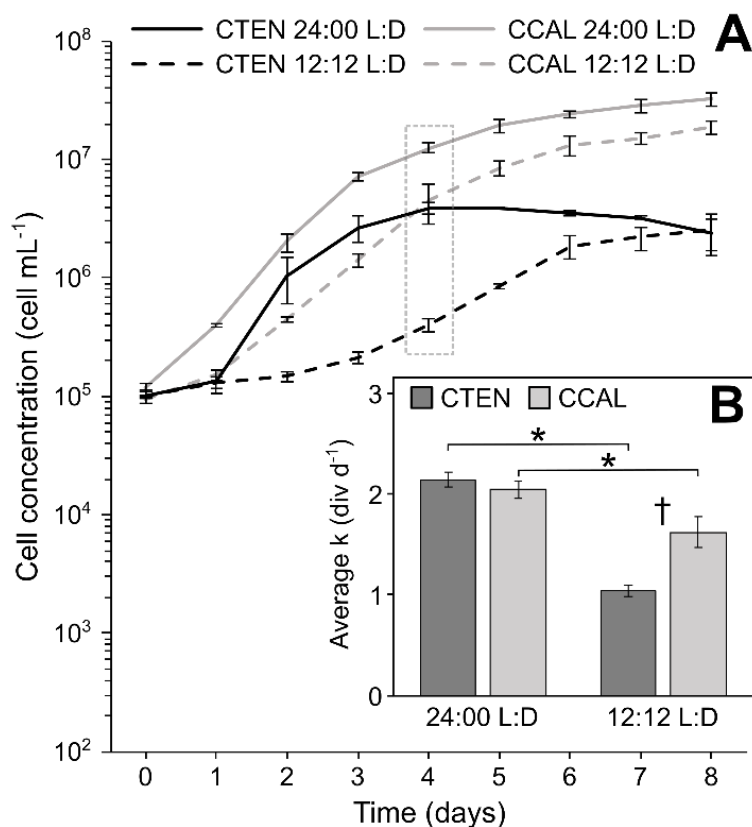


Figure 2 Cell growth of CTEN and CCAL depending on photoperiod treatment. A: Evolution of cell concentration (cell mL⁻¹; mean \pm SD; n=3) for CTEN (black lines) and CCAL (grey lines) cultures under 24:00 L:D (full lines) and 12:12 L:D (dot lines) photoperiod treatments. B: Average growth rate (k; div d⁻¹) for CTEN (dark grey) and CCAL (light grey) at each photoperiod; the periods considered for calculation were the following: day 1 – day 3 for CTEN 24:00, day 0 – day 2 for CCAL 24:00, day 3 – day 6 for CTEN 12:12 and day 1 – day 4 for CCAL 12:12. Error bars represent the standard deviation between replicate cultures (n = 3). Statistical comparisons (Kruskal-Wallis test) were made between photoperiods (*; p-value < 0.05) and between species (†; p-value < 0.05). The grey box on day 4 indicates the samples taken for the biochemical analyses of pigment and lipid contents.

The CTEN cultures showed morphological changes during cultures, with cell chain formation during exponential growth, whereas CCAL cultures remained containing solitary cells (Supplementary – Annexe IV – Figure S1). From micrograph analyses, CTEN cultures showed an average cell section area (mean \pm SD) of 51 ± 28 μ m² and CCAL showed similar results, with an average cell section area of 37 ± 9.3 μ m² (Figure 3; Supplementary – Annexe IV – Table S2). The calculated cell section areas for CTEN were larger in the 24:00 L:D photoperiod compared to the 12:12 L:D photoperiod. Under the 24:00 L:D photoperiod, strong variations in cell section areas were observed during growth in CTEN cultures with a significant decrease (p-value < 0.05) between day 0 (59

$\pm 21 \mu\text{m}^2$) and day 2 ($34 \pm 10 \mu\text{m}^2$), then levelling till on day 3 during exponential growth, followed by a significant gradual increase during late growth period between day 3 ($46 \pm 10 \mu\text{m}^2$) and day 8 ($91 \pm 42 \mu\text{m}^2$). Under the 12:12 L:D photoperiod, a first significant decrease (p-value < 0.05) in cell section areas of CTEN was observed between day 0 ($66 \pm 20 \mu\text{m}^2$) and day 4 ($28 \pm 6.5 \mu\text{m}^2$) followed by a significant gradual increase until day 7 ($49 \pm 16 \mu\text{m}^2$). Under both photoperiods, CCAL cultures mostly showed minor variations of cell section areas throughout growth, and overall, similar section area averages although slightly lower under the 12:12 L:D photoperiod (Figure 3; Supplementary – Annexe IV – Table S2).

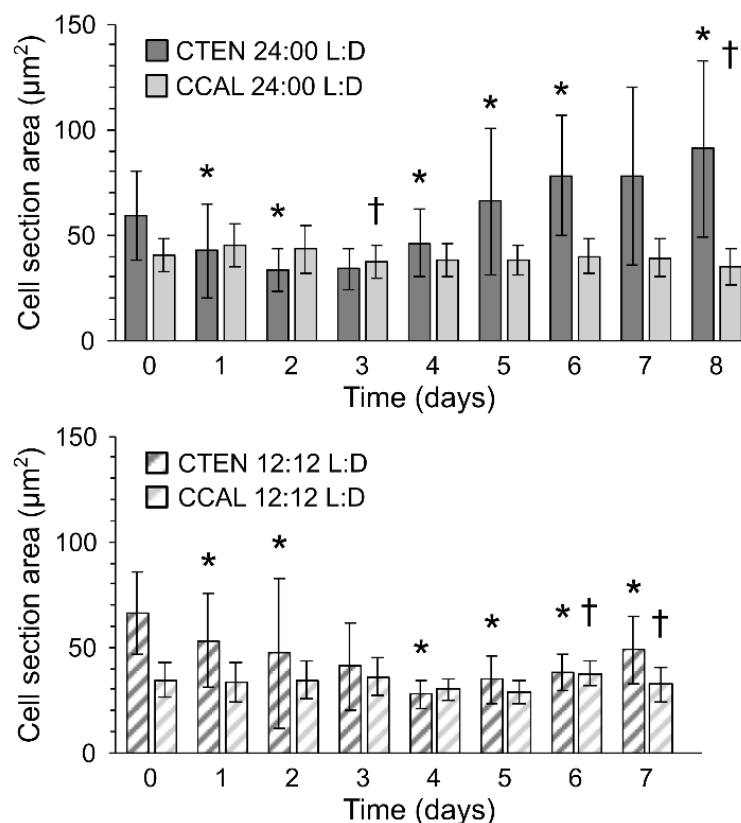


Figure 3 Variation in cell section area during photoperiod experiments (μm^2 ; mean \pm SD) of CTEN (dark grey) and CCAL (light grey) cultures under 24:00 L:D photoperiod (full bar) or 12:12 L:D photoperiod (hatched bar). Error bars represent the standard deviation between replicate cultures (n = 3). Significant differences (Kruskal-Wallis test) for CTEN (*) (p-value < 0.05) and CCAL (†) (p-value < 0.05) are expressed for time n compared to time n-1.

3.2.2 *Chlorophyll a and photosynthetic activity*

Throughout the growth of cultures, the cellular content of *chl a* showed statistically significant variations in the two strains and under the two photoperiods (Figure 4; Supplementary – Annexe IV – Table S2). Under the 24:00 L:D photoperiod in CTEN cultures, cellular *chl a* content at the inoculation time ($0.35 \pm 0.06 \text{ pg cell}^{-1}$) was divided by ~ 4 on day 2 down to $0.08 \pm 0.01 \text{ pg cell}^{-1}$, then gradually recovered to return to the initial value on day 8, with a sharp ~ 3 -fold increase from day 4 (from 0.11 ± 0.05

pg cell⁻¹) (Figure 4; Supplementary – Annexe IV – Table S2). In CCAL cultures, mean *chl a* content ranged between 0.11 ± 0.05 pg cell⁻¹ on day 4 and 0.34 ± 0.04 pg cell⁻¹ on day 0 without significant variations from day to day. In cultures grown under the 12:12 L:D photoperiod, the two strains showed a decreasing trend in their *chl a* content (Figure 4). In CTEN cultures, cellular *chl a* content was maximum in inoculated cells (0.32 ± 0.1 pg cell⁻¹ on day 0) and decreased all along growth till day 8 down to 0.12 ± 0.02 pg cell⁻¹, with a significant decrease between day 4 (0.18 ± 0.005 pg cell⁻¹) and day 6 (0.13 ± 0.02 pg cell⁻¹; p-value < 0.05). CCAL cultures showed a similar decreasing trend of *chl a* content between the inoculation day and day 6, down to 0.10 ± 0.02 pg cell⁻¹, before doubling back up in the late growth period until day 8.

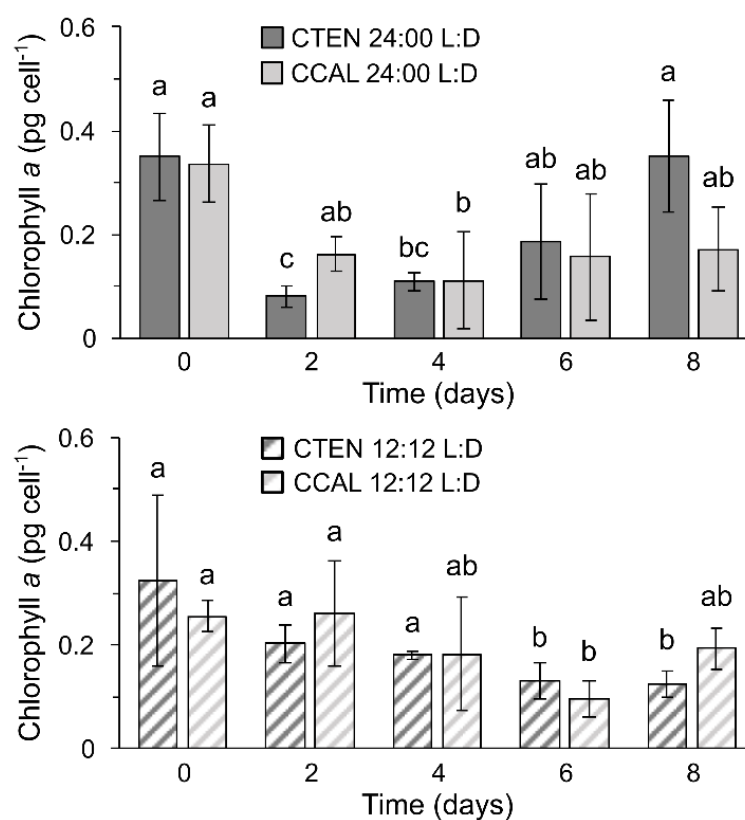


Figure 4 Variation in cellular *chl a* content (pg cell⁻¹; mean \pm SD) during photoperiod experiments for CTEN (dark grey) and CCAL (light grey), under 24:00 L:D (full bar) or 12:12 L:D (hatched bar) photoperiod. Error bars represent the standard deviation (n = 3). Statistical comparisons (Kruskal-Wallis test) were made between days for each photoperiod treatment and between strains (different letters represent significant differences (p-value < 0.05) between days).

In the monitoring of photosynthetic activity, overall, the Fv/Fm values measured in the CTEN cultures were lower than in the CCAL cultures (Figure 5). Under the 24:00 L:D photoperiod, CTEN cultures showed average Fv/Fm values between 0.21 ± 0.02 (day 8) and 0.62 ± 0.01 (day 2). A significant increase was observed between day 0 (0.39 ± 0.01) and day 2 followed by successive significant decreases until day 8. In CCAL cultures, average Fv/Fm values were between 0.60 ± 0.01 on day 2 and 0.68 ± 0.01 on day 6. Only

one significant increase was observed between day 2 and day 4 (0.66 ± 0.02). Under the 12:12 L:D photoperiod, the average Fv/Fm varied between 0.41 ± 0.01 (day 0) and 0.61 ± 0.02 (day 6) for the CTEN cultures. Although no significant difference was observed from day to day, a significant increase was measured between days 0 and 4 (0.60 ± 0.004). In CCAL cultures, average Fv/Fm values were between 0.56 ± 0.02 on day 0 and 0.71 ± 0.02 on day 8. Successive significant increases were calculated from day to day between day 0 and day 8 (p-value < 0.05; Figure 5).

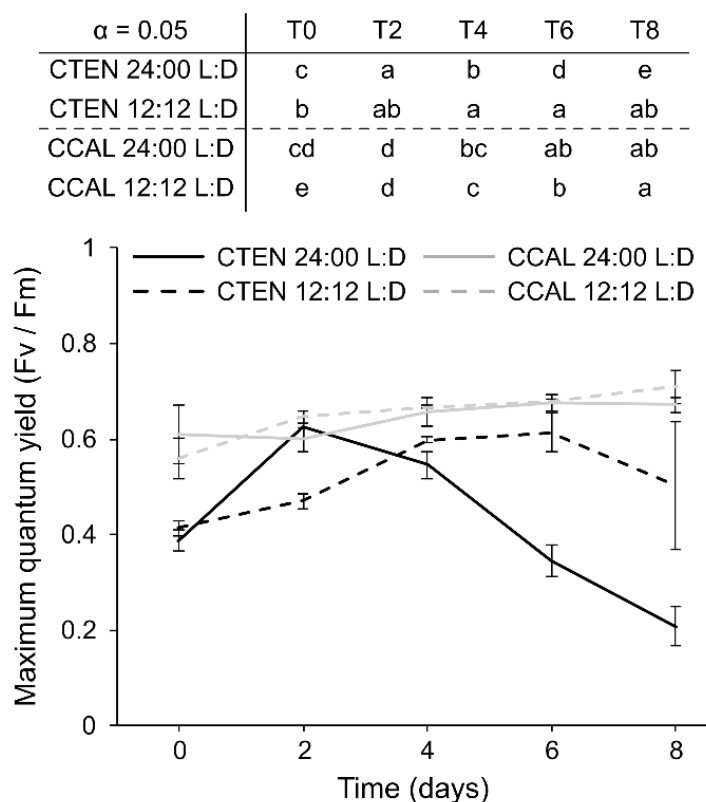


Figure 5 Variation of maximum quantum yield (Fv/Fm) during the photoperiod experiments (mean \pm SD) for CTEN (black lines) and CCAL (grey lines) cultures under 24:00 L:D (full lines) or 12:12 L:D (dot lines) photoperiod. Error bars represent the standard deviation (n = 3). Statistical comparisons (Kruskal-Wallis test) were made between times and significant differences (p-value < 0.05) are reported in the table at the top and represented by different letters.

3.2.3 Pigment and lipid composition

On day 4, xanthophyll (i.e. sum of fucoxanthin, diadinoxanthin and diatoxanthin), chlorophyllid *a* and β -carotene mean concentrations (mean \pm SD) were quantified on CTEN and CCAL cultures (Table 1; see pigment and lipid content expressed in mg L⁻¹ in Supplementary – Annexe IV – Table S3). Overall, cellular concentrations of these pigments were higher in CCAL cells than in CTEN cells whatever the photoperiod, except for chlorophyllid *a*. Regarding cultures under the 24:00 L:D photoperiod, CTEN cells showed xanthophyll concentrations of 0.09 ± 0.02 pg cell⁻¹, chlorophyllid *a* concentrations of 0.17 ± 0.07 pg cell⁻¹ and β -carotene concentrations of

0.01 ± 0.001 pg cell⁻¹. Conversely, CCAL cultures exhibited higher concentrations of xanthophyll (0.32 ± 0.02 pg cell⁻¹), chlorophyllid *a* values below the detection limit (LD = 0.3 ng L⁻¹) and β -carotene concentrations similar to CTEN with 0.01 ± 0.003 pg cell⁻¹ (Table 1). Under the 12:12 L:D photoperiod, CTEN cultures showed concentrations of xanthophyll, chlorophyllid *a* and β -carotene of 0.19 ± 0.01 pg cell⁻¹, 0.15 ± 0.01 pg cell⁻¹ and 0.01 ± 0.001 pg cell⁻¹, respectively. Conversely, CCAL cells displayed higher concentrations of xanthophyll (0.34 ± 0.02 pg cell⁻¹) and β -carotene (0.02 ± 0.001 pg cell⁻¹). Chlorophyllid *a* values were also below the detection limit.

Under the 24:00 L:D photoperiod, the CTEN cultures showed average total lipid concentrations of 2.4 ± 0.1 pg cell⁻¹ with a slight dominance of the neutral lipid fraction (62%) compared to the polar lipid fraction (38%) (Figure 6; Table 1). CCAL cultures showed higher total lipid concentrations (4.9 ± 0.2 pg cell⁻¹; Table 1) with quite similar proportions of neutral (59%) and polar (41%) lipid fractions (Figure 6). Overall, total lipids were evenly distributed between SFAs, MUFAs and PUFAs for both *Chaetoceros* species. However, the polar lipid fraction was dominated by PUFAs with 48% and 56% for CTEN and CCAL respectively (Figure 6). Conversely, CCAL exhibited a low percentage of PUFAs in the neutral lipid fraction (16%) compared to SFAs and MUFAs (Figure 6). Regarding essential lipids, CTEN cultures showed average concentrations of 0.46 ± 0.2 pg cell⁻¹ and 0.05 ± 0.01 pg cell⁻¹ for the Omega-3 and Omega-6 subgroups respectively (Table 1). These essential lipids were equally distributed between neutral and polar fractions. EPA represented 80% (0.37 ± 0.1 pg cell⁻¹) and DHA represented 15% (0.07 ± 0.02 pg cell⁻¹) of the Omega-3 subgroup (Table 1). CCAL cells displayed higher average concentrations of Omega-3 (0.73 ± 0.03 pg cell⁻¹) and Omega-6 (0.24 ± 0.04 pg cell⁻¹) subgroups than CTEN cultures (Table 1). A large dominance was observed for the polar lipid fraction ($\approx 70\%$) compared to the neutral lipid fraction for the two subgroups. In CCAL cultures, EPA represented 85% (0.62 ± 0.02 pg cell⁻¹) and DHA represented 8% (0.06 ± 0.003 pg cell⁻¹) of the Omega-3 subgroup (Table 1).

Table 1 Cellular pigment and lipid content (pg cell^{-1} ; mean \pm SD) in CTEN and CCAL cultures under the two photoperiod treatments (24:00 L:D; 12:12 L:D) on day 4. Statistical comparisons (Kruskal-Wallis test) were made between photoperiod treatments (*; p -value < 0.05) and between strains (\dagger ; p -value < 0.05).

Pigments & Lipids (pg cell^{-1})		CTEN		CCAL	
		24:00 L:D	12:12 L:D	24:00 L:D	12:12 L:D
Pigment composition	Xanthophyll ⁽¹⁾	0.091 \pm 0.036	0.194 \pm 0.012 *	0.324 \pm 0.036 \dagger	0.335 \pm 0.027 \dagger
	Fucoxanthin	0.083 \pm 0.034	0.167 \pm 0.011 *	0.288 \pm 0.034 \dagger	0.295 \pm 0.024 \dagger
	Diadinoxanthin	0.008 \pm 0.003	0.019 \pm 0.001 *	0.035 \pm 0.003 \dagger	0.040 \pm 0.003 \dagger
	Diatoxanthin	< LD ⁽⁴⁾	0.008 \pm 0.001	0.001 \pm 0.000	< LD ⁽⁴⁾
	Chlorophyllid <i>a</i>	0.167 \pm 0.125	0.155 \pm 0.024	< LD ⁽⁴⁾	< LD ⁽⁴⁾
	β -carotene	0.009 \pm 0.001	0.011 \pm 0.001 *	0.014 \pm 0.003 \dagger	0.019 \pm 0.001 * \dagger
Total lipids	Total	2.426 \pm 0.794	2.561 \pm 0.185	4.898 \pm 0.687 *	2.060 \pm 0.197
	SFA	0.787 \pm 0.242	0.950 \pm 0.071 \dagger	1.681 \pm 0.318 *	0.474 \pm 0.045
	MUFA	0.759 \pm 0.267	0.714 \pm 0.049 \dagger	1.640 \pm 0.270 *	0.475 \pm 0.060
	PUFA	0.880 \pm 0.285	0.897 \pm 0.066	1.578 \pm 0.100 *	1.111 \pm 0.092 \dagger
	Omega-6 ⁽²⁾	0.046 \pm 0.010	0.033 \pm 0.001 \dagger	0.241 \pm 0.041 *	0.026 \pm 0.003
	Omega-3 ⁽³⁾	0.465 \pm 0.165	0.442 \pm 0.029	0.731 \pm 0.030 *	0.491 \pm 0.021
	EPA	0.369 \pm 0.132	0.349 \pm 0.021	0.621 \pm 0.018 *	0.411 \pm 0.014 \dagger
	DHA	0.068 \pm 0.023	0.061 \pm 0.004 \dagger	0.059 \pm 0.003 *	0.037 \pm 0.004
Polar lipids	Total	0.916 \pm 0.141	1.570 \pm 0.144	1.989 \pm 0.123	1.820 \pm 0.178
	SFA	0.257 \pm 0.039	0.402 \pm 0.035	0.460 \pm 0.010 *	0.367 \pm 0.036
	MUFA	0.220 \pm 0.042	0.495 \pm 0.050	0.423 \pm 0.022	0.394 \pm 0.053
	PUFA	0.438 \pm 0.060	0.674 \pm 0.060	1.106 \pm 0.091	1.060 \pm 0.089 \dagger
	Omega-6 ⁽²⁾	0.028 \pm 0.003	0.025 \pm 0.001	0.162 \pm 0.015 *	0.025 \pm 0.003
	Omega-3 ⁽³⁾	0.213 \pm 0.028	0.354 \pm 0.028	0.522 \pm 0.048	0.476 \pm 0.022 \dagger
	EPA	0.143 \pm 0.006	0.291 \pm 0.021	0.442 \pm 0.043	0.400 \pm 0.015 \dagger
	DHA	0.055 \pm 0.018	0.049 \pm 0.004 \dagger	0.050 \pm 0.003 *	0.035 \pm 0.004
Neutral lipids	Total	1.510 \pm 0.667	0.990 \pm 0.066 \dagger	2.910 \pm 0.717 *	0.240 \pm 0.024
	SFA	0.530 \pm 0.203	0.548 \pm 0.042 \dagger	1.221 \pm 0.324 *	0.108 \pm 0.010
	MUFA	0.539 \pm 0.226	0.219 \pm 0.004 \dagger	1.217 \pm 0.286 *	0.081 \pm 0.008
	PUFA	0.441 \pm 0.238	0.222 \pm 0.020 \dagger	0.472 \pm 0.108 *	0.051 \pm 0.006
	Omega-6 ⁽²⁾	0.017 \pm 0.001	0.008 \pm 0.001 \dagger	0.078 \pm 0.001 *	0.001 \pm 0.001
	Omega-3 ⁽³⁾	0.252 \pm 0.149	0.087 \pm 0.013 \dagger	0.208 \pm 0.056 *	0.015 \pm 0.002
	EPA	0.226 \pm 0.138	0.058 \pm 0.004 \dagger	0.178 \pm 0.046 *	0.011 \pm 0.001
	DHA	0.013 \pm 0.005	0.011 \pm 0.013	0.009 \pm 0.002 *	0.002 \pm 0.001

⁽¹⁾ Sum of pigments fucoxanthin, diadinoxanthin and diatoxanthin

⁽²⁾ Sum of lipids C18:2n-6; C18:3n-6; C20:3n-6; C20:4n-6; C22:4n-6; C22:5n-6

⁽³⁾ Sum of lipids C18:4n-3; C20:4n-3; C20:5n-3 (EPA); C22:5n-3; C22:6n-3 (DHA)

⁽⁴⁾ Below the detection limit

Under the 12:12 L:D photoperiod, the CTEN cells showed average total lipid concentrations of $2.6 \pm 0.1 \text{ pg cell}^{-1}$. Unlike the 24:00 L:D photoperiod, here the polar lipid fraction (61%) dominated slightly over the neutral lipid fraction (39%) (Figure 6; Table 1). CCAL cultures showed similar total lipid concentrations ($2.1 \pm 0.1 \text{ pg cell}^{-1}$; Table 1) as CTEN and a large dominance of the polar lipid fraction (88%) over the neutral lipid

fraction (12%) (Figure 6). Similar to the previous results, total lipids were evenly distributed among SFAs, MUFAs, and PUFAs for CTEN cultures (Table 1). However, CCAL cells showed a higher percentage of PUFAs (54%) in the total lipid fraction compared to SFAs (23%) and MUFAs (23%). Regarding essential lipids, CTEN cultures showed average concentrations of 0.44 ± 0.03 pg cell⁻¹ and 0.03 ± 0.001 pg cell⁻¹ for the Omega-3 and Omega-6 subgroups respectively (Table 1). Here, essential lipids showed a greater proportion in the polar lipid fraction (> 80%) than in the neutral lipid fraction. In the Omega-3 subgroup, EPA represented 80% (0.35 ± 0.02 pg cell⁻¹) and DHA represented 14% (0.06 ± 0.005 pg cell⁻¹) of the subgroup (Table 1). CCAL cells displayed mean concentrations similar to those of CTEN for Omega-3 (0.49 ± 0.02 pg cell⁻¹) and Omega-6 (0.03 ± 0.003 pg cell⁻¹) subgroups (Table 1). CCAL cultures also showed a large dominance of the polar lipid fraction (> 90%) compared to the neutral lipid fraction of the two subgroups. Finally, EPA represented 84% (0.41 ± 0.01 pg cell⁻¹) and DHA represented 8% (0.04 ± 0.004 pg cell⁻¹) of the Omega-3 subgroup as in CTEN cultures (Table 1).

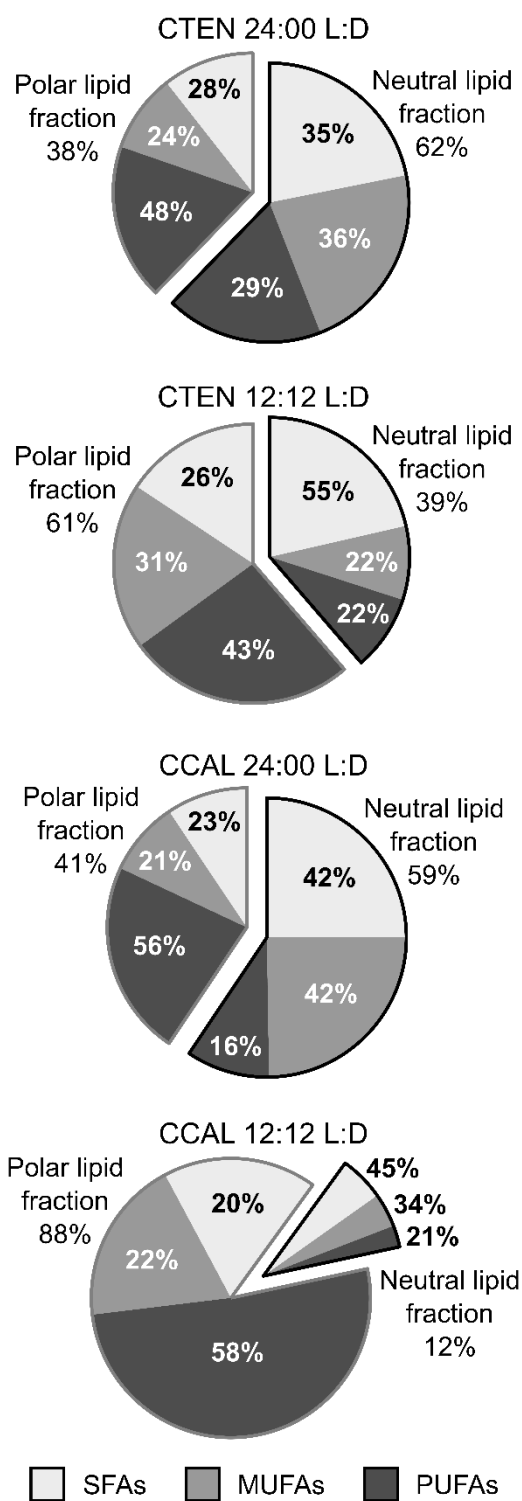


Figure 6 Cellular lipid content ratio (by weight) in CTEN and CCAL cultures, depending on the photoperiod treatment, on the fourth day of cultivation. Lipid content (which is detailed in Table 1) is expressed in percentage (%) for the different lipid fractions: the polar (grey outline) and neutral (black outline) fractions are represented; then for the neutral and polar lipid fractions separately, the percentage composition of PUFAs (dark grey), MUFAs (medium-dark grey) and SFA (light grey) are shown.

4. DISCUSSION

4.1 Effects of photoperiod

4.1.1 Growth dynamics

Maximal densities of *C. simplex* var. *calcitrans* (CCAL) were obtained on the last experimental day, during the stationary phase and for both photoperiods tested, while for *C. tenuissimus* CT16ED (CTEN), maximal cellular densities were obtained at day 5 (24:00 L:D) and day 8 (12:12 L:D), similarly to results obtained during inoculum density experiments.

Growth of microalgae are known to be strongly depending from culture conditions and especially from light settings, like photoperiod (e.g. Parmar et al. 2011; Krzemińska et al. 2014). Due to the major influence of culture conditions (e.g. light intensity, temperature), it is difficult to compare our results to those from other studies. Nevertheless, Figueroa-Torres et al. (2021)'s estimation of maximal cellular densities between 7×10^6 and 13×10^6 cell mL⁻¹ (24:00 L:D) is congruent with our results concerning CCAL. Likewise, Robert et al. (2004) observed cellular densities (28.5×10^6 cell mL⁻¹) and growth rates (1.99 div d⁻¹) which are close to our observations. Based on our findings and corroboration by some previous studies, it seems that the 24:00 L:D photoperiod allows a better growth efficiency for CCAL. Indeed, the 24:00 L:D photoperiod is commonly applied in aquaculture in order to maximize biomass of microalgae cultures (e.g. Fakhri et al. 2015; Beigbeder & Lavoie 2022).

Regardless of inoculum concentration and growth conditions implemented in our experiments, CTEN reached stationary phase with a plateau settling at around $4\text{-}5 \times 10^6$ cell mL⁻¹. These results are congruent with other studies on similar species, which showed maximal cellular densities similar to our findings, reaching between 1×10^6 to 4×10^6 cell mL⁻¹ (e.g. Shirai et al. 2008; Hano & Tomaru 2019; Figueroa-Torres et al. 2021), except that, to our knowledge, no previous studies highlighted the plateau we observed in CTEN cellular densities. Assuming that no nutrient or CO₂ limitation occurred, relative to high nutrient richness of culture medium and CO₂ supply as well as no significant pH variation (data not shown), it is not clear what was involved in explaining this limitation of maximal cell concentration in cultures. From these observations, it is suggested here that growth inhibition occurred due to cell-to-cell contact (favored by aeration generating small-scale turbulence inside culture). This could take place particularly at the long setae of this organism (Grzebyk et al., 2022) and could correspond to a kind of quorum sensing phenomenon. Costas et al. (1993) identified growth inhibition due to cell-to-cell contact in *Prorocentrum lima* species and attributed this phenomenon to a self-control

mechanism against cellular proliferation that can manifest in natural environment during phytoplankton bloom events.

The CTEN strain was described with cells sizing 7 to 12 μm long, 3 to 6 μm large, and having long setae, reaching 25 to 30 μm in length (Grzebyk et al., 2022). With this data it is possible to estimate the volume occupation of a CTEN cell, approximated to a sphere, ranging from $100 \times 10^3 \mu\text{m}^3$ to $207 \times 10^3 \mu\text{m}^3$, and accordingly, the obtained theoretical maximal density, without any contact between cells, would range between 4.8×10^6 and $10 \times 10^6 \text{ cell mL}^{-1}$. This theoretical density range corresponds to the limit densities observed during our experiments, hence supporting the hypothesis of growth inhibition induced by cell-to-cell contact. Furthermore, during our measurements of cellular section area, we noticed that some CTEN cells had setae reaching a length up to 40 μm , thus scaling theoretical maximal densities (without contact between cells) down to 2.3×10^6 to $2.8 \times 10^6 \text{ cell mL}^{-1}$. In another calculation (for a cell radius fixed at 25 μm going from the cell center to the end of a seta), it can be estimated that two cells would be separated from each other by less than an equivalent cellular spherical volume for a cell concentration above $2 \times 10^6 \text{ cell mL}^{-1}$. Therefore, taking into account the turbulent movements in the culture medium, cell-to-cell contacts by the setae may occur more frequently above $2 \times 10^6 \text{ cell mL}^{-1}$, and we hypothesize that these cell-to-cell contacts cause the inhibition of cell growth and induce the passage of the culture into stationary phase, resulting in an early plateauing of the cell concentration.

The growth observed for CTEN showed strong differences according to the photoperiod. Under the 12:12 L:D photoperiod, CTEN was characterized by a slow and constant growth, until reaching stationary phase on day 6. The associated specific growth rates are then generally low, but still positive. Conversely, under the 24:00 L:D photoperiod, CTEN showed a rapid growth, associated with high growth rate until day 3 and followed by a stationary phase, characterized by the downfall of growth rates until the end of the experiments. This was confirmed by the presence of chlorophyllid *a* pigment at day 4, especially under the photoperiod 24:00, which was not detectable in CCAL cultures and which is usually associated with diatom's senescence, indicating a mortality of the cells (Bidigare et al., 1986 and references herein).

4.1.2 Chlorophyll *a* and photosynthetic activity

Under the 24:00 L:D photoperiod, CCAL showed a strong decline of the cellular concentrations of *chl a* between day 0 and day 2, while no decrease was observed under the 12:12 L:D photoperiod. This could be due to protection mechanisms against cellular damage from excess energy input and the formation of reactive oxygen species (ROS). In fact, according to Thorel et al. (2014), strong irradiation can cause a decrease in the

cellular content of *chl a* as a photoacclimation adaptive strategy of the organisms. For CTEN, a significant reduction in *chl a* cellular content was also observed between day 0 and day 2 under the 24:00 photoperiod and this could support the hypothesis of a photoacclimation process (Thorel et al., 2014). Afterwards, *chl a* concentrations in CTEN increased, until reaching values close to the initial ones and in line with results obtained by Doblin et al. (1999) and Sarker et al. (2016) for other *C. tenuissimus* strains. These observations could indicate a stress on organisms exposed to 24:00 L:D photoperiod: it is possible that the excess of light energy received under continuous irradiance provoke the formation of ROS, thus causing potential cell damage (Zhang et al., 2017). Also, maybe the light intensity used for our experiments was too strong for CTEN, thus inducing stress on this species (Wahidin et al., 2013). Besides, the natural 12:12 L:D photoperiod seems the most appropriate to guarantee an optimal growth and maintenance of this new CTEN strain, issued from natural environment.

An interesting feature, observed during the photoperiod experiments, is the strong variation in cellular section area for CTEN during the different growth phases (see morphology in Supplementary – Annexe IV – Figure S1). This was particularly evident under the 24:00 L:D photoperiod, when cells were two to three fold bigger towards the end of the experiments compared to the start. Regardless of the photoperiod, these progressive increases in cells sizes took place when the density plateau was reached and cultures entered the beginning of the stationary phase. In their work, Robert et al. (2004) described the evolution of cellular densities and biovolumes of *Chaetoceros "minus"* and demonstrated an increase in cells size throughout the growth of this species. Similar to our observations, the authors could identify a dispersion in cells size distribution during growth. In our study, the augmentation in cells section area during the stationary phase was paralleled by an increase in *chl a* cellular content, regardless of the photoperiod.

These observations may indicate that the shift from the reaching of the cellular density plateau to the beginning of the stationary phase of the cultures is associated to an impoverishment of the culture medium. Decreases in cellular contents of *chl a* during the shift to the stationary phase in cultures are documented in literature and linked to nutrient limitation in the cultivation medium (e.g. Phatarpekar et al. 2000). However, our results on CTEN cultures show stable (12:12 L:D) or increasing (24:00 L:D) *chl a* levels during the stationary phase. Moreover, during our inoculum essays, no CTEN culture showed the senescent phase typical of the impoverishment of the culture medium, not even after nine days in the stationary phase. An alternative hypothesis can thus be that the observed growth inhibition, observed in all CTEN cultures during the study, could be linked to contact-inhibition between cells, previously discussed.

The maximal photosynthetic efficiency of photosystem II (Fv/Fm) is widely used as a proxy for the estimation of photosynthetic stress in plants (e.g. Schreiber 1983; White et al. 2011). Concerning microalgae and algae in general, Fv/Fm values ranging between 0.6 – 0.65 are universally considered an indicator of good health state of the organisms (e.g. Maxwell & Johnson 2000; Parkhill et al. 2001). During our experiments, CCAL showed relatively contrasting and elevated Fv/Fm values. Hence, we can affirm that our CCAL cultures maintained a good health status during the whole study and that photoperiod did not significantly affect the photosynthetic efficiency of CCAL. These observations are hence congruent with those reported by Zhang et al. (2017) on *C. calcitrans*. As for CTEN, under both photoperiods the Fv/Fm values were initially low, in accordance with a study by Kottuparambil & Agusti (2020) on another strain of *C. tenuissimus* from natural environment. Under 12:12 L:D photoperiod, CTEN generally showed increasing Fv/Fm values throughout the entire duration of the experiments, reaching a maximum at day 6 and globally indicating a good health status of the organisms (e.g. Maxwell & Johnson 2000; Parkhill et al. 2001). On the other hand, under 24:00 L:D photoperiod, CTEN's Fv/Fm evolution was characterized by a significant increase between day 0 and day 2, followed by significant successive decreases up until the end of the experiments. This decrease corresponded to the stationary phase period previously commented, and might explain the drop down of growth rates.

4.1.3 Pigment and lipid content

Pigments are of great interest for aquaculture industry, mainly for the pigmentation and organoleptic characteristics of the fish flesh (Patras et al., 2019; Rizwan et al., 2018; Schüler et al., 2017). The importance of *C. calcitrans* regarding aquaculture applications and pigment production is universally known and our results on CCAL strain can confirm knowledge from literature about pigment production of this species (Whyte, 1987; Zhang et al., 2017). During our experiments, pigment content in CCAL was not affected by photoperiod, while for CTEN, the 12:12 photoperiod resulted more suitable for pigment production. In fact, under the 12:12 L:D photoperiod a stronger xanthophyll concentration could be detected for CTEN, of which 89% was constituted by the light-harvesting fucoxanthin. Nevertheless, when compared to CCAL, CTEN did not show any particularly interesting feature in pigment production.

Like other species of the *Chaetoceros* genus, *C. calcitrans* is known for its high content in essential lipids, as notably EPA (e.g. Volkman et al. 1989; Brown 2002). The cellular concentrations of total lipids and their fractions' proportions can vary widely, depending on the growth phase and culture conditions (e.g. Muller-Feuga et al. 2003; Miller et al. 2014). For CCAL, lipid analyses were performed between the end of

the exponential growth phase (12:12 L:D) and the beginning of stationary phase (24:00 L:D). Cellular concentrations of total lipids were significantly higher under 24:00 L:D than 12:12 L:D photoperiod. In *C. calcitrans* forma *pumilum* under continuous light, Ponis et al. (2003) estimated a mean cellular concentration of total lipids of 3.0 ± 0.2 pg cell⁻¹ during the stationary phase, while Miller et al. (2014) reported concentrations between 3.5 and 7.4 pg cell⁻¹ following the growth phase. Similarly, Robert et al. (2004) estimated cellular concentrations of total lipids in CCAL of 2.2 pg cell⁻¹ and 5.1 pg cell⁻¹ during the exponential and stationary phases, respectively. Our results are hence in the range of total lipids' concentrations described in literature for CCAL.

A closer look on lipids fractionation and on different groups among the total lipids highlights higher proportions of PUFAs (54%), including Omega-3 (24%) and EPA (20%), for CCAL under the 12:12 L:D photoperiod. Multiple studies have described strong PUFA's proportions under photoperiods including long dark phases (Krzemińska et al., 2014). Lim & Zaleha (2013) hypothesized that under light-limiting conditions (12:12 L:D), the organisms increase thylakoid membrane surface, the expansion of which is hence associated to a strong need of polar PUFAs as major component of membranes. In our study, for similar cell amounts of total polar lipids and polar PUFAs, the polar fraction under the 12:12 L:D photoperiod represented 88% of total lipids and polar PUFAs fraction alone represented 51% of cell amount of total lipids, vs. 40.6 and 22.6 % under continuous light, respectively.

Based on these observations regarding the relative richness of essential lipids in CCAL cultures, the 12:12 L:D photoperiod is a better condition in term of PUFA production, of EPA in particular, compared to continuous light.

For lipid content in CTEN, total lipid cellular concentrations did not show a marked distinction between the two photoperiods. Muller-Feuga et al. (2003) estimated that *Chaetoceros* genus shows total lipid concentrations of around 2 pg cell⁻¹ on average. In their work on a species defined as *Chaetoceros "tenuissimus-like"*, Robert et al. (2004) estimated total lipids contents of 1.1 pg cell⁻¹ and 1.3 pg cell⁻¹ during the exponential and stationary phases, respectively. These observations are congruent with our results, even though CTEN showed slightly higher values than those documented in literature.

The different groups constituting the total lipids showed similar proportions between the two photoperiods, among the SFAs, the MUFAs and the PUFAs as well as between the Omega-3 and the Omega-6. Nevertheless, we observed opposite proportions between the two photoperiods: under the 12:12 L:D photoperiod 61% of total lipids was constituted by the polar lipid fraction and under the 24:00 L:D photoperiod 62% was of the neutral fraction. These findings are in accordance with knowledge from literature, showing energy stocking under the form of neutral lipids during the stationary phase (e.g. Mansour et al. 2003; Miller et al. 2014). These neutral lipids are then used as energy

resources for the aerobic metabolism of the cells (Miller et al., 2014). However, our results do not allow to determine whether either photoperiod is more suitable for essential lipids production (Omega-6; Omega-3 of which EPA and DHA) in this new strain of *C. tenuissimus* CT16ED.

4.2 *Chaetoceros tenuissimus* CT16ED as a potential strain for aquaculture

4.2.1 General contributions of the study

This study describes for the first time the potential for *C. tenuissimus* CT16ED strain biotechnological applications. It constitutes a preliminary essential step in evaluating potential aquaculture exploitation of this strain. Nevertheless, it was difficult to compare our findings with other studies on the physiological properties and growth of microalgae, both due to culture conditions, but also due to the lack of knowledge and exhaustive descriptions of species and strains used elsewhere. In this study, the selected strains are well known as they are characterized genetically (Grzebyk et al., 2022) and morphologically (panel photos in Supplementary – Annex IV – Figure S1). Hence, since there is no confusion about strains identification, this work is also a valuable contribution for future studies as it provides a solid base for comparison.

Our study compared two culture setups with different photoperiods tested, which represent interesting conditions in the aquaculture domain. The 24:00 L:D photoperiod is widely used in aquaculture in order to favor microalgal growth and specifically to obtain high biomasses in a short time span (e.g. Fakhri et al. 2015; Beigbeder & Lavoie 2022), while the 12:12 L:D photoperiod is particularly suitable for potential applications of natural aquaculture systems, like outdoor plants. This is relevant, since nowadays the outdoor cultivation systems are widely used for the production of microalgae at large scale (Pérez et al., 2017). In light of the present context requiring energy sobriety, this kind of culture, exploiting natural solar radiation as source of energy, seems a very suitable option (Guo et al., 2015).

To our knowledge, only few studies have reported on the description of growth and features or biochemical composition of *C. tenuissimus* in comparison with other species of the same genus. Diatoms of the *Chaetoceros* genus are particularly appreciated in the aquaculture domain, due to their rapid growth, high cellular densities in culture and high content of essential lipids (e.g. Volkman et al. 1989; Brown 2002; Robert et al. 2004). Amongst these species, *C. simplex* var. *calcitrans* is commonly used (e.g. Volkman et al. 1989; Brown 2002) and was hence chosen for this study as comparison organism to evaluate the potential aquaculture interest of the strain *C. tenuissimus* CT16ED (CTEN) originating from a lagoon environment. This is particularly

interesting since estuarine and lagoon species are already known to have peculiar characteristics in comparison to their pelagic counterparts, even within the same species. For instance, the estuarine strain (3H) of diatom *Thalassiosira pseudonana* showed a higher tolerance to salinity and temperature variations, and different pollution sensitivity, than its pelagic strain (13-1) counterpart (Fisher & Schwarzenbach, 1978). Also, a local species, issued from natural environment, would provide multiple advantages in this context, like a stronger resistance towards disturbance and environmental variations (e.g. salinity, temperature) and a better adaptability to local conditions, since it would better fit with the conditions of the region of origin (Hotos & Avramidou, 2021; Tzovenis et al., 2009). Hence, the use of a species, issued from a high hydrologically variable natural system, like a lagoon environment, makes it an adapted option for an outdoor production, even more efficiently at local industry scale (Cheregi et al., 2019). Thus, this work can contribute to the development of technological applications of a new strain to enhance local aquaculture activity.

4.2.2 Interesting features of CTEN strain

During exponential growth phase (after four days in culture), despite showing lower maximal cellular densities than CCAL, CTEN exhibited a biomass dietary quality similar to those observed in CCAL. Moreover, CTEN growth rates in the exponential phase were similar to those obtained for CCAL. Hence, these characteristics indicate that an utilisation of CTEN as diet for aquaculture seems appropriate.

With CTEN, the increases of *chl a* content and size of cells along the stationary phase indicated nutrient-replenished cells in term of nitrogen and phosphorus, and hence with a high particulate carbon content (Riemann et al., 1989), including proteins and lipids (e.g., membrane phospholipids). These characteristics are particularly interesting for the cultivation of mollusks and shrimps larvae in hatchery (Muller-Feuga et al., 2003). Mollusk larvae, depending on their size, are able to ingest a large size-range of preys (from 0.5 to 30 µm diameter), with an optimum varying according to mollusk species, and a positive correlation exists between the size of larvae and that of ingested preys (Muller-Feuga et al., 2003). In shrimp hatchery, the larvae do not show selective prey ingestion according to size but rather feed on a large size range of the preys, from 5 to 20 µm of diameter (Muller-Feuga et al., 2003). Furthermore, Galgani & AQUACOP (1988) reported that the stadia I and II of zoeae of the Penaeidae family can feed on preys of 35 µm and 50 µm diameter, respectively.

As we demonstrated during our study, a large size range of cells is provided from CTEN cultures: this feature can hence be an important asset for the mollusk and shrimp hatchery (Phatarpekar et al., 2000). In fact, usually in these kinds of aquaculture,

multiple stages of development, and hence multiple larval sizes, are present simultaneously. In this context, a variety of adapted preys' sizes is hence required. CTEN could also be suitable for the feeding of live preys (e.g. *Artemia*, copepods, rotifers) subsequently used as nourishment in fish aquaculture (Muller-Feuga et al., 2003). Furthermore, numerous studies already underlined the beneficial effects of using mixes of different microalgae species as food supply for aquaculture species (e.g. Gomes et al. 2021). Therefore, the use of CTEN as food supplement in aquaculture seems to be a potential interesting application, thanks to the particular characteristics of this species (e.g. size variety, lipid content).

However, under the 24:00 L:D photoperiod, CTEN showed a poor health status and a short-time lasting culture maintenance. Moreover, numerous studies have already proven the 24:00 L:D photoperiod unsuitable for the production of high lipid concentrations in microalgae (e.g. Amini Khoeyi et al., 2012; Lim & Zaleha, 2013; Wahidin et al., 2013). Indeed, it seems that a photoperiod comprising a longer dark phase is more suitable for the production of microalgae rich in essential lipids, such as PUFAs. Hence, it is more pertinent to assess the nutritional potential and performances of CTEN under the 12:12 L:D photoperiod, under which CTEN showed indeed a general good health and higher biomass values than those of CCAL on day 4.

Overall, under this photoperiod, both species showed similar cellular concentrations of total lipids, with the polar lipids fraction being dominant for both. Given the growth phase of the two species at day 4 (exponential growth phase for CTEN and beginning of the stationary phase for CCAL), these results are congruent with knowledge from literature (Miller et al., 2014). CTEN showed a higher proportion of neutral lipids (39% of total lipids) compared to that of CCAL (12% of total lipids) and this was true for all fractions analyzed, except for DHA. This suggests that CTEN can store energy reserves under neutral lipid form more rapidly than CCAL. Furthermore, CTEN showed total DHA content significantly higher than those found in CCAL, and making a higher DHA/EPA ratio around 0.18 against 0.10 for CCAL. Like EPA, the DHA is an Omega-3 which is essential for the development of larval stadia of numerous aquaculture species (e.g. Brown 2002; Ragg et al. 2010) and for the good functioning of some organs (Tocher, 2003).

Hence, despite the low cellular densities attained for CTEN, which can remain an obstacle for the use of this species in aquaculture production, results of our study point out a promising nutritional potential for CTEN, close to that of CCAL. Finally, the maintain of good health of CTEN under the 12:12 L:D photoperiod, together with the results obtained in terms of lipid production, allows to consider the culture of this species in outdoor systems.

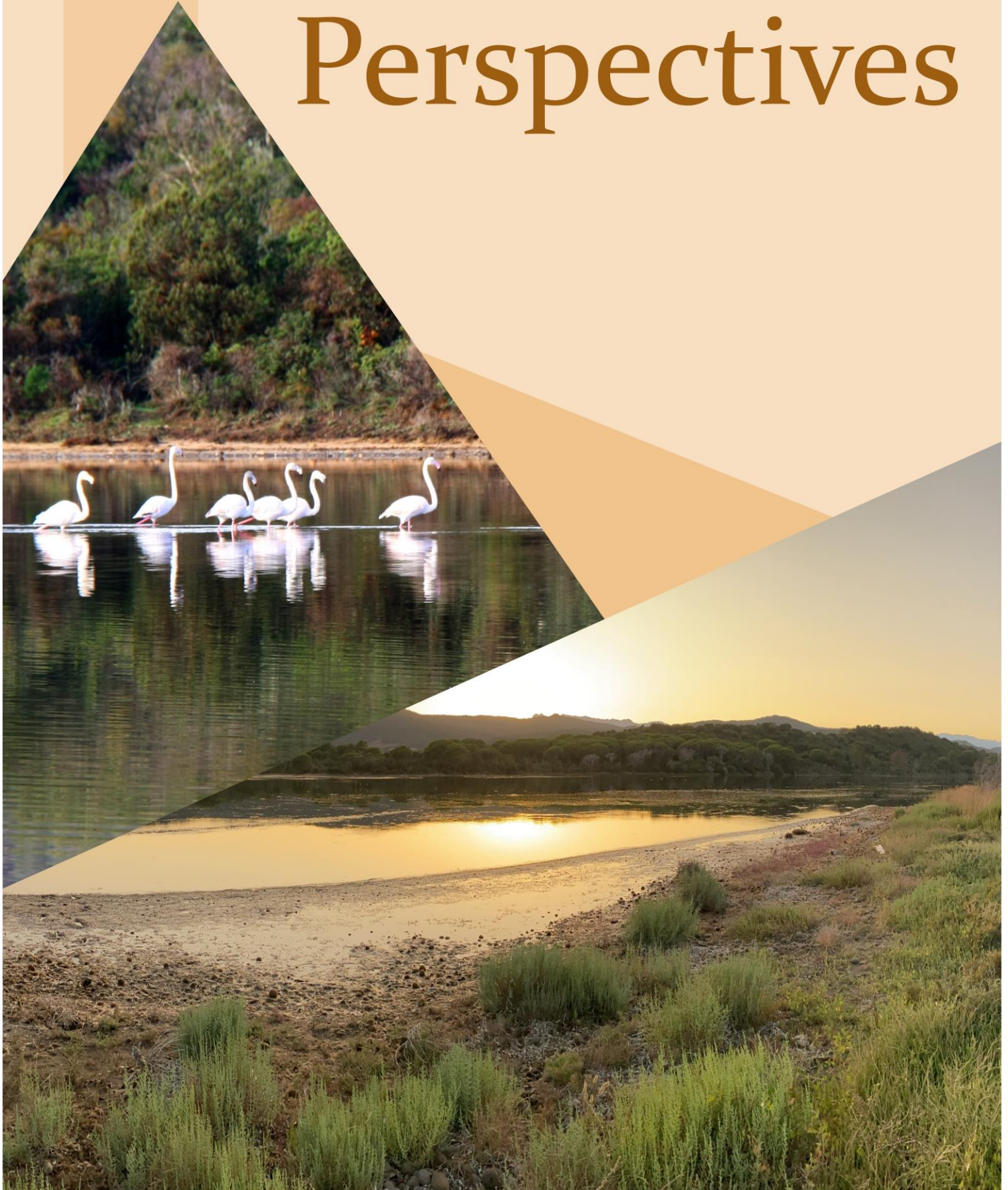
The most interesting feature of CTEN concerns lipids' production and especially their composition. It might be useful to test growth and biochemical compounds production of CTEN under conditions specifically conceived to primarily favor lipid production. For instance, EPA production was enhanced under nitrogen repletion and low light intensities (at 50-60 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) in *Nannochloropsis* sp., whereas for DHA increase high light intensity (at 460 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$) resulted more suitable for multiple species (Schüler et al., 2017 and references herein). Moreover, pH variations in nutrients-limited conditions and biphasic culture method, involving successive nitrogen supplementation and starvation phases, already resulted as quite efficient in modulating lipid production and composition in multiple microalgae species (Ratha et al., 2013; Alkhamis et al., 2022). Also, the use of different irradiance spectrum provided by color LED can be brought into play to induce modifications in the biochemical production and composition of microalgae (Suhaimi et al., 2021). Further experiments on different culture conditions, involving nutrient, light, temperature and pH variations, could be useful to explore and enhance CTEN's lipid production, as well as potentially trigger a better performance in the production of other compounds, such as the combined induction of PUFAs and carotenoids through culture medium changes (Schüler et al., 2017).

5. CONCLUSION

In this study, the growth, the photosynthetic activity and the pigment and lipid contents were investigated together for the first time on a lagoon strain of *C. tenuissimus* (CT16ED).

Through experimental essays under two photoperiods (24:00 L:D; 12:12 L:D), this work allowed to determine the potential for exploitation of this strain in aquaculture applications. A marked influence of the photoperiod on growth, photosynthetic activity and nutritional potential of CTEN was observed. The comparison with *Chaetoceros simplex* var. *calcitrans*, made it possible to discover some specific characteristics of CTEN, which make it a promising species for aquaculture purposes, linked to its natural origin and hence its adaptation to natural and highly instable environment. Despite relatively low cellular densities obtained with CTEN strain, when compared to CCAL strain of *C. calcitrans*, a commonly used *Chaetoceros* species in aquaculture, CTEN seems suitable for aquaculture production owing to: i) its lipid content, rich in essential PUFAs; ii) its high cell-size variability and richness in chlorophyll *a*; iii) its good maintenance under the 12:12 L:D photoperiod, allowing the consideration of its application in outdoor cultures.

Discussion et Perspectives



DISCUSSION ET PERSPECTIVES

La position des lagunes côtières dans l'histoire anthropique a évolué rapidement, en passant de milieux à supprimer pour garantir l'assainissement et créer des terrains exploitables à des milieux à conserver (Ghiotti, 2019; Pérez-Ruzafa et al., 2019b).

La gestion de ces milieux aujourd'hui dépasse le seul objectif de préservation de la qualité de l'eau et de la biodiversité, et vise actuellement à inclure des éléments bien plus larges, qui impliquent non seulement l'Homme, mais aussi une échelle plus longue qui concerne l'Humanité dans un futur plus lointain, comme la lutte contre l'érosion côtière, l'élévation du niveau de la mer et les inondations, ainsi que la protection et la persistance des activités et de l'urbanisation des zones retrolittorales (Ghiotti, 2019). La problématique de la conservation des lagunes devient donc une problématique qui englobe l'avenir du littoral de façon intégrée, qui est d'ailleurs un objectif international synthétisé notamment dans le cadre du protocole sur la Gestion Intégrée des Zones Côtières (GIZC¹).

En effet, des aspects socio-économiques non négligeables sont en jeu, car les lagunes sont une spécificité des **systèmes littoraux à intérêts multiples**. Banalement, elles font partie de la côte et leur valeur paysagère est considérée comme l'un des plus importants services écosystémiques, avec un impact économique direct dans les domaines du tourisme et immobilier (Robert, 2014). Le pouvoir de cette valeur paysagère est tellement fort qu'elle est aussi source de conflits, entre particuliers, mais touche aussi des collectivités locales et territoriales, à travers la constructibilité des terrains qui évolue en fonction de la vue sur le paysage (Robert, 2014). La perte des systèmes lagunaires côtiers constituerait aussi une menace pour les terrains de l'arrière-pays, en augmentant le risque d'érosion et d'inondation des zones urbanisées du retrolittoral (Chapman, 2012; Ferrarin et al., 2014; Ghiotti, 2019; Taylor et al., 2021). De plus, de nombreuses activités se fondent sur ces écosystèmes (Pérez-Ruzafa et al., 2011a). L'Homme profite de la productivité des lagunes en exploitant ces systèmes pour des activités de pêche, d'aquaculture et de conchyliculture (Newton et al., 2018; Pérez-Ruzafa et al., 2019b, 2020). Souvent, d'autres activités se développent sur les plans d'eau et sur les terrains attenants, comme l'extraction de sel, des sports nautiques et des

¹ La gestion intégrée des zones côtières (GIZC) consiste en un protocole et un outil de gouvernance des territoires littoraux visant un développement durable. La GIZC est définie comme « un processus dynamique de gestion et d'utilisation durables des zones côtières, prenant en compte simultanément la fragilité des écosystèmes et des paysages côtiers, la diversité des activités et des usages, leurs interactions, la vocation maritime de certains d'entre eux, ainsi que leurs impacts à la fois sur la partie marine et la partie terrestre » (Ministère des affaires étrangères, 2013). La gestion intégrée des espaces et des ressources terrestres et marines est promue, en prenant en compte les aspects économiques et sociaux de la zone littorale dans sa complexité. Dans ses objectifs, la planification rationnelle des activités, la préservation de l'intégrité et de la qualité paysagère et la cohérence des initiatives politique à différentes échelles, relativement aux zones littorales, sont compris, avec un but d'exploitation et développement durable des ressources et des services fournis par ces milieux, ainsi que de la prévention et/ou réduction des effets du changement climatique et des actions humaines dans le futur (Deboudt, 2012; Ministère des affaires étrangères, 2013).

stations touristiques, en constituant donc une source de richesse importante pour la société (Pérez-Ruzafa et al., 2019b, 2020).

Le besoin de conservation de ces milieux touche ainsi non seulement à l'écologie, mais aussi à des problématiques économiques et sociales qui ont un poids dans la prise de décision et la fixation des objectifs (Folke et al., 2001; Ostrom, 2009; Robards et al., 2011; Berkes, 2012; Benessaiah & Sengupta, 2014; Grafton et al., 2019). Dans ce cadre, l'établissement des objectifs se fait typiquement à l'échelle humaine. Toutefois, l'Homme a ses limites, notamment une mémoire courte par rapport à l'échelle temporelle des systèmes naturels. La perception du « comment c'était avant » n'est pas stable et change de génération en génération, générant un « oubli progressif », connu sous le nom de « amnésie environnementale générationnelle », qui provoque cette problématique dite « *Shifting Baseline Syndrome* » (Pauly, 1995; Kahn, 2002). Si la gestion veut dépasser cette frontière temporelle et incorporer efficacement l'**avenir des écosystèmes lagunaires** (et la globalité des systèmes littoraux en particulier), il est essentiel d'en comprendre le fonctionnement et les dynamiques dans leur complexité et leur évolution historique.

Pour cela, il paraît donc logique de réaliser des suivis sur du long terme des écosystèmes et de reconstruire leurs **trajectoires**, à travers des approches historiques, rétrospectives et l'élaboration de frises chronologiques (Pulina et al., 2012; Biggs et al., 2015; Mariani et al., 2015; De Wit et al., 2020; Erostate et al., 2022). L'évolution et l'adaptation de la biodiversité aux changements, historiques et futurs, sont un point primordial (Chapman, 2012; Ghiotti, 2019). Ces objectifs imposent la nécessité de trouver des éléments marqueurs de l'état et du fonctionnement des milieux. En ce sens, le **phytoplancton** est un **indicateur** très utile des milieux aquatiques. Toutefois, dans les milieux lagunaires, la complexité du système souvent demande la prise en compte d'autres éléments en jeu pour la reconstruction des interactions et du fonctionnement écologique et de ses trajectoires (Elmqvist et al., 2003; Boudouresque et al., 2020; Pasqualini et al., 2020). Les variations environnementales sont fortement affectées de la **saisonnalité**, en particulier dans les systèmes lagunaires, et déterminent les dynamiques du phytoplancton à travers les fluctuations d'une multitude de facteurs (Margalef, 1978; Cloern, 1996, 1999; Reynolds, 2006; Trombetta et al., 2019). En particulier, les lagunes présentent typiquement des **salinités** variables en fonction des saisons et des équilibres et échanges avec les bassins versants et la mer (Pérez-Ruzafa et al., 2011c, 2019a, 2019b). La salinité est un des facteurs les plus importants dans la structuration des communautés phytoplanctoniques et est aussi prévu comme l'un de plus impacté par le **changement climatique** en milieu lagunaire (Robert & Mazzilli, 2007; Pulina et al., 2012; Ferrarin et al., 2014). Toutefois, des prévisions sur les potentielles réponses de ces milieux à ces scénarios futurs restent toujours méconnues

(Dube et al., 2010; Pulina et al., 2012). En outre, le vaste spectre de conditions que les lagunes peuvent offrir (rien qu'en termes de taille, origine, hydrologie...) détermine la nécessité de questionner ces problématiques dans plusieurs types de systèmes. Notamment, hypothétiquement la taille de la surface lagunaire devrait impliquer une différente réactivité des systèmes, en relation avec une mineure capacité de mitigation et une interaction accrue du plan d'eau avec ses systèmes attenants (Downing, 2010; Doughty et al., 2019). Parallèlement, en raison de leurs cadres très anthropisés, les lagunes sont considérées comme des **socio-écosystèmes**, et il est donc logique d'inclure, parallèlement aux trajectoires de l'environnement, les éléments humains qui peuvent avoir modifié dans le passé, ou impacté dans le présent et le futur, les systèmes lagunaires des bassins versants jusqu'à la mer (Berkes et al., 2003; Redman et al., 2004; Walker et al., 2006; Bullock et al., 2011; Cote & Nightingale, 2012; Folke, 2016; Ghiotti, 2019; Grafton et al., 2019; Walker, 2020).

1. PHYTOPLANCTON ET ÉCOSYSTÈMES LAGUNAIRES : QUELS FONCTIONNEMENTS ET QUELLES TRAJECTOIRES D'ÉVOLUTION ?

1.1 Comment les communautés phytoplanctoniques ont-elles évolué ?

L'**approche rétrospective** appliquée à l'étude des lagunes en Corse a permis d'identifier certaines trajectoires dans l'histoire de ces écosystèmes, ainsi que de comparer leurs évolutions avec d'autres systèmes au niveau méditerranéen et mondial, afin de tracer des **tendances globales** et déterminer des **spécificités locales**. En particulier, des éléments récurrents ont pu être identifiés à travers l'étude des communautés phytoplanctoniques, marqueurs de l'évolution écologique de ces milieux.

Un des phénomènes les plus remarquables ressorti des études menées dans cette thèse est le changement de la composition des communautés phytoplanctoniques, montrant un **shift** d'une dominance de diatomées à **une dominance de dinoflagellés**. Ce phénomène était particulièrement marquant pour la lagune de Biguglia, dans l'analyse de son évolution écologique (Ligorini et al., 2022b - **Chapitre II**). Ces observations sont en lien avec d'autres études, qui démontrent une récente prolifération de dinoflagellés dans plusieurs environnements côtiers, au détriment des diatomées (Xiao et al., 2018; Fischer et al., 2020). Les *drivers* de ce phénomène global ont été identifiés dans le changement climatique, l'eutrophisation (« eutrophisation culturelle », Malone & Newton, 2020), des conséquences des actions de gestion et le succès écologique de certaines espèces mixotrophes capables de profiter des conditions dégradées (Aligizaki et al., 2009; Collos et al., 2009; Fischer et al., 2020; Hallegraeff, 2010; Kudela et al., 2015; Xiao et al., 2018).

Globalement, une tendance à l'**intensification des phénomènes de blooms** phytoplanctoniques a été observée pour des lagunes différentes par leurs morphologies, fonctionnements et contextes : les étangs de Biguglia, Diana et Urbino (Ligorini et al., 2022a, 2022b - **Chapitres I et II**). De plus, certains **effets saisonniers** ont été mis en évidence, comme l'augmentation de la magnitude de *blooms* d'une diatomée potentiellement toxique, *Pseudo-nitzschia* spp., en automne à Urbino et en hiver et au printemps à Diana (Ligorini et al., 2022 - **Chapitre I**). Sur l'étang de Biguglia, les *blooms* phytoplanctoniques sont devenus de plus en plus fréquents et étalés sur l'année entière (Ligorini et al., 2022b - **Chapitre II**). Ces éléments sont supportés par des observations dans d'autres systèmes, lagunaires et côtiers. Notamment, l'augmentation des *blooms* et des HABs en particulier est un phénomène connu pour les milieux lagunaires et côtiers au niveau mondial et bien décrit dans la littérature (Smayda, 1997b; Hallegraeff, 2010; Kudela et al., 2015; Husson et al., 2016; Melliti Ben Garali et al., 2020). L'élément saisonnier est aussi connu, notamment, en Méditerranée, Trombetta et al. (2019) ont identifié des *shifts* dans la saisonnalité des *blooms* phytoplanctoniques dans la lagune française de Thau, avec des *blooms* hivernaux à haute magnitude, induits par des températures douces. Ces altérations avaient ensuite impacté la saison suivante, à travers l'accumulation d'une biomasse inférieure à celle typiquement rencontrée dans les *blooms* printaniers de la lagune. Ce genre d'évènements est familier dans le milieu côtier et attendu s'accroître dans le futur en lien avec l'augmentation des températures engendrée par le changement climatique (Martens, 2001; van Beusekom et al., 2009; Trombetta et al., 2021, 2019). Par conséquent, les perturbations au niveau d'une saison peuvent entraîner des altérations au niveau du cycle saisonnier entier des communautés phytoplanctoniques et potentiellement affecter le réseau trophique et le fonctionnement écosystémique des lagunes (Trombetta et al., 2021).

L'**émergence d'espèces potentiellement toxiques** a aussi été observée dans le cadre de la thèse. En particulier, l'émergence du dinoflagellé invasif *Prorocentrum cordatum* en 2010 a signé le début d'un *shift* progressif vers une forte dominance de dinoflagellés et de *blooms* dans la lagune de Biguglia (Ligorini et al., 2022b - **Chapitre II**). L'intensification des *blooms* de certaines espèces potentiellement nuisibles, notamment *Pseudo-nitzschia* spp. et *Prorocentrum* spp., qui ont été observées à plusieurs reprises dans les années plus récentes au cours des travaux présentés, intéresse plusieurs systèmes lagunaires et côtiers (Aligizaki et al., 2009; Husson et al., 2016; Skarlato et al., 2018b; Fischer et al., 2020; Melliti Ben Garali et al., 2020). Dans la lagune de Biguglia, au cours des années récentes, plusieurs dinoflagellés potentiellement toxiques ont montré de plus en plus de succès, comme *Gonyaulax* spp., *Akashiwo sanguinea*, *Dinophysis* sp., profitant de la dégradation progressive du milieu (Ligorini et al., 2022b - **Chapitre II**). Parallèlement, des dominances et des *blooms* persistants de

certaines de ces dinoflagellés nuisibles ont été aussi observés dans les lagunes de petites surfaces en Corse-du-Sud, surtout les espèces *Prorocentrum micans*, *Prorocentrum cordatum*, *Akashiwo sanguinea* et *Kryptoperidinium foliaceum* dans les lagunes d'Arasu et de Santa Giulia en particulier, les plus touchées par les activités anthropiques, mais aussi ponctuellement dans la lagune de Balistra, considérée comme très peu impactée par l'anthropisation (Ligorini et al., 2023 - **Chapitre III**). En même temps, l'augmentation des blooms et le *shift* vers une dominance de dinoflagellés semblent entraîner une **perte de diversité** des communautés phytoplanctoniques, qui deviennent de plus en plus homogènes (Ligorini et al., 2022b - **Chapitre II**; Ligorini et al., 2023 - **Chapitre III**).

Les phénomènes décrits sont donc observés dans plusieurs lagunes présentant des fonctionnements différents en Corse et sont aussi confirmés dans d'autres systèmes ailleurs dans le monde (Collos et al., 2009; Xiao et al., 2018; Derolez et al., 2020b; Fischer et al., 2020). Toutefois, il est difficile d'identifier des processus globaux et des spécificités locales sont souvent en jeu. Par exemple, dans la lagune de Thau, l'émergence d'un dinoflagellé toxique, *Alexandrium catenella*, a été mise en relation avec la trajectoire d'oligotrophisation de l'étang, suite à l'application de mesures de gestion pour la diminution des apports en nutriments dans la lagune (Collos et al., 2009). Au contraire, la parution de *P. cordatum* dans l'étang de Biguglia semble être liée plutôt à des diminutions de salinité et de forts apports en nutriments, en grande partie dus à des conséquences inattendues d'une intervention de gestion pour l'amélioration de la circulation d'eau dans la lagune, i.e. le faucardage et nettoyage du canal du Fossone, qui lie le bassin sud de l'étang au fleuve Golo (Cecchi et al., 2016; Garrido et al., 2016; Ligorini et al., 2022b - **Chapitre II**).

Il est donc nécessaire d'approfondir les causes des évolutions et tendances observées, en intégrant plusieurs facteurs, biotiques et abiotiques, et une vision globale du milieu.

1.2 Quelles sont les principales causes des évolutions observées ?

Les changements observés au niveau des communautés phytoplanctoniques dénotent surtout des processus agissants à l'échelle globale et sont symptômes d'une dégradation progressive des milieux lagunaires. Cette dégradation, évidente à large échelle, est à attribuer à plusieurs facteurs en jeu, parfois locaux et/ou liés à des problématiques ou phénomènes globaux, qui agissent conjointement en formant des interactions complexes.

Un des principaux facteurs en jeu est la qualité des eaux tributaires des lagunes, de surface et souterraines, qui joue un rôle essentiel dans le fonctionnement écologique des milieux lagunaires et dans leurs histoires. En particulier l'**eutrophisation et les pollutions anthropiques** sont parmi les causes majeures de dégradation et de changement dans les milieux côtiers (Cloern, 2001; Lloret et al., 2008; Zaldívar et al., 2008; Pérez-Ruzafa et al., 2019b). Plusieurs lagunes méditerranéennes ont subi des processus d'eutrophisation dans leurs histoires, notamment les lagunes de Mar Menor (Espagne) et Thau (France) en sont des exemples connus (e.g. Souchu et al., 1998, 2010; Pérez-Ruzafa et al., 2018; Derolez et al., 2019; Álvarez-Rogel et al., 2020 et références citées). Les conséquences sur les communautés biotiques sont parfois catastrophiques, en provoquant des proliférations de macroalgues, des *blooms* phytoplanctoniques et parfois des mortalités massives de la faune, suite à des phénomènes d'anoxie et malaïgue, avec des conséquences économiques très graves, par exemple dans le cadre d'une exploitation halieutique (e.g. Souchu et al., 1998; Derolez et al., 2019; Álvarez-Rogel et al., 2020). Ces phénomènes très évidents ont poussé au développement de plusieurs stratégies de gestion visant à diminuer les apports aux lagunes côtières. Ces mesures ont été dans certains cas efficaces, comme dans le cas de l'étang de Thau, qui est désormais passé à une trajectoire d'oligotrophisation (Collos et al., 2009; Le Fur et al., 2019; Derolez et al., 2020b). Toutefois, malgré l'amélioration de la qualité des eaux lagunaires par rapport à certains indicateurs (notamment dans le cadre de la DCE), les systèmes montrent toujours des signes de dégradation. Notamment, le cas de l'étang de Biguglia s'insère parfaitement dans ce contexte : la ville de Bastia, au sud de laquelle la lagune se situe, a montré une expansion remarquable au cours du dernier siècle, parallèlement à une modification des activités agricoles et cela a entraîné une augmentation graduelle des apports à l'étang et l'accumulation de nutriments et autres polluants anthropiques (Erostate et al., 2018, 2019, 2022). En particulier, les forts apports en nitrates ont impacté les communautés phytoplanctoniques en favorisant les *blooms* et la parution d'espèces nuisibles (Cecchi et al., 2016; Garrido et al., 2016). Malgré les efforts de gestion et l'effective amélioration de la qualité des eaux lagunaires, certains critères d'évaluation restent non-satisfaisants. Notamment, comme montré dans le **Chapitre II** (Ligorini et al., 2022b), dans le cadre de la DCE l'état écologique de la lagune a été classé comme « médiocre » en 2018, avec le phytoplancton, les macrophytes et les invertébrés benthiques comme paramètres déclassants. Parallèlement, les observations au niveau du phytoplancton (augmentation de *blooms*, *shift* vers une dominance de dinoflagellés, émergence d'espèces nuisibles) et d'autres niveaux trophiques, indiquent que, malgré les améliorations et les efforts, la lagune présente toujours un fonctionnement altéré. La raison de ce retard dans la réponse du système aux améliorations est partiellement due à un côté rétroactif, lié à l'histoire du milieu. L'augmentation de la population et le récent

développement touristique ont soumis la lagune à des apports de plus en plus massifs en différents types de polluants (nutriments, produits pharmaceutiques, éléments traces...), parfois difficiles à dégrader et s'accumulant rapidement dans les eaux souterraines (Erostate et al., 2019). Également, la lagune est soumise à une pollution inertielle due à l'accumulation de nutriments dans les eaux souterraines tributaires, résultant de plusieurs décennies d'activités anthropiques sur le bassin versant (Erostate et al., 2018, 2022). Ces polluants, en particulier les nitrates, sont ainsi relâchés progressivement dans le bassin avec un décalage temporel (Erostate et al., 2018, 2022). Cet effet inertiel des pollutions anthropiques constitue une difficulté supplémentaire pour les actions de gestion, notamment dans le cadre des actions de réduction d'apports en nutriments du bassin versant, en créant une inertie dans la réponse du système lagunaire aux actions mises en place à ce jour.

L'importance de la qualité des eaux tributaires et la nécessité d'identifier les sources de pollution anthropique ont été appliquées à l'étude des lagunes de petites surfaces (Ligorini et al., 2023 – **Chapitre III**). Bien que l'impact de l'urbanisation soit bien moins important que sur l'étang de Biguglia, cette approche a permis d'identifier des sources de pollution anthropique (nitrates) laissant supposer des problématiques d'assainissement sur les bassins versants de ces petits systèmes, pouvant potentiellement impacter leurs communautés biotiques, même sur le long terme (Ligorini et al., 2023 – **Chapitre III**).

La capacité de stockage de polluants, nutriments et autres apports au sein des lagunes est également affectée par le fonctionnement hydrique du système. Les observations précédemment décrites ont mis en évidence l'importance de **la circulation des eaux, du bassin versant jusqu'à la mer**, dans le fonctionnement et la dégradation des milieux lagunaires, car ce facteur détermine le niveau de confinement des bassins. Dans ce contexte, une première problématique émergente de l'analyse des communautés phytoplanctoniques dénote une spécificité plutôt locale, mais applicable à d'autres systèmes : la **perte de continuité écologique** et la création de barrières déterminent des altérations dans le fonctionnement du système. Dans la lagune d'Arasu, coupée en plusieurs bassins dans les années 1960 avec l'objectif de réaliser un petit port de plaisance, la composition des communautés phytoplanctoniques témoigne d'une circulation altérée entre les bassins, consécutive à l'artificialisation (Ligorini et al., 2023 - **Chapitre III**). En particulier, le bassin le plus proche de la zone urbanisée du bassin versant montre des signes de dégradation, avec des communautés phytoplanctoniques en faible état de santé et une absence de macrophytes malgré la connexion avec la mer, tandis que les bassins les plus confinés sont caractérisés par une dominance de dinoflagellés formant souvent de *blooms* (Ligorini et al., 2023 - **Chapitre III**). Des effets similaires ont été observés dans d'autres lagunes méditerranéennes en association avec

des altérations mécaniques, le confinement, les apports en nutriments, des pollutions en cours ou inertielles (Sarno et al., 1993b; Lafabrie et al., 2013; Sfriso et al., 2017, 2019, 2021).

Ces différents éléments relatifs à la qualité et à la circulation de l'eau, émergés de façon marquante dans le cadre de cette thèse, dénotent que la **perte de continuité hydrologique** entre bassin versant, lagune et mer compromet le bon fonctionnement du milieu, en particulier pour les lagunes de petites surfaces, plus réactives, mais aussi pour les grandes lagunes. Notamment, la lagune de Biguglia a montré dans son évolution des altérations de salinité fortement dépendantes des connexions à la mer et des apports du bassin versant (Ligorini et al., 2022b - **Chapitre II**). Cela semble affecter le phytoplancton en particulier, comme précédemment évoqué, mais aussi d'autres compartiments biotiques, en particulier les macrophytes, dont la régression semble liée à la désalinisation progressive, et les espèces invasives, qui semblent être généralement favorisées par des diminutions de salinité (Ligorini et al., 2022b - **Chapitre II**). Ces conditions se produisent notamment quand l'étang est isolé de la mer à cause de la fermeture de son grau (Ligorini et al., 2022b - **Chapitre II**). Pour les lagunes de petites surfaces, une tendance similaire semble se dessiner : les communautés phytoplanctoniques se penchent vers un état de santé médiocre, elles sont souvent dominées par des dinoflagellés (parfois nuisibles), et présentent des *blooms* persistants et une faible diversité, en lien avec les sources de pollutions anthropiques identifiées au sein des bassins versants et le niveau de connectivité des lagunes aux systèmes attenants (Ligorini et al., 2023 - **Chapitre III**). La déconnexion et l'**isolement** des plans d'eau de leurs systèmes adjacents peuvent déterminer des phénomènes d'assèchement et des altérations des périodes hydrologiques, ainsi que des modifications des cycles des nutriments et de la circulation des sédiments, en affectant *in fine* les communautés biotiques, comme cela a été le cas pour la lagune de Santa Giulia pendant l'été en 2020 (Ligorini et al., 2023 - **Chapitre III** ; Angeler et al., 2010; Rojo et al., 2012; Sahraoui et al., 2013). Notamment, la perte de connectivité à la mer des milieux lagunaires a été associée à une augmentation de l'eutrophisation et de la biomasse phytoplanctonique et à la parution d'espèces nuisibles tolérant le stress (Pereira Coutinho et al., 2012; Sahraoui et al., 2013; Jones et al., 2018). Au contraire, un bon échange avec la mer a été mis en relation avec une meilleure circulation de l'eau et une mitigation des enrichissements nutritifs dans différentes ICOLLs (Schallenberg et al., 2010b; Hyman & Stephens, 2020).

Le fonctionnement hydrologique et la connectivité des lagunes à leurs systèmes attenants dépendent fortement de deux facteurs principaux : le **changement climatique** et les **interventions de gestion**.

La **tendance à la fermeture des graus** est exacerbée par les modifications des périodes hydrologiques, en particulier par une diminution des pluies ou bien leur concentration dans des périodes plus courtes et intenses (MedECC, 2020). Cela implique un apport mineur en eau douce aux bassins lagunaires et une accumulation de sédiments, qui ne peuvent pas être chassés par la force sortante (insuffisante), et qui ont donc la tendance à colmater les graus (Ligorini et al., 2022b - **Chapitre II**). Ce phénomène, en association avec l'augmentation des températures et en particulier les vagues de chaleur estivales, détermine une forte pression d'évaporation sur les milieux lagunaires, qui engendrent des **variations de salinité et de température** importantes dans les plans d'eau. Ces modifications ont déjà été mises en relation avec des altérations des communautés biotiques, notamment pour les lagunes de Diana et Urbino, pour lesquelles un lien entre changement climatique et modifications des communautés phytoplanctoniques a été identifié (Ligorini et al., 2022 - **Chapitre I**), mais surtout pour les lagunes de petites surfaces en Corse-du-Sud, notamment en relation directe avec les dynamiques d'ouverture des graus, et en particulier à travers l'expérimentation à différents niveaux de salinités, mimant des scénarios de changement climatique (Ligorini et al., 2023 - **Chapitre III; Chapitre IV**). Malgré l'instabilité intrinsèque des milieux lagunaires, des fortes variations de salinité liées au changement climatique et au niveau de connexion de ces systèmes, peuvent entraîner de forts bouleversements des communautés biotiques, comme la diminution de la diversité phytoplanctonique, des altérations de l'efficacité photosynthétique et la parution d'espèces potentiellement nuisibles (Ligorini et al., 2023 - **Chapitre III ; Chapitre IV**). Des résultats similaires, dus à la perte de connectivité à la mer et aux variations de salinité conséquentes, ont été aussi observés dans d'autres systèmes lagunaires ou estuariens dans le monde (Schallenberg et al., 2010b; Camacho et al., 2012; Pereira Coutinho et al., 2012; Jones et al., 2018). Cela indique que le changement climatique devient l'un des plus grands *drivers* de changement en milieu lagunaire.

La gestion environnementale agit aussi fortement sur le fonctionnement hydrologique des systèmes lagunaires, notamment avec le **management des activités sur le bassin versant**. Toute décision prise au niveau des alentours des lagunes peut impacter les plans d'eaux dans leur complexité, parfois de façon directe et immédiate, parfois sur le long terme. Par exemple, la déforestation du bassin versant pour faire place à des terrains d'agriculture autour d'une lagune peut entraîner des altérations dans le ruissellement et les apports d'eau douce au plan d'eau, et donc des modifications importantes de la salinité du milieu, comme c'était le cas pour la Laguna de Terminos (Mexique) (Fichez et al., 2017). L'**usage de l'eau** en amont des lagunes, comme le prélèvement d'eau pour l'usage humain, la construction de barrages et digues, l'altération des canaux et cours d'eau détermine une modification des apports d'eau en

aval, potentiellement impactant certains services écosystémiques lagunaires, comme la recharge des nappes phréatiques, entre autres (MEA, 2005; Pérez-Ruzafa et al., 2019a; Erostate et al., 2020). Parallèlement, les **interventions d'ouverture et gestion des graus** sont souvent utilisées en milieu lagunaire pour contrôler les rejets d'eau et les échanges entre les systèmes de transition et la mer, souvent en association avec les activités de pêche et aquaculture pour le recrutement d'espèces d'intérêt ou pour garantir une bonne circulation et oxygénation des eaux (Schallenberg et al., 2010b; Pérez-Ruzafa et al., 2018). Parfois, ces graus sont aménagés, autrement dit, ils sont artificialisés pour permettre une connexion permanente à la mer, comme il est le cas pour la lagune de Diana en Corse. Pourtant, ces actions et ces aménagements entraînent des altérations de la salinité des milieux lagunaires et, dans certains cas, elles peuvent créer des modifications profondes du fonctionnement des systèmes lagunaires (Gunaratne et al., 2011; Camacho et al., 2012).

1.3 Quelles sont les conséquences des évolutions observées ?

L'ensemble des résultats et des observations sur les trajectoires et les états des lieux réalisés sur les systèmes lagunaires dans le cadre de cette thèse ont montré des signaux de dégradation qui sont alarmants si considérés à la lumière des changements futurs, *drivers* de ces altérations. Des altérations ont été identifiées sur les fonctionnements hydrologiques des lagunes. Les conséquences de ces bouleversements sont particulièrement évidentes au niveau des communautés phytoplanctoniques, mais intéressent plus globalement les communautés biotiques, à la fois par action directe des pressions précédemment décrites et par des effets en cascade induits des modifications au sein du phytoplancton sur les niveaux trophiques supérieurs. Tous ces éléments interrogent sur l'avenir des systèmes lagunaires et sur les conséquences relatives à la perte de ces milieux.

En premier lieu, une des causes majeures d'altération a été identifiée dans le changement climatique. Dans ce cadre, les estimations des projections dessinent pour les lagunes méditerranéennes une hausse de température des eaux jusqu'à 15 % plus élevées et des augmentations de salinité de plus que quarante fois plus fortes qu'en mer (Ferrarin et al., 2014). Ainsi, il existe une tendance à l'homogénéisation de ces écosystèmes qui déterminerait la **perte de la mosaïque d'habitats** que les lagunes constituent (Figure 12), d'un côté si important pour le maintien de la biodiversité, mais aussi constituant une protection contre les changements futurs, à travers la potentialité d'une variété de réponses au changement (Downing, 2010; Ferrarin et al., 2014).

Selon les observations dans le cadre de cette thèse, les implications des prévisions du changement climatique porteront à une exacerbation de la perte de connectivité des lagunes à la mer, à travers la fermeture progressive des graus, et la diminution d'apports en eau douce. Le travail mené dans le **Chapitre III** démontre la forte vulnérabilité des lagunes de petites surfaces (Ligorini et al., 2023). Les conséquences sur les variations de salinité sont évidentes et les scénarios de **salinités extrêmes**, enquêtés pendant le travail présenté dans le **Chapitre IV**, pourront passer de phénomènes ponctuels à la normalité (Figure 12). Cela, associé au **risque d'assèchement** (Figure 12) et perte des milieux lagunaires, en particulier ceux de petites surfaces, fait qu'il existe un besoin d'intégrer ces projections dans le management futur de ces milieux et de mitiger les possibles conséquences afin de préserver l'intégrité des systèmes et les services écosystémiques fournis.

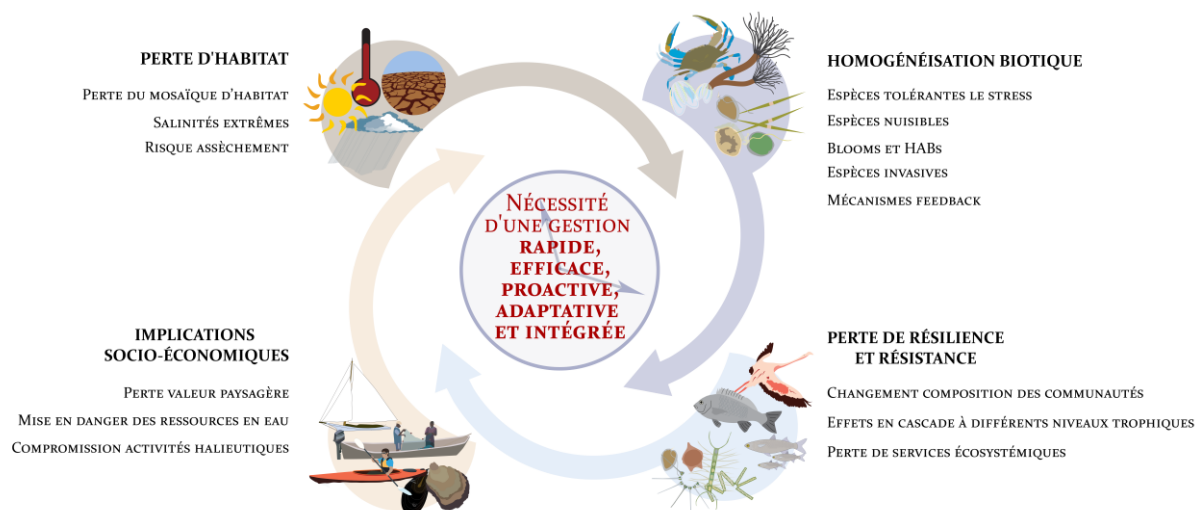


Figure 12 Schéma synthétique des principales conséquences envisageables pour l'avenir des écosystèmes lagunaires sur la base des trajectoires et drivers de dégradation identifiés au cours de la thèse.

Au niveau biotique, selon les observations, on peut s'attendre à ce que l'augmentation des pressions anthropiques et la progression du changement climatique amèneront à l'augmentation de conditions environnementales stressantes, en termes de fréquence et intensité, et donc à la favorisation, d'espèces tolérant le stress. Ce phénomène a été en effet déjà observé et démontré au cours de la thèse relativement aux communautés phytoplanctoniques, à travers des manifestations comme l'émergence d'espèces tolérant le stress, souvent potentiellement toxiques, et l'exacerbation des phénomènes de *bloom* en association à des pressions anthropiques et des scénarios et conditions liés au changement climatique (Ligorini et al., 2022a, 2022b, 2023 – **Chapitres I, II et III ; Chapitre IV**).

Ces phénomènes sont donc attendus s'intensifier dans le futur proche. L'une des principales conséquences visibles est l'**homogénéisation biotique** (Figure 12), qui a été

déjà observée à plusieurs reprises dans les communautés biotiques au cours de travaux réalisés, en particulier sur l'étang de Biguglia. En effet, les communautés phytoplanctoniques de cette lagune se sont révélées de plus en plus dominées par une ou peu d'espèces, notamment le dinoflagellé potentiellement toxique et invasif *P. cordatum* (Ligorini et al., 2022b - **Chapitre II**). Toutefois, cette espèce n'est pas la seule **espèce invasive** dans l'étang de Biguglia. Effectivement, l'étude des trajectoires écologiques de cette lagune a permis de faire émerger une autre observation, soit la récente augmentation d'espèces non natives et leur explosion dans les dernières années en particulier (Figure 12 ; Ligorini et al., 2022b - **Chapitre II** ; Marambio et al., 2013; Cilenti et al., 2015; Diciotti et al., 2016; Fuentes, 2019; Taybi & Mabrouki, 2020; Marchessaux & Belloni, 2021). L'installation et prolifération d'espèces exotiques envahissantes est une problématique qui intéresse plusieurs lagunes côtières (Boudouresque & Verlaque, 2012). Notamment, le cténophore *Mnemiopsis leidyi* et le crabe bleu, *Callinectes sapidus*, ont colonisé une multitude de lagunes méditerranéennes différentes dans la dernière vingtaine d'années (Boudouresque & Verlaque, 2012; Delpy et al., 2012; Marambio et al., 2013; Cilenti et al., 2015; Tordoni et al., 2019; Culurgioni, 2020; Kara & Chaoui, 2021; Mancinelli et al., 2021; Marchessaux & Belloni, 2021). À l'échelle globale, les dynamiques de l'invasion biologique n'ont pas encore été identifiées de manière claire et universelle : un lien avec la dégradation des écosystèmes a été démontré dans certains cas, mais les processus subjacents la vulnérabilité des systèmes à l'invasion restent toujours l'un des plus grands défis de l'écologie moderne et plusieurs approches ont été développées pour explorer ce sujet (Mack et al., 2000; Beisel, 2010; Blackburn et al., 2011; Boudouresque & Verlaque, 2012). La parution et prolifération de ces espèces invasives, souvent reconduites au changement climatique et à l'action anthropique (directe ou indirecte), contribuent à l'homogénéisation biotique des lagunes côtières et à la destruction des habitats. Avec la dégradation progressive des milieux lagunaires, l'invasion biologique sera favorisée et soutiendra à son tour la dégradation ultérieure à travers des **mécanismes de feedback** (Figure 12 ; Sullivan, 2004; Fischer et al., 2013; Marambio et al., 2013; Diciotti et al., 2016; Fuentes, 2019; Qiu et al., 2019; Dalu et al., 2022; Ligorini et al., 2022b - **Chapitre II**).

Globalement, les altérations décrites, à travers une dégradation progressive, engendrent une graduelle **perte de la capacité de résistance et résilience des milieux lagunaires** (Figure 12 ; Scheffer et al., 2001; Walker et al., 2006; Carpenter et al., 2012; Nyström et al., 2012; Pérez-Ruzafa et al., 2018). Cela implique un accroissement de la vulnérabilité aux menaces croissantes. De ce fait, sur le long terme, les systèmes lagunaires pourront ne plus être capables de réagir aux bouleversements : par conséquent, une pression, même de faible intensité, pourra potentiellement les faire

tomber dans des états alternatifs dégradés et non-souhaités d'un point de vue socio-économique (Ligorini et al., 2022b - **Chapitre II** ; Folke et al., 2001, 2010; Folke, 2006; Walker et al., 2006; Cote & Nightingale, 2012).

Les **effets en cascade** (Figure 12) des modifications environnementales et surtout biotiques précédemment décrites pourront avoir aussi des impacts à large échelle et sur différents niveaux trophiques, notamment sur les stocks de poissons et sur le comportement des oiseaux migrateurs (Bruschetti et al., 2009; Pejchar & Mooney, 2009; Maceda-Veiga et al., 2017). Par exemple, sous les scénarios de salinités extrêmes enquêtés au cours du **Chapitre IV**, les communautés phytoplanctoniques ont répondu principalement à travers la favorisation d'espèces tolérantes le stress et l'émergence d'espèces initialement rares, au détriment des dominantes, causant donc des changements profonds dans la composition des communautés. Les changements en termes de classes de taille, composition et abondance au sein des communautés phytoplanctoniques soutiennent la perte de biodiversité et peuvent avoir des répercussions importantes aux niveaux trophiques supérieurs (Astorg et al., 2022). Par exemple, comme des groupes taxonomiques différents ont de différentes valeurs nutritionnelles, un changement de composition peut impacter l'apport nutritif aux niveaux zooplanctoniques et supérieurs (e.g. impacter les stocks de poissons d'intérêt commercial) et compromettre leur capacité de résister aux conditions stressantes, notamment à cause d'un apport insuffisant en lipides (Astorg et al., 2022). Ainsi, les altérations des communautés phytoplanctoniques et l'invasion biologique contribueront de plus en plus à la dégradation des milieux lagunaires, à la perte de leur capacité de résistance et résilience et, *in fine*, à la **perte des services écosystémiques** (Figure 12), notamment dans le cas des activités de pêche et aquaculture au sein des lagunes (Boudouresque & Verlaque, 2012; Tordoni et al., 2019; Ligorini et al., 2022a, 2022b - **Chapitres I et II ; Chapitre IV**).

En effet, la protection et conservation des milieux lagunaires est importante du point de vue écologique bien sûr, mais les **implications économiques et sociales** subjacentes ne sont pas négligeables (Figure 12). Le remplacement des services écosystémiques perdus, normalement fournis gratuitement par ces milieux, serait difficile ou, en tout cas, impliquerait un coût trop élevé. En effet, à titre d'exemple, Costanza et al. (1997) ont estimé la valeur du potentiel économique des systèmes côtiers de transition à 22 000 US\$ ha⁻¹ par année. La perte des zones humides littorales, déjà en cours et exacerbée du changement climatique (comme l'augmentation du niveau de la mer et des températures et les changements de salinité), compromet la protection des côtes à travers par exemple l'aggravation de l'érosion côtière, de l'intrusion saline et du risque d'inondation. Par conséquent, les services écosystémiques associés risquent d'être compromis. Banalement, à travers une **perte de valeur paysagère** (Figure 12) : la vue

sur le littoral attire touristes et randonneurs, gonfle les prix hôteliers (jusqu'à + 10 % pour dix régions touristiques méditerranéennes majeures) et les prix du marché immobilier (Robert, 2014). Ensuite, à travers la **mise en danger des ressources en eaux** (Figure 12) : les eaux souterraines exploitées pour la consommation humaine peuvent être mises en danger par une réduction de la recharge des nappes et l'intrusion saline (Erostate et al., 2020). Encore, la diversité des milieux lagunaires, la mosaïque d'habitats et les gradients environnementaux qui les caractérisent les rendent des systèmes essentiels pour le soutien de la biodiversité et le développement de ressources. Notamment, dans le cadre de cette thèse, la dépendance des activités halieutiques des milieux lagunaires a été bien explorée et des risques émergents ont été soulignés : par exemple, l'augmentation d'espèces phytoplanctoniques potentiellement toxiques peut constituer une **menace pour les activités aquacoles et de pêche** (Figure 12 ; Smayda, 1997b; Tatters et al., 2012; Sahraoui et al., 2013; Salcedo-Garduño et al., 2019; Zingone et al., 2021; Ligorini et al., 2022a, 2022b - **Chapitres I et II**) et déterminer des arrêts de pêche ou de vente de produits d'aquaculture de plus en plus fréquentes dans le futur, en déterminant une grave perte économique (Smayda, 1997b; Salcedo-Garduño et al., 2019). À l'échelle globale, les difficultés dans le domaine de la pêche entraînent un intérêt progressif vers l'aquaculture, ainsi qu'une demande de plus en plus croissante pour des solutions écologiques et peu coûteuses, surtout en relation avec la sobriété énergétique qui est demandée pour le futur dans un cadre d'épuisement progressif des ressources (Day et al., 2009; Tzovenis et al., 2009; Eryalçın et al., 2015; Guo et al., 2015; Jusoh et al., 2020; Hotos & Avramidou, 2021).

1.4 Quelles sont les implications pour de potentielles applications biotechnologiques ?

Dans ce cadre de carence énergétique et de défi technologique pour la production aquacole, le phytoplancton peut offrir un service à la société : l'exploration des **potentialités d'application biotechnologique du phytoplancton lagunaire** dans le cadre de cette thèse a mis en évidence l'importance des caractéristiques particulières qui peuvent être développées par des organismes adaptés à des milieux instables (**Chapitre V**). En effet, la souche ciblée de *Chaetoceros tenuissimus* a révélé des potentialités prometteuses pour l'aquaculture, e.g. principalement une variété de tailles cellulaires, et la production d'une composition lipidique attrayante (**Chapitre V**). La variabilité en termes de taille des cellules joue un rôle important dans la sélectivité alimentaire de prédation de la part d'organismes produits en éclosion (Muller-Feuga et al., 2003; González-Araya et al., 2012). La production lipidique observée résulte riche en lipides neutres, et plus particulièrement en acide docosahexaénoïque (DHA),

fondamentaux pour le développement larvaire de plusieurs organismes d'intérêt économique (**Chapitre V** - Brown, 2002; Ragg et al., 2010).

À l'échelle locale, il existe un intérêt particulier pour l'application immédiate de cette nouvelle souche dans le domaine de l'aquaculture : les chercheurs en Corse sont particulièrement investis dans l'amélioration des connaissances sur le développement de certaines espèces d'intérêt économique, pour de potentielles applications dans la restauration de population dans le milieu naturel et/ou pour fournir des technologies utiles pour le développement d'une exploitation halieutique et aquacole durable et rentable. Le laboratoire Stella Mare (UAR 3514 CNRS Université de Corse) étudie plusieurs espèces ciblées avec l'objectif d'implémenter les connaissances sur leur reproduction et développement pour des perspectives de restauration écologique et d'aquaculture.

Notamment, *Ostrea edulis* (l'huître plate européenne) figure parmi les espèces d'intérêt au sein de la plateforme, en raison de ses propriétés organoleptiques remarquables et de sa présence naturelle dans la région, en particulier au sein de l'étang de Diana, qui abrite une exploitation ostréicole historique et qui assure à ce jour une production d'huîtres dans l'ordre de 200 t par an (Buestel et al., 2009). *Magallana gigas* (huître creuse) est toutefois l'espèce d'huître plus largement cultivée, au niveau de la Corse et européen (Buestel et al., 2009; Pernet et al., 2010). Dans les années récentes, la surexploitation et certaines épidémies, comme des parasitoses, ont conduit à la diminution globale des populations naturelles de bivalves et en ont compromis l'aquaculture. Dans ce contexte, *O. edulis* constitue une ressource prometteuse pour le développement de l'ostréiculture (Buestel et al., 2009; Pernet et al., 2010), spécialement en Corse : en effet, la population corse semble être génétiquement différente d'autres populations, et ses individus sont particulièrement adaptés aux conditions environnementales fluctuantes et résistants aux épizooties (e.g. Bonamiose), qui ont décimé leurs homologues européens (Gervais et al., 2019).

Dans ce cadre, les attentes sont fortes pour l'utilisation de la souche isolée dans l'étang de Diana pour l'ostréiculture et les résultats du travail présenté dans le **Chapitre V** s'insèrent dans les objectifs de recherche de la plateforme Stella Mare. Les résultats émergents de cette étude montrent que la nouvelle souche possède des caractéristiques prometteuses pour son application biotechnologique dans la production d'huîtres en éclosion et leur cultivation. Par exemple, l'allocation des ressources préférentiellement dans la croissance de la taille cellulaire plutôt que dans la densité cellulaire de cette souche est attrayante, car il a été déjà démontré que *O. edulis* a une préférence alimentaire pour des microalgues de grande taille (González-Araya et al., 2012a). Encore, les proportions plus élevées de DHA dans la production lipidique observée pourraient être d'intérêt, car de hauts contenus en acides gras polyinsaturés constituent une valeur

nutritionnelle fortement demandée pour les microalgues utilisées dans la culture de *O. edulis* et pour les juvéniles, en particulier (Ronquillo et al., 2012). Grâce à cette production lipidique intéressante, cette nouvelle souche pourrait aussi être un bon candidat pour des alimentations mixtes dans la production d'huîtres : en effet, il a été prouvé que les juvéniles et les larves de *O. edulis* sont favorisés par l'utilisation d'alimentations mixtes de microalgues (Savina & Pouvreau, 2004; González-Araya et al., 2011; Ronquillo et al., 2012). Ronquillo et al. (2012) ont comparé de différentes alimentations mixtes et leurs effets sur la croissance des juvéniles de *O. edulis* et ont démontré que des alimentations mixtes, fournissant une meilleure production et transfert aux bivalves d'acides gras polyinsaturés, étaient les plus efficaces. Cela ouvre des perspectives d'expérimentation, finalisées à évaluer la contribution de la nouvelle souche en termes de lipides dans une alimentation mixte appliquée à la production de *O. edulis* dans les éclosiers du laboratoire Stella Mare. D'autres expérimentations avec des alimentations basées sur cette souche ou mixtes pourraient être réalisées sur *O. edulis* à de différents stades larvaires ou de développement pour mesurer les taux de croissance, le développement, la fécondité, l'absorption et le transfert des nutriments à haute valeur alimentaire, et donc pour évaluer *in fine* la faisabilité et la rentabilité de l'application de la nouvelle souche dans la production et l'aquaculture de *O. edulis*. En outre, au laboratoire Stella Mare d'autres espèces pourraient faire l'objet d'études sur de potentielles applications de cette nouvelle souche. Notamment, *Paracentrotus lividus* (l'oursin violet) est aussi une des espèces ciblées et produites au sein du laboratoire, principalement pour un objectif de restauration des populations naturelles, intensivement exploitées autour de la Corse. En effet, cette espèce a un intérêt commercial dans plusieurs régions méditerranéennes (Paredes et al., 2015; Gomes et al., 2021) et la surexploitation des populations naturelles a augmenté la demande pour sa production en aquaculture (Pais et al., 2012; Bertocci et al., 2014; Ouréns & Naya, 2015). Comme des alimentations mixtes basées sur *Chaetoceros calcitrans* ont déjà montré des résultats positifs sur le taux de survie des larves en échiniculture (Gomes et al., 2021), la nouvelle souche de *Chaetoceros tenuissimus* pourrait être un potentiel candidat pour l'alimentation dans la production d'oursins en éclosier.

À l'échelle régionale, notamment dans le cadre des objectifs de la plateforme Stella Mare, l'utilisation d'une espèce locale pourrait être particulièrement intéressante pour la production d'individus destinés à être relâchés dans le milieu naturel pour la restauration de population, car cela permettrait une croissance et un développement des organismes sous une alimentation similaire aux conditions environnementales locales. Également, l'intérêt de la souche locale utilisée pendant ce projet de thèse présente aussi un aspect captivant par rapport à son origine, qui a permis l'exploration du lien entre cette espèce phytoplanctonique et l'activité d'aquaculture menée dans cet étang pour

des perspectives d'applications biotechnologiques locales (**Chapitre V**) : le fait que la nouvelle souche ait été isolée dans l'étang de Diana (Grzebyk et al., 2022), la lagune corse dans laquelle l'ostréiculture est pratiquée, la rend particulièrement intéressante pour la production ostréicole régionale, car, en premier lieu, elle devrait être plus adaptée aux conditions locales et lagunaires en particulier, et, deuxièmement, elle constitue une composante naturelle de l'alimentation des huîtres dans le milieu.

De plus, l'affinité de cette nouvelle souche pour la photopériode 12 h lumière et 12 h obscurité dénote l'adaptation au milieu naturel et semble donc être intéressante pour de potentielles applications en cultures en plein air, particulièrement appréciées pour leur entretien à bas coût énergétique, qui constitue un avantage économique non négligeable (Guo et al., 2015; Pérez et al., 2017).

En effet, au niveau local, l'utilisation d'une espèce issue du milieu naturel apporte des avantages en termes d'adaptation aux conditions de la zone d'origine et une majeure résistance aux fluctuations environnementales, en particulier pour les **espèces lagunaires, adaptées à des milieux fortement instables** (Tzovenis et al., 2009; Cheregi et al., 2019; Hotos & Avramidou, 2021). L'utilisation d'espèces lagunaires dans des applications aquacoles s'est déjà révélée particulièrement intéressante, comme une meilleure résistance aux fluctuations de salinité et température par rapport aux souches marines des mêmes espèces (Fisher & Schwarzenbach, 1978; Tzovenis et al., 2009 et références citées; Hotos & Avramidou, 2021).

De ce fait, au vu des potentialités aquacoles des espèces lagunaires soulignées et sans compter toutes les autres perspectives d'application de molécules d'intérêt dans d'autres domaines (médecine, cosmétique, nutrition humaine, biocarburants...), la conservation des systèmes lagunaires est aussi importante pour préserver des **potentialités de développement de ressources biotechnologiques** qui pourraient être utiles pour le soutien d'un développement et une exploitation durable, à différentes échelles.

En conclusion, l'intérêt à conserver les milieux lagunaires réside donc en plusieurs fronts de type hydrologique, biologique, sociologiques et économiques, tous strictement liés sous l'écologie de ces milieux. Dans ce cadre et en raison des observations et projections précédemment décrites, il est évident que la conservation des écosystèmes lagunaires demande une **gestion rapide, efficace, proactive, adaptative et intégrée** (Figure 12), comprenant toute la complexité de ces milieux, dans leur cadre d'insertion : le littoral.

2. VERS UNE GESTION DURABLE DES ÉCOSYSTÈMES LAGUNAIRES

2.1 Quelles sont les problématiques pour une gestion durable ?

Malgré la dégradation progressive des systèmes lagunaires côtiers méditerranéens et la conscience qu'il existe un fort besoin de les préserver, leur gestion rencontre à ce jour plusieurs **obstacles**.

En premier lieu, souvent un des freins à la prise de décision réside en un **manque de connaissances** sur l'état et les dynamiques des systèmes lagunaires (Figure 13 ; Latron et al., 2022; Ligorini et al., 2023 - **Chapitre III**). Les lagunes de petites surfaces en sont un exemple flagrant. Les travaux menés dans le cadre de cette thèse ont fourni des éléments clés dans la compréhension de ces milieux au niveau local, mais aussi en application à d'autres lagunes similaires dans la région méditerranéenne et dans le monde (Ligorini et al., 2023 - **Chapitre III**). Les analyses ont révélé l'importance des aspects locaux et du contexte de ces petits systèmes très réactifs, mais aussi des points communs de fonctionnement, et leur vulnérabilité face aux pressions anthropiques et au changement climatique a été démontrée (Ligorini et al., 2023 - **Chapitre III**). Toutefois, même les lagunes les plus connues rentrent parfois dans cette problématique à cause de la **difficulté de comprendre les dynamiques de réaction et les trajectoires de restauration (inertie, hystérésis ; Figure 13)**. Les deux exemples relatifs aux lagunes de Biguglia et Thau, montrant des effets indésirables suivant des actions de restauration (Collos et al., 2009; Cecchi et al., 2016; Garrido et al., 2016; Pasqualini et al., 2017; Derolez et al., 2020b; Ligorini et al., 2022b - **Chapitre II**), sont donc intéressants, car ils ont permis de mettre en lumière le fait que les trajectoires de restauration sont souvent complexes et parfois des effets secondaires inattendus se produisent suite à des interventions de gestion. Encore, les trajectoires de restauration de ces systèmes lagunaires sont fortement méconnues et dépendent largement de l'état d'eutrophisation ou de dégradation et de la capacité de résilience de ces systèmes (Le Fur et al., 2019). D'où l'intérêt de regarder le plus largement possible, et pas qu'un seul compartiment, pour pouvoir individuer et évaluer les éléments favorisant les propriétés de résilience et prévoir les potentielles réponses du système, afin de planifier des actions de gestion efficaces (Walker et al., 2006; Hobbs et al., 2009; Biggs et al., 2015; García-Ayllón, 2017; Boudouresque et al., 2020; De Wit et al., 2020; Ligorini et al., 2022b - **Chapitre II**; Ligorini et al., 2023 - **Chapitre III**).

Une problématique centrale qui interroge les gestionnaires et les scientifiques opérant dans les milieux lagunaires est d'**intégrer le changement constant à la planification des stratégies de gestion**, et en particulier la question de la **gestion des**

graus (Figure 13). Avec la progression du changement climatique, la réduction de l'apport d'eau due à la diminution des pluies engendrera de plus en plus la fermeture de graus. Grâce à l'analyse sur le long terme et à travers la création de frises chronologiques, ce phénomène apparaît évident dans le cas de l'étang de Biguglia : la diminution des pluies engendre une pression sortante insuffisante qui détermine à son tour l'accumulation de sédiments et une tendance à la fermeture du grau. Dans le cas de Biguglia cet isolement de la lagune du milieu marin entraîne malgré tout une baisse progressive de la salinité, car le même phénomène de comblement intéresse aussi l'embouchure du fleuve Golo tributaire de la lagune : la fermeture combinée de ces deux embouchures conduit à un isolement du plan d'eau de la mer et un apport d'eau douce plus élevé du bassin versant (Ligorini et al., 2022b - Chapitre II). Dans d'autres cas, l'isolement des systèmes lagunaires de la mer, en association à l'augmentation de températures et donc de l'évaporation, entraîne une augmentation du confinement de ces milieux et les expose au risque d'assèchement.

C'est notamment le cas des lagunes de petites surfaces, plus réactives, comme cela s'est produit pour la lagune de Santa Giulia en 2020 (Ligorini et al., 2023 - Chapitre III). La nécessité de maintenir la connexion à la mer, et pour des raisons de circulation de l'eau et pour des raisons de connexion biologique (par exemple, pour le recrutement d'espèces d'intérêt) nécessaire pour le soutien des activités, notamment la pêche, déterminera un besoin croissant de rétablir ces connexions de façon artificielle, avec des **interventions actives d'ouverture des graus** (Figure 13). Ces opérations sont toutefois coûteuses en termes de temps, énergie et argent, de plus, elles ne sont pas forcément résolutes, justement en raison de cette tendance à l'accumulation de sédiment entraînée par le changement climatique. Encore une fois, le socio-écosystème de l'étang de Biguglia en est l'exemple plus classique : les interventions d'ouverture artificielle du grau sont souvent inefficaces si la profondeur creusée n'est pas suffisante, car le grau se ferme à nouveau plutôt rapidement, sans laisser le temps à la lagune de réagir (Ligorini et al., 2022b - Chapitre II). Ces solutions d'intervention deviendront donc de plus en plus difficiles et de moins en moins rentables au cours du temps, ce qui constitue un problème pour la gestion qui, au contraire, demande et recherche des solutions alternatives à bas coût et haute performance pour la gestion et restauration des écosystèmes (Elliott et al., 2007a).

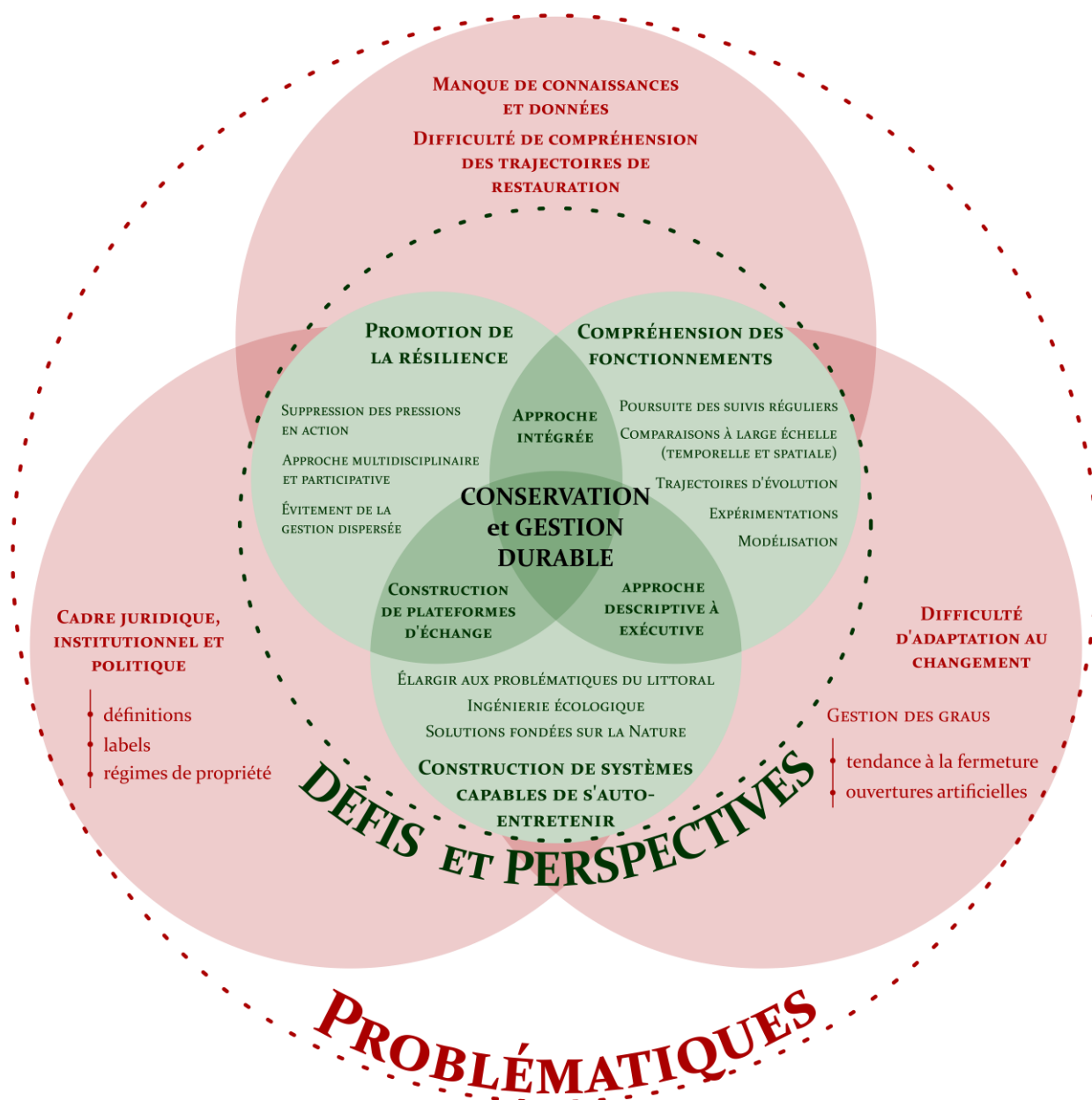


Figure 13 Représentation schématisée des principaux freins à la gestion, des défis pour l'avenir de ces milieux et du processus vers une gestion intégrée et durable pour la conservation des écosystèmes et des services écosystémiques fournis.

Parallèlement, le **cadre juridique, institutionnel et politique** autour des lagunes ne rend pas plus facile leur gestion (Figure 13). En premier lieu, la définition des lagunes, toujours en évolution, est une problématique non négligeable, car la classification de ces systèmes affecte les cadres normatifs applicables et donc les objectifs fixés pour la conservation (Cizel, 2017; Ghiotti, 2019; Latron et al., 2022). Les lagunes de petites surfaces enquêtées pendant ce travail (Ligorini et al., 2023 - Chapitre III), ainsi que les lagunes temporaires, en sont un exemple, car elles sont exclues de la DCE, mais elles sont incluses dans la définition de « lagunes méditerranéennes habitat 1150* »

établie par la DHFF (Cizel, 2017; Ghiotti, 2019; Barre et al., 2020). En outre, la nature de transition de ces systèmes fait qu'ils sont encadrés par plusieurs types de directives, cadres juridiques, normes et objectifs, et, en effet, au moins cinq normes différentes peuvent concerner les lagunes (Ghiotti, 2019): la Directive Cadre sur l'Eau (DCE ; 2000/60/EC European Union (EU), 2000), la Directive Habitats-Faune-Flore (DHFF ; 92/43/EEC European Union (EU), 1992), la Directive Inondation (DI ; 2007/60/EC European Union (EU), 2007), la Directive Cadre Stratégie pour le Milieu Marin (DCSMM ; 2008/56/EC European Union (EU), 2008), et la Directive Eaux Souterraines (DES ; 2006/118/EC European Union (EU), 2006).

De plus, souvent les lagunes cumulent des labels pour leur conservation en tant que zones d'intérêt à préserver. Toutefois, souvent ces statuts ne résultent pas en une protection effective des milieux, car ils ne posent pas de mesures de protection contraignantes ou alors, car il y a des problématiques d'attribution de ces labels ou de construction et mise en action de plans de gestion, liées à un manque de financement et/ou de ressources humaines députées à ces fonctions (Cizel, 2017; Popoff et al., 2021). Parfois, ce manque de mise en action de plans de gestion est dû à des problématiques de régimes de propriété privés ou mixtes, comme c'est le cas des lagunes de petites surfaces traitées dans le **Chapitre III** (Ligorini et al., 2023), qui complexifient et ralentissent le développement des stratégies de gestion (De Wit et al., 2021; OEC, 2022).

Au niveau pratique, donc, les gestionnaires sont confrontés à **plusieurs défis** : la pluralité des problématiques des systèmes lagunaires mène à l'implication de nombreux acteurs, ce qui nécessite d'une concertation complexe pour la prise de décisions. Parallèlement, la gestion est aussi menée à concilier des objectifs et des impositions à la fois internationales ou nationales (par exemple les cadres réglementaires GIZC, DCE...), mais aussi des réformes et contraintes territoriales.

2.2 *Quels sont les défis et les perspectives pour une conservation durable ?*

Les obstacles à la gestion des lagunes côtières portent atteinte au développement de différentes stratégies, ou bien d'approches et réflexions qui peuvent aider à sortir des impasses et progresser vers la promotion de la conservation et la durabilité de ces écosystèmes.

En premier lieu, l'amélioration de la **compréhension des fonctionnements écologiques** des milieux lagunaires est un des premiers défis pour envisager une gestion efficace (Figure 13). L'acquisition de connaissances doit être poursuivie, notamment avec des observations empiriques et des **suivis réguliers**, surtout pour les milieux peu

connus, comme les lagunes de petites surfaces (Figure 13). La construction de bases de données sur le long terme et l'investigation des écosystèmes permettra la poursuite des études des **trajectoires d'évolution** et le développement de **comparaisons entre différents systèmes à large échelle (temporelle et spatiale)**, afin de déduire des processus globaux (Figure 13). Parallèlement, persévérer dans la réalisation d'**expérimentations** permettra de prévoir de potentielles réponses des systèmes aux changements futurs (Figure 13 ; Ligorini et al., 2023 - **Chapitre III** ; **Chapitre IV**). Notamment, dans le cadre du travail présenté dans le **Chapitre IV**, qui met en évidence les effets significatifs des changements de salinité sous différents scénarios d'évènements climatiques extrêmes envisageables dans le futur proche, la nécessité de tester d'autres conditions est évoquée. Par exemple, les effets synergiques des variations de salinité et de l'augmentation des températures ou des modifications dans les apports en nutriments ont déjà été observés sur d'autres systèmes, mais restent méconnus sur les communautés des milieux lagunaires et ceux de petite taille en particulier (Ganguly et al., 2013; Fouilland et al., 2017; Stefanidou et al., 2018; Hernando et al., 2020). Également, il existe un besoin d'explorer les réponses à ce genre d'altérations environnementales de la part de communautés complexes, pour comprendre les dynamiques de réponses en tenant compte des différentes interactions biotiques en jeu (Barnes & Wurtsbaugh, 2015; Fouilland et al., 2017).

En outre, l'intérêt d'étudier ces dynamiques utilisant les lagunes côtières et leurs communautés biotiques réside dans la potentialité de systèmes sentinelles de ces milieux, qui peuvent donc fournir des éléments essentiels sur le futur des écosystèmes côtiers sous l'action de différentes pressions en raison de leur réactivité (Robert & Mazzilli, 2007; Ferrarin et al., 2014).

De plus, les connaissances acquises dans les cadres décrits sont aussi constitutives pour le développement de modèles numériques (Gunaratne et al., 2011; Jones et al., 2018; Doughty et al., 2019; Pérez-Ruzafa et al., 2019a; Pete et al., 2020; Teixeira & Solari, 2020). La **modélisation** est un outil fondamental pour le partage et le support à la discussion entre les scientifiques et un public non-scientifique, qui est pourtant confronté à l'analyse de situations complexes et surtout à la prise de décision en matière de gestion environnementale (Figure 13 ; Pete et al., 2020; Ligorini et al., 2022b - **Chapitre II** ; Ligorini et al., 2023 - **Chapitre III**). La modélisation peut permettre de dessiner différents scénarios possibles pour le futur et prévoir les réponses du système, en intégrant par exemple des options plausibles sous l'application de mesures de protection ou de restauration, afin de concilier le langage scientifique avec la compréhension de la part d'acteurs de différents domaines (politiques, professionnels...), et fournir ainsi une base pour le dialogue.

Afin de développer des outils de modélisation et poursuivre l'acquisition de connaissances sur les milieux lagunaires et sur leur fonctionnement écologique, la meilleure approche est la prise en compte de plusieurs compartiments, biotiques et abiotiques, ainsi que la continuité hydrologique des plans d'eau lagunaires avec leurs bassins versants et la mer. Idéalement, cette démarche permettra d'appliquer une approche écosystémique aux investigations et donc de construire l'image holistique de l'écosystème, dont la gestion a besoin pour pouvoir comprendre le fonctionnement du milieu (Ligorini et al., 2022b - **Chapitre II**).

En termes de gestion environnementale des lagunes en dégradation, la meilleure solution pour la conservation des écosystèmes est souvent prouvée être la **protection de la résilience naturelle du système** (Elliott et al., 2007a; Pérez-Ruzafa et al., 2018; Ligorini et al., 2022b - **Chapitre II**). Cet objectif constitue un enjeu majeur pour la gestion environnementale des milieux lagunaires, surtout en raison du grand nombre d'acteurs impliqués (Figure 13 ; Cote & Nightingale, 2012; Grafton et al., 2019; Walker, 2020; De Wit et al., 2021). La **suppression des pressions en action** est considérée comme une action centrale dans la protection et la restauration des systèmes naturels, dont la non-application peut compromettre l'efficacité d'autres mesures de gestion (Figure 13 ; Schallenberg et al., 2010b; Rodrigo et al., 2013; Pérez-Ruzafa et al., 2018; Prado et al., 2019). Toutefois, les lagunes côtières sont des socio-écosystèmes au sein du système complexe du littoral, donc la présence de l'Homme demande le maintien de certaines activités et services et « l'impact zéro » est utopique. Par conséquent, les futures études sur ces milieux devraient évoluer en intégrant le côté sociologique et économique de façon opérationnelle, à travers une **démarche multidisciplinaire et participative** (Figure 13 ; Redman et al., 2004; Robards et al., 2011; Berkes, 2012; Cote & Nightingale, 2012; Benessaiah & Sengupta, 2014). Seulement avec la construction d'une vision globale et intégrée de l'écosystème dans sa complexité, il est possible d'établir le spectre d'états désirés par la société vers lequel faire converger les efforts d'investissement en ressources (humaines et financières), en concertation avec tous les acteurs en jeu (Elmqvist et al., 2019; Grafton et al., 2019; Walker, 2020). En perspective, l'approche idéale à l'enquête sur ces systèmes multifacettes est une approche socio-écologique, qui permettrait de comprendre les interactions et les changements écosystémiques, et d'accompagner les stratégies de gestion par la recherche et l'expertise, à travers un partage de connaissances et compétences. Ce couplage est le fondement pour garantir la durabilité des écosystèmes lagunaires côtiers et des services qu'ils fournissent (Redman et al., 2004; Ostrom, 2009; Cataudella et al., 2015; Virapongse et al., 2016; Elmqvist et al., 2019). Le scientifique ne doit pas être isolé dans ses enquêtes : les questions de gestion doivent remonter aux scientifiques, mais parallèlement les expertises des acteurs, ainsi que les attentes et la perception du milieu de la part des

usagers, doivent être prises en compte dans les interrogations scientifiques (Cote & Nightingale, 2012; Grafton et al., 2019; Walker, 2020). Les moyens à déployer sont les plus variés : un exemple qui s'est révélé plutôt efficace est la réalisation d'enquêtes au sein de la société, portant sur la perception de la qualité du système lagunaire d'intérêt et son évolution dans le temps, en lien avec la gestion (Audouit et al., 2019).

Afin d'obtenir cette harmonisation entre les différentes parties impliquées dans l'écosystème, l'attention devrait se focaliser sur le **développement de plateformes ou outils d'échange** entre les différents acteurs en jeu, afin de partager le savoir et les compétences et **éviter la gestion dispersée** qui parfois affecte les lagunes côtières en raison de leur caractère transitoire, de leurs régimes de propriété complexes et leurs statuts de protection multiples (Figure 13 ; Redman et al., 2004; Ghiotti, 2019; Grafton et al., 2019; De Wit et al., 2021; Walker, 2020).

Dans ce contexte, des actions à plus large échelle (temporelle et spatiale) émergent, par exemple en relation aux fonctions de protection de la côte exercées par les lagunes côtières et aux implications de leur perte sous la progression du changement climatique (e.g. élévation du niveau de la mer, érosion côtière, risque d'inondation...). L'objectif d'une gestion efficace de ces milieux est d'atteindre la **durabilité des écosystèmes littoraux**, à une échelle temporelle qui dépasse celle des générations humaines (objectif GIZC ; Chapman, 2012; Deboudt, 2012; Ghiotti, 2019; Taylor et al., 2021). Dans cette optique, il existe une demande croissante pour des solutions de restauration écologique qui puissent **créer des écosystèmes capables de s'auto-entretenir et s'auto-supporter**, sans qu'ils nécessitent de gestion ultérieure (Figure 13 ; Elliott et al., 2007a; Day et al., 2009). Ces éléments amènent à **élargir la conservation des lagunes aux problématiques de conservation du littoral** (Figure 13) : la gestion environnementale des systèmes littoraux est amenée à être proactive, pour intégrer les potentielles réponses des systèmes, mais aussi adaptative, pour permettre au système de persister dans un processus d'adaptation dynamique au changement (Day et al., 2009; Chapman, 2012; Mitsch, 2012; Pérez-Ruzafa et al., 2019b; Taylor et al., 2021).

Ces propriétés peuvent être mises en œuvre à travers de solutions d'**ingénierie écologique**², dans une optique d'amélioration et renforcement des propriétés de résistance et résilience des écosystèmes naturels (Figure 13 ; Gattie et al., 2003; Mitsch, 2012; De Wit et al., 2017, 2020). Selon Day et al. (2009), dans le futur proche la

² Le terme « ingénierie écologique » a été introduit par Howard T. Odum dans les années 1960 et porte au concept innovant de couplage des principes scientifiques avec des pratiques d'autres domaines relatives aux besoins de la société, vers une amélioration de la qualité de vie (Gattie et al., 2003). Les deux objectifs de l'ingénierie écologique sont i) la restauration des écosystèmes fortement perturbés par les activités humaines, et ii) le développement de nouveaux écosystèmes durables qui aient une valeur et écologique et humaine (Mitsch, 2012). Cette discipline est relativement jeune, parfois encore contradictoire et complexe, qui nécessite toujours d'un développement plus profond, notamment au niveau académique (Mitsch, 2012).

restauration et la gestion durable des écosystèmes sera aussi importante que la protection des zones naturelles déjà existantes. Parallèlement, cette approche à la conservation devra évoluer pour s'adapter à des écosystèmes qui deviendront de plus en plus des mosaïques de zones intensivement exploitées/impactées (Day et al., 2009). La pauvreté en ressources et surtout en énergie forcera l'Homme à se baser sur l'ingénierie écologique pour atteindre une gestion écosystémique durable (Day et al., 2009; Mitsch, 2012).

Au sein de cette discipline, les **Solutions fondées sur la Nature (SfN)** ont subi un vrai développement récent et sont considérées comme des outils à explorer pour la gestion environnementale (Figure 13 ; Moraes et al., 2022; Reguero et al., 2022). Les SfN sont définies par le UICN comme « des actions visant à protéger, gérer de manière durable et restaurer des écosystèmes naturels ou modifiés pour relever directement les défis de société de manière efficace et adaptative, tout en assurant le bien-être humain et en produisant des bénéfices pour la biodiversité », de façon que, aux objectifs purement écologiques, des objectifs de développement durable sont aussi étayés (Bridges et al., 2022; Moraes et al., 2022; Reguero et al., 2022). L'ancienne approche à la protection et à la restauration des systèmes naturels était la construction d'infrastructures solides et immuables, par exemple la construction de digues pour la protection de la zone côtière des vagues et de l'érosion (Gattie et al., 2003; Chowdhury et al., 2021). Toutefois, ces systèmes non seulement peuvent introduire de nouvelles problématiques, comme l'altération de l'hydrologie, la perte de complexité du substrat et conséquentes pertes en biodiversité et favorisation d'espèces invasives, mais, en raison de leur nature stationnaire, ils ne sont pas des solutions à long terme, car ils ne peuvent pas s'adapter aux changements (e.g. l'élévation du niveau de la mer) (Waltham & Dafforn, 2018; Chowdhury et al., 2021). L'ingénierie écologique et les SfN en particulier constituent l'opportunité de créer des designs à travers l'exploration de nouveaux matériaux pour enrichir, améliorer des infrastructures déjà existantes ou en créer des nouvelles, avec un faible impact écologique et la reconstitution de la valeur et des fonctions écologiques perdues (Waltham & Dafforn, 2018; Chowdhury et al., 2021; Bridges et al., 2022). De plus, les SfN offrent une flexibilité et adaptabilité aux changements en pouvant évoluer, au contraire des infrastructures rigides, et des bénéfices pour la lutte contre le changement climatique (Bridges et al., 2022).

Des exemples d'application de ces solutions existent désormais dans plusieurs environnements, mais elles montrent une efficacité variable. Une des applications plus classique est la **protection du littoral** de l'érosion et du risque d'inondation. Parfois, ces projets aboutissent à des **échecs**, par exemple, la plantation de mangroves sur les côtes de l'Océan Indien pour la protection du littoral contre les tsunamis s'est révélée parfois inefficace (voir synthèse dans Mitsch, 2014). Souvent, les causes d'échec de ces

projets résident en une connaissance du milieu trop sommaire ou un engagement des usagers insuffisant (e.g. zone non propice à l'établissement des mangroves et conflits avec les aquaculteurs dans l'élevage de crevettes, pour l'exemple cité ; Mitsch, 2014). D'autres exemples montrent au contraire l'efficacité de ces SfN, notamment pour la restauration de zones humides dans la baie du Delaware, grâce au respect de l'action naturelle du fonctionnement du système dans le design du projet, en permettant d'épargner énormément de ressources financières et humaines (Mitsch, 2014). Un autre système largement utilisé et efficace pour la protection des côtes est l'installation des récifs à huîtres, qui permet non seulement de créer des habitats complexes favorisant la diversité, mais aussi d'obtenir des **structures « vivantes » qui peuvent s'adapter au changement à long terme**, comme l'élévation du niveau de la mer (Chowdhury et al., 2021). Selon des études de modélisation, en outre, il semble y avoir un intérêt dans le **couplage de plusieurs SfN en parallèle pour optimiser l'attente des objectifs de restauration**, comme l'application combinée de rechargement en sable et végétalisation en mer à travers la plantation de phanérogames dans la zone infralittorale pour renforcer la résistance du milieu côtier (Chen et al., 2022).

Les problématiques des milieux lagunaires décrites au cours de ce travail pourraient faire l'objet de projets d'ingénierie écologique et SfN. Notamment, des techniques de contrôle des flux à travers des systèmes d'écluses se sont déjà révélées efficaces en Tunisie (Pergent & Kempf, 1993) et ont été utilisées dans un projet d'ingénierie écologique dans la lagune de Venise pour régler les flux d'eau douce d'un canal reliant le fleuve Sile au plan d'eau (Boscolo Brusà et al., 2022). Un système de ce type pourrait potentiellement être envisagé notamment dans le cas de l'étang de Biguglia, pour limiter, ou en tout cas contrôler, les apports du fleuve Golo à travers le canal du Fossone, surtout en cas de fermeture de l'embouchure du fleuve à la mer afin d'éviter un apport excessif d'eau douce (avec sa charge en sédiments, nutriments, polluants...) à la lagune.

Les trajectoires d'eutrophisation, ou les problématiques liées aux apports des activités (surtout agricoles) des bassins versants en général, remarquées à plusieurs reprises pendant les travaux réalisés et en particulier sur la lagune de Biguglia, pourraient être adressées à travers des SfN. Par exemple, des études pilotes sur l'utilisation de bioréacteurs à bois autour de la lagune eutrophisée du Mar Menor, en Espagne, ont montré une efficacité remarquable dans la réduction des nitrates des rejets agricoles (Álvarez-Rogel et al., 2020).

Encore, la problématique de la gestion des graus pose un défi encore plus important lié au changement climatique, comme précédemment discuté. Les SfN semblent alors fournir un outil très prometteur, en abordant le problème à travers la **lutte contre**

l'accumulation de sédiments et l'optimisation de la circulation hydrique. Cela peut se produire notamment à travers le renforcement du littoral sableux, par exemple grâce à la végétalisation des dunes, et la protection de la côte contre les vagues et l'érosion par le biais des récifs artificiels (e.g. récifs à huîtres, structures biodégradables ; Chowdhury et al., 2021; Boscolo Brusà et al., 2022). Différentes SfN peuvent être couplées pour atteindre le résultat désiré (Boscolo Brusà et al., 2022; Chen et al., 2022; Pathak et al., 2022), notamment, pour la lagune de Pulicat (Inde), l'utilisation combinée de mécanismes de protection côtière et végétalisation du lido a été suggérée pour contraster de façon durable l'envasement et la fermeture des graus (Santhanam et al., 2022). Malgré une efficacité parfois faible (Schallenberg et al., 2010b; Rodrigo et al., 2013), la transplantation de phanérogames pour reconstituer des herbiers au sein des lagunes s'est révélée parfois un outil de restauration écologique efficace (Sfriso et al., 2019, 2021, 2022). Ce système pourrait être utilisé en couplage avec d'autres SfN pour améliorer la dynamique des sédiments : en lagune, pour ralentir la dispersion et trapper les sédiments en les stockant au fond, et en mer, pour protéger le littoral de l'érosion et de la force des vagues (Boscolo Brusà et al., 2022; Bridges et al., 2022; Chen et al., 2022). En effet, ce système a déjà été prouvé comme efficace en milieu côtier et lagunaire (Boscolo Brusà et al., 2022; Chen et al., 2022).

Le défi posé par l'ingénierie écologique et les SfN est toutefois complexe. Ces actions demandent une connaissance scientifique approfondie des écosystèmes, un fort engagement des acteurs en jeu et un travail d'engagement mutuel entre pratiques et connaissances d'écologie et d'ingénierie (Mitsch, 2012; Moraes et al., 2022). Néanmoins, **il est désormais demandé à l'écologue de passer de l'approche descriptive classique à une nouvelle approche exécutive** (Day et al., 2009; Mitsch, 2012; Moraes et al., 2022).

Il faut se permettre d'agir pour contraster la dégradation progressive des écosystèmes naturels et préserver leurs services pour les générations futures. Les outils sont à disposition et l'action produira forcément un changement, positif ou négatif. Quel que soit le résultat, ces informations sont indispensables pour progresser : même l'erreur peut constituer un progrès et l'ingénierie écologique constitue un « *acid test* » pour les connaissances écologiques, pouvant corroborer ou démentir des théories écologiques (Mitsch, 2012).

L'application pratique de ces actions aux systèmes lagunaires est freinée par leur complexité au niveau global et local : l'obtention d'une réponse claire et nette sur la réactivité de ces écosystèmes est difficile, notamment dans une perspective d'application d'un projet de restauration *via* l'ingénierie écologique. Dans cette optique, les avis scientifiques et les scénarios modélisés sont des guides et des appuis à la prise de décision.

Néanmoins, les principes sur lesquels l'ingénierie écologique se fonde sont des points de réflexion centraux dans la planification des actions de restauration et pour la gestion écosystémique en général, et résumant bien les recommandations discutées au cours de ce travail pour une gestion efficace et durable : les problèmes écologiques doivent être résolus avec une vision intégrée du système, qui inclut l'Homme aussi (« **system thinking** ») ; la nature doit contribuer au design des solutions, qui doivent donc intégrer le fonctionnement du système (« **self-design** ») ; l'utilisation de ressources naturelles doit être privilégiée dans une optique de sobriété énergétique (« **natural energy use** ») ; et la conservation des écosystèmes doit être intégrée, adaptative et à long terme dans un contexte de changement continu (« **ecosystem conservation** ») (Mitsch, 2012). Cette approche souligne, encore une fois, la nécessité d'un haut niveau d'interdisciplinarité, où l'écologie doit s'approprier des pratiques d'autres disciplines (l'ingénierie, l'architecture de paysage, la sociologie...) pour élaborer des solutions efficaces et rentables (Day et al., 2009; Mitsch, 2012). Pour aller encore plus loin, la démarche idéale de recherche serait la transdisciplinarité, la forme plus poussée de l'interdisciplinarité : le vrai enjeu est d'arriver à appliquer cette approche intégrée, où plusieurs disciplines et acteurs non-académiques (e.g. gestionnaires, usagers, grand public) sont engagés dans une combinaison d'interdisciplinarité et approche participative pour générer de nouveaux concepts, méthodes et savoirs autour d'une problématique écologique à résoudre (Klein, 2008; Stock & Burton, 2011; Butt & Dimitrijević, 2022). Seulement à travers la **recherche**, l'**interdisciplinarité**, le **partage** et le **dialogue**, il est possible de définir la meilleure option pour la **conservation durable** des systèmes lagunaires et des services écosystémiques fournis face aux changements globaux.



Conclusion générale



CONCLUSION GÉNÉRALE

L'objectif général de cette thèse était de fournir des éléments d'appui pour les acteurs impliqués dans la gestion environnementale, afin de fournir un soutien pour la conservation et la restauration des lagunes côtières, ainsi que d'explorer les potentielles applications biotechnologiques d'une diatomée isolée dans une lagune corse dans le domaine de l'aquaculture.

En premier lieu, cette thèse constitue un apport important au savoir territorial. Les travaux dans le cadre de cette thèse ont permis en effet d'améliorer les connaissances sur les milieux lagunaires au niveau régional de la Corse. Cela a fourni donc un **apport à la communauté scientifique territoriale** et une **continuité** importante **dans la recherche et la valorisation locale**, en poursuivant les nombreux efforts de recherche qui ont été menés dans les années passées. Parallèlement, les éléments mis en lumière pendant ces travaux ont une **application au niveau global**, à l'échelle méditerranéenne et mondiale, à la fois avec un apport de connaissances qui peuvent servir de base de comparaison ou avec l'apport de questions ou découvertes applicables à des systèmes similaires présents ailleurs dans le monde.

À travers le travail présenté dans le **Chapitre I**, concernant les lagunes de Diana et Urbino, des **dynamiques de saisonnalité** ont été détectées pour les lagunes oligotrophes, à travers une approche d'analyse des **trajectoires sur le long terme** des communautés phytoplanctoniques. Parallèlement, des tendances inquiétantes, comme **l'augmentation des blooms** et de **certaines espèces potentiellement toxiques**, ont été mises en évidence. Ces observations sont en ligne avec des observations à l'échelle mondiale, ce qui indique un symptôme de processus globaux impactant les lagunes, en particulier le changement climatique. Ces observations, en raison des activités menées sur les étangs, notamment **l'aquaculture** et surtout dans les étangs profonds et marinisés comme ceux d'origine tectonique, amènent à des **questions sur la durabilité** de ces activités dans le futur.

L'application des trajectoires sur le long terme a mis en évidence la nécessité de prendre en compte plusieurs compartiments dans l'écosystème, à côté de l'indicateur « phytoplancton ». L'étude présentée dans le **Chapitre II**, qui a pour objet l'étang de Biguglia, montre que seulement avec cette approche globale, il est possible de construire **l'image holistique du système et de son fonctionnement**. Cela est indispensable pour reconstruire les trajectoires du système et d'en évaluer les dynamiques, la linéarité (ou pas) et « l'élasticité », en termes de résistance et résilience du milieu face aux perturbations. Un autre aspect fondamental qui a été mis en évidence est la nécessité de

prendre en compte l'Homme dans l'étude des trajectoires écologiques. Quelle est sa place dans l'écologie du système ? L'**approche écosystémique** est donc appliquée à un **socio-écosystème**. En perspective, une **approche socio-écosystémique**, avec l'implication des sciences sociales et des études sur les aspects socio-économiques et de gouvernance, sera donc nécessaire pour établir le spectre d'états désirés et **favoriser les échanges** entre les différents acteurs impliqués dans la gestion des milieux lagunaires.

L'approche appliquée à l'étude des **lagunes de petites surfaces**, objet du **Chapitre III**, avec les trois lagunes études de cas, Arasu, Santa Giulia et Balistra, est conséquent aux idées maturées pendant le travail réalisé en **Chapitre II**. La conscience sur l'importance écologique (et socio-économique) des lagunes de petites surfaces a porté les gestionnaires à prioriser les études sur ces milieux pour combler la **connaissance fragmentaire** dont l'on dispose. L'approche rétrospective n'est pas possible dans ces cas en raison d'un manque d'information. L'avantage est que l'étude de ces systèmes peu connus peut débiter avec une sorte de « maturité écologique » en appliquant cette approche globale, déjà prouvée efficace sur de grands systèmes, dès le départ des enquêtes sur les petits systèmes. L'étude présentée dans le **Chapitre III** montre un élan préliminaire vers cette **approche socio-écosystémique**, demandée pour le développement d'une gestion efficace : les systèmes lagunaires sont considérés des hydrosystèmes en connexion avec leurs systèmes adjacents et sont étudiés avec une approche interdisciplinaire, écologique et hydrologique ; ils sont aussi considérés comme des socio-écosystèmes avec une composante humaine à ne pas négliger, et sous les aspects d'impact anthropique (pollution, rejets, usage de l'eau, tourisme...) et sous les aspects socio-économiques et gouvernementaux (valeurs et services fournis, usage et demande des usagers, propriété foncière et problématiques de gestion...). L'ensemble de ces éléments a porté à définir certains facteurs agissant sur les potentielles variations (locales et globales) et des évidences que ces petits systèmes sont à la fois fragiles face aux changements et au changement climatique en particulier, mais aussi des **sentinelles des changements**.

Ces observations ont porté à s'interroger sur l'**avenir** de ces systèmes lagunaires. Comment les systèmes et leurs services peuvent varier dans le futur et sous de différents scénarios possibles ? Le monde en dynamisme constant et soumis à un taux de changement en augmentation exige une certaine **adaptabilité**, une **gestion proactive** pour garantir la conservation et la durabilité des écosystèmes. Les réponses à ces questions peuvent être étudiées à travers des **essais expérimentaux**. Le travail présenté dans le **Chapitre IV** offre un exemple de cette approche, en prenant une lagune de petite surface (Santa Giulia) comme objet d'étude, en raison de son rôle de sentinelle précédemment discuté. L'enquête est portée sur la **salinité**, un facteur très important

dans le milieu lagunaire, qui va être fortement impacté par le **changement climatique** et dont les effets sous différents scénarios de changement sont encore méconnus. Ce travail démontre que des variations de salinité prévues pour le futur vont produire des modifications importantes des communautés phytoplanctoniques lagunaires, malgré une certaine capacité de résistance, car habituées à un milieu fortement instable. Ces variations entraînent des répercussions au niveau écosystémique et des implications donc au niveau de la gestion écologique. Les questions qui se posent identifient en particulier la **gestion intégrée** des bassins versants et de l'entretien des graus comme moyens pour **mitiger** les impacts du changement climatique et donc les variations de salinité dans les systèmes lagunaires.

Le changement climatique futur et les changements locaux et globaux liés à la croissance et l'évolution humaine forcent aussi l'humanité à trouver de **nouvelles solutions** pour **soutenir le développement et le bien-être** d'un monde anthropisé en croissance continue. Par exemple, le déclin de l'exploitation halieutique provoque une augmentation de la demande par rapport à l'aquaculture. Cela engendre un **défi technologique** pour des productions de plus en plus **rentables, à bas coût économique, et énergétique**. Le phytoplancton, élément fondamental dans la production aquacole, peut fournir un service à la société dans ce cadre. Le travail présenté dans le **Chapitre V**, sur la diatomée *Chaetoceros tenuissimus* issue de l'étang de Diana, démontre que des **souches issues du milieu naturel** (et celui lagunaire en particulier) peuvent montrer des caractéristiques biochimiques et physiologiques d'intérêt. Les lagunes, qui sont des milieux extrêmement instables ont un potentiel dans ce cadre : elles peuvent fournir des espèces particulièrement résistantes aux variations environnementales, donc au changement des paramètres dans les milieux de culture et potentiellement produisant des molécules d'intérêt en raison de leur adaptation à un milieu variable par rapport à des souches cultivées, habituées à des conditions constantes. De plus, l'étude présentée dans le **Chapitre V** apporte une contribution importante au niveau territorial, en s'inscrivant parfaitement dans les objectifs de restauration et développement du laboratoire Stella Mare et en posant une première pierre vers le développement des entrepreneuriats locaux en Corse, à travers l'exploitation d'une ressource locale, adaptée aux conditions régionales, dans un potentiel d'activité aquacole.

Chapitre I Trajectoires, blooms, HABs et aquaculture

Ce premier travail a évalué les trajectoires sur le long terme et la saisonnalité des communautés phytoplanctoniques dans deux **lagunes tectoniques** (profondes et oligotrophes). À travers cette **approche long-terme**, des modifications dans la structure des communautés et dans la magnitude et fréquence des **blooms** ont été démontrées et mises en relation avec des processus agissant à l'échelle globale (changement climatique). Les limites de cette étude consistent en un manque de vision globale qui empêche la compréhension optimale des facteurs en jeu sur les systèmes et sur leurs communautés. Malgré cela, ce travail constitue une **alerte** pour la gestion future des milieux lagunaires en particulier dans le cadre de leur **exploitation aquacole**, dans un contexte de **changement climatique**.



Chapitre II Trajectoires d'un socio-écosystème

Cette étude, réalisée sur une lagune perturbée, intègre aux dynamiques sur le long terme une **approche écosystémique**. Les résultats ont montré l'importance de considérer le système lagunaire comme un **continuum hydrologique** avec son bassin versant et le milieu marin attenants, dans une optique de **socio-écosystème**. Certaines actions de gestion sur le système ont révélé des effets secondaires pour le fonctionnement écologique global. Malgré une bonne capacité de la lagune d'absorber les bouleversements, le système a récemment montré des signes de dégradation et une diminution de la capacité de **résistance** et **résilience**. L'**image holistique et rétrospective** restituée par ce travail fournit un élément de réflexion essentiel et une approche innovante pour la gestion future des systèmes lagunaires méditerranéens.



Chapitre III Lagunes de petites surfaces : diversité, réactivité, vulnérabilité

Ce travail fournit un premier **inventaire** des lagunes côtières de Corse et également un important message relatif à l'**approche intégrée** à appliquer pour le développement de connaissances sur les écosystèmes lagunaires de **petites surfaces** et pour leur future gestion. Les plans d'eau sont considérés en continuité avec leurs **bassins versants** et la **mer**, avec une **approche interdisciplinaire éco-hydrologique**. Des **éléments sociaux** sont discutés et invitent à développer une approche socio-écosystémique sur ces milieux si importants et **vulnérables** face aux **pressions anthropiques** et au **changement climatique**.



Chapitre IV Salinité : lagunes sentinelles du changement climatique

Cette étude expérimentale analyse de **potentielles réponses** des communautés phytoplanctoniques lagunaires au **changement climatique**. Les systèmes lagunaires, et ceux de petite surface en particulier, s'avèrent particulièrement réactifs aux variations de salinité et peuvent être considérés des sentinelles du changement. Les implications des changements observés au niveau du phytoplancton sur le fonctionnement écosystémique sont discutées afin de fournir des éléments utiles à la **gestion proactive** de ces milieux.

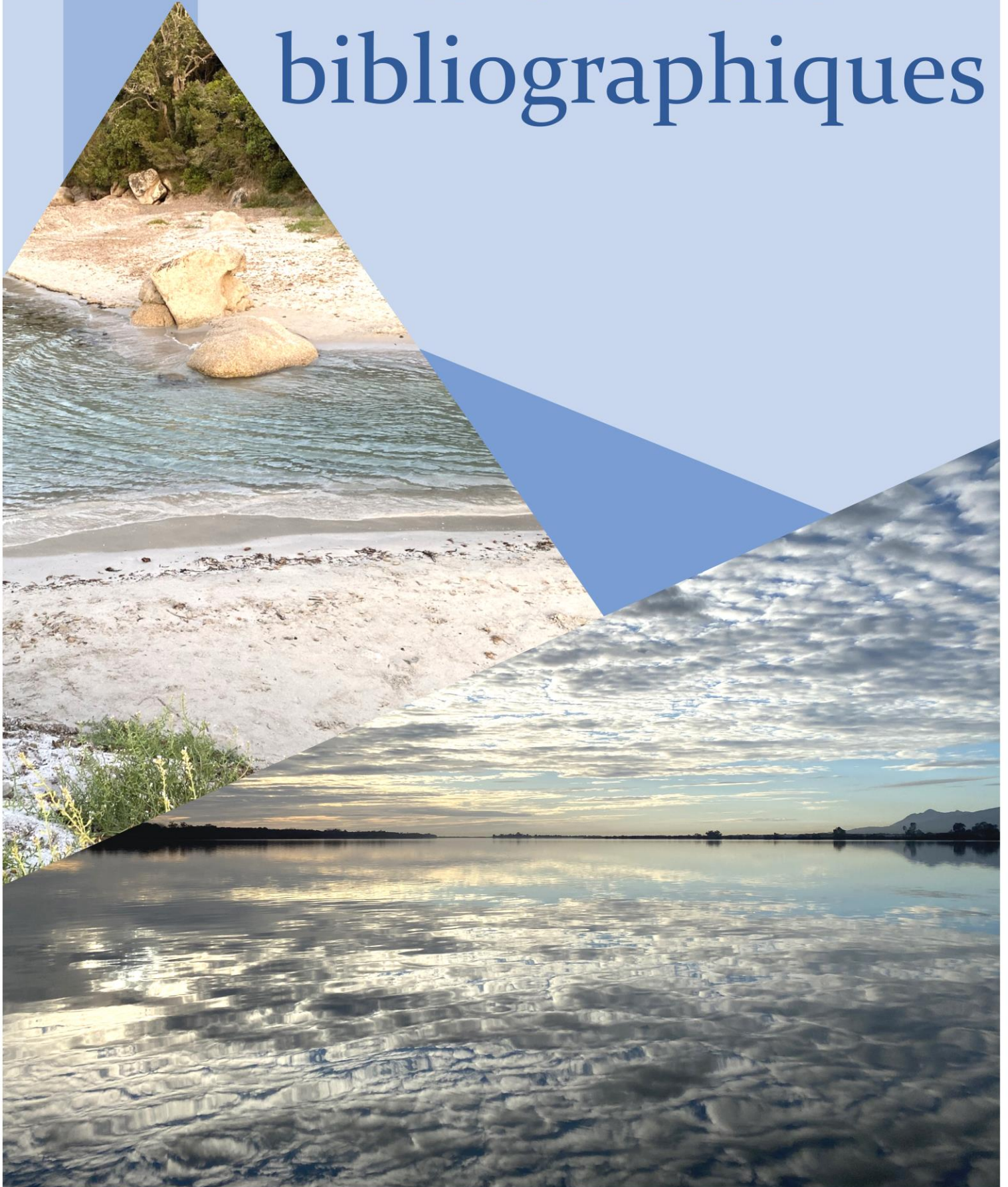


Chapitre V Phytoplancton lagunaire : une ressource pro- metteuse

Ce dernier travail se focalise sur les **potentialités biotechnologiques du phytoplancton**. L'espèce issue du milieu lagunaire, comparée avec une espèce issue de collections et communément utilisée en **aquaculture**, a montré des potentialités surtout en termes de contenu lipidique, de grand intérêt dans le domaine de l'aquaculture. Ce travail démontre l'intérêt de la recherche sur les espèces phytoplanctoniques naturelles. Le phytoplancton peut offrir à la société une solution technologique contre les défis économiques dans un monde perturbé, vers une **exploitation durable** et la **valorisation** de ressources naturelles et locales.



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Pour la réalisation des figures dans ce manuscrit, les pictogrammes ont été obtenus des sites *Flaticon* (<https://www.flaticon.com>) et *Integration and Application Network, University of Maryland Center from Environmental Science* (<https://ian.umces.edu/media-library>).

Annexes



ANNEXE I – SUPPLEMENTARY MATERIAL (LIGORINI ET AL., 2022A)

Table S1 Summary description for each lagoon of the different databases retrieved for each lagoon from the REPHY - French Observation and Monitoring program for Phytoplankton and Hydrology in coastal waters - monitoring network (REPHY, 2019).

Database	Diana					Urbino				
	Begin/end	Samplings per month	Samplings per season	Total number samples	Counting strategy	Begin/end	Samplings per month	Samplings per season	Total number samples	Counting strategy
FLORTOT 2001-2019	2001/01/29 2019/09/16	0 to 3	Winter: 103 Spring: 123 Summer: 112 Autumn: 116	454	all taxa present in the sample are counted					
FLORIND 2008-2015	2008/01/02 2015/12/21	1 to 5	Winter: 74 Spring: 78 Summer: 61 Autumn: 71	284	selected toxic taxa + taxa cellular density > 100 000 cell L ⁻¹	2008/01/02 2015/12/21	1 to 5	Winter: 66 Spring: 60 Summer: 55 Autumn: 59	240	selected toxic taxa + taxa cellular density > 100 000 cell L ⁻¹
FLORTOX 1998- 2017/2019	1998/01/26 2019/09/09	0 to 5	Winter: 156 Spring: 182 Summer: 139 Autumn: 147	624	only selected toxic taxa are counted systematically	1998/01/26 2017/04/10	0 to 5	Winter: 167 Spring: 175 Summer: 137 Autumn: 142	621	only selected toxic taxa are counted systematically

Table S2 Summary table for environmental variables and nutrient concentration, from 1998 to 2019, based on monthly medians historical database. Number of samples (n), minimal (min), maximal (max), median (median) and mean (mean) values are displayed for each season. Standard error (SE) for the mean are also shown.

		Diana						Urbino					
		n	min	max	median	mean	SE	n	min	max	median	mean	SE
Temperature (°C)	Winter	65	7.30	14.89	10.03	10.16	0.19	59	6.85	14.40	10.05	9.89	0.21
	Spring	66	10.18	22.23	15.87	16.27	0.44	59	10.30	23.90	16.15	16.62	0.51
	Summer	65	22.03	29.47	26.87	26.58	0.22	61	22.10	31.00	27.60	27.28	0.23
	Autumn	64	12.09	28.00	21.04	20.51	0.48	56	11.00	26.50	20.86	20.30	0.54
Salinity (PSU)	Winter	65	32.08	39.32	36.59	36.54	0.20	59	27.05	39.87	36.33	35.78	0.33
	Spring	65	31.23	38.27	36.78	36.39	0.18	58	29.80	37.90	35.63	35.25	0.27
	Summer	65	35.90	40.71	38.39	38.33	0.11	61	31.60	41.23	38.05	37.55	0.24
	Autumn	64	34.93	40.55	38.58	38.36	0.14	56	32.60	40.58	38.68	38.19	0.23
Turbidity (FNU)	Winter	63	0.30	9.07	1.25	1.54	0.15	56	0.39	6.20	1.30	1.58	0.15
	Spring	65	0.30	8.75	1.00	1.28	0.14	58	0.20	3.95	1.02	1.39	0.12
	Summer	64	0.20	3.10	1.23	1.29	0.07	61	0.18	3.90	1.10	1.25	0.09
	Autumn	63	0.05	4.10	1.65	1.72	0.11	56	0.15	5.50	1.26	1.65	0.16
Dissolved Oxygen (mg L⁻¹)	Winter	30	6.87	10.60	8.71	8.61	0.16	24	5.35	10.38	8.58	8.47	0.26
	Spring	31	5.08	13.30	7.56	7.77	0.24	24	4.75	11.55	7.72	7.62	0.25
	Summer	45	2.84	13.30	6.69	6.75	0.28	25	4.30	11.08	6.20	6.55	0.30
	Autumn	32	3.48	8.47	7.16	6.85	0.21	24	4.10	9.70	6.91	6.81	0.28
DIN (µmol L⁻¹)	Summer	49	0.02	2.10	0.23	0.45	0.07	48	0.00	4.00	0.24	0.47	0.10
DIP (µmol L⁻¹)	Summer	49	0.00	1.69	0.08	0.14	0.04	48	0.00	0.67	0.07	0.10	0.02
Silicates (µmol L⁻¹)	Summer	37	0.20	59.90	6.16	7.95	1.74	34	6.10	92.70	46.36	43.80	3.71

Table S3 Summary table for Chlorophyll *a* variable, from 2001 to 2019 on Diana lagoon, based on monthly medians historical database. Number of samples (n), minimal (min), maximal (max), median (median) and mean (mean) values are displayed for each season. Standard error (SE) for the mean are also shown.

		Diana					
		n	min	max	median	mean	SE
Chlorophyll <i>a</i> (µg L⁻¹)	Winter	56	0.03	13.39	0.69	1.03	0.25
	Spring	55	0.05	6.94	0.44	0.62	0.13
	Summer	54	0.24	4.50	1.06	1.37	0.14
	Autumn	52	0.05	6.65	1.05	1.32	0.17

Table S4 PERMANOVA (a) and PAIRWISE (b) tests results on Diana phytoplankton community, based on FLORTOT database. Significant values are highlighted in bold.

a)		Df	SumsOfSqs	MeanSqs	Pseudo-F	Pr(>F)
	Season	3	0.19	0.06	8.45	0.001
	Residuals	421	3.23	0.01	0.94	
	Total	424	3.43	1.00		

b)	pairs	Df	SumsOfSqs	Pseudo-F	p.adjusted
	Winter vs Spring	1	0.06	8.65	0.001
	Winter vs Summer	1	0.07	8.44	0.001
	Winter vs Autumn	1	0.07	8.82	0.001
	Spring vs Summer	1	0.09	12.42	0.001
	Spring vs Autumn	1	0.05	7.71	0.001
	Summer vs Autumn	1	0.04	5.08	0.002

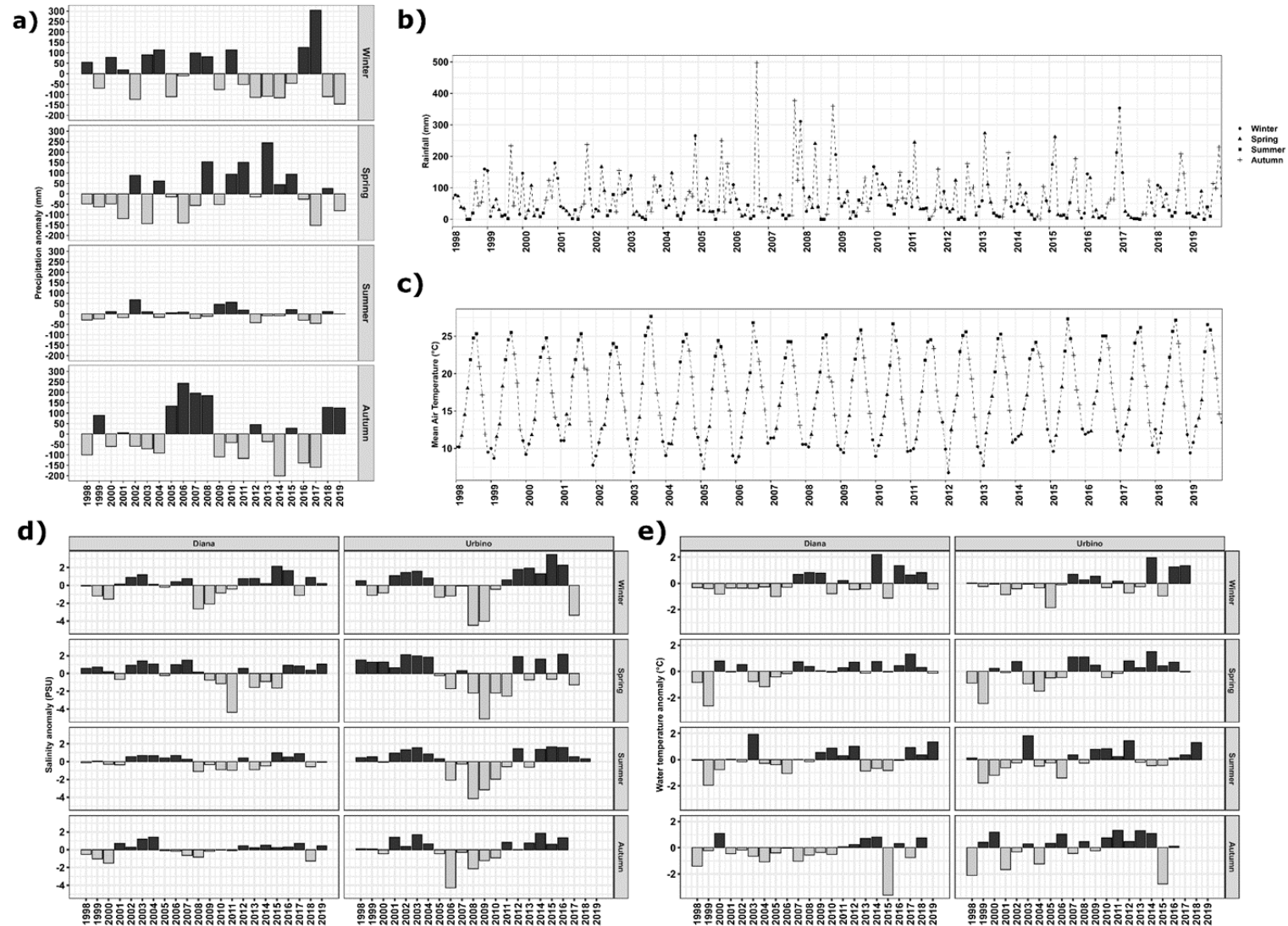


Figure S1 Meteorological conditions described as annual positive and negative anomalies relative to the average level of seasonal cumulative rainfall (S1a, mm), monthly cumulative rainfall (S1b, mm) and monthly mean air temperature (S1c, °C) registered at Solenzara weather station (Météo-France) from 1998 to 2020. Environmental patterns described as annual positive and negative anomalies relative (i) to the mean seasonal salinity (S1d), and (ii) to the mean seasonal water temperature (S1e, °C), recorded from 1998 to 2019 in Diana and from 1998 to 2018 in Urbino.

ANNEXE II – SUPPLEMENTARY MATERIAL (LIGORINI ET AL., 2022B)

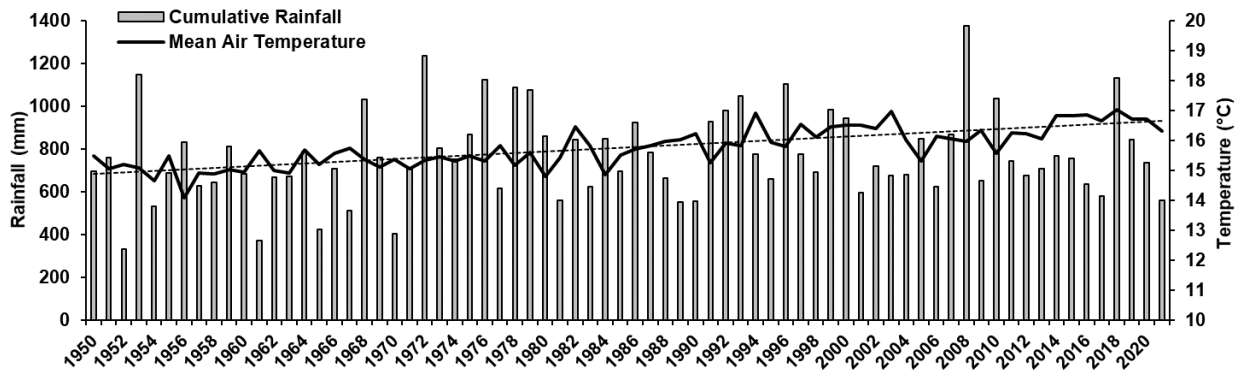


Figure S1 Meteorological conditions at Bastia Airport weather station over the period 1950–2021: annual cumulative rainfall (histogram, scale on the left, mm) and annual mean air temperature (dark line, scale on the right, °C; with linear trend (dashed dark line)). MK test highlighted a significant increasing trend in annual mean air temperature on the overall period (1950–2021) (p value < 0.001 , Sen's Slope = 0.025), indicating a temperature rise of more than 1.7 °C between 1950 and 2020.

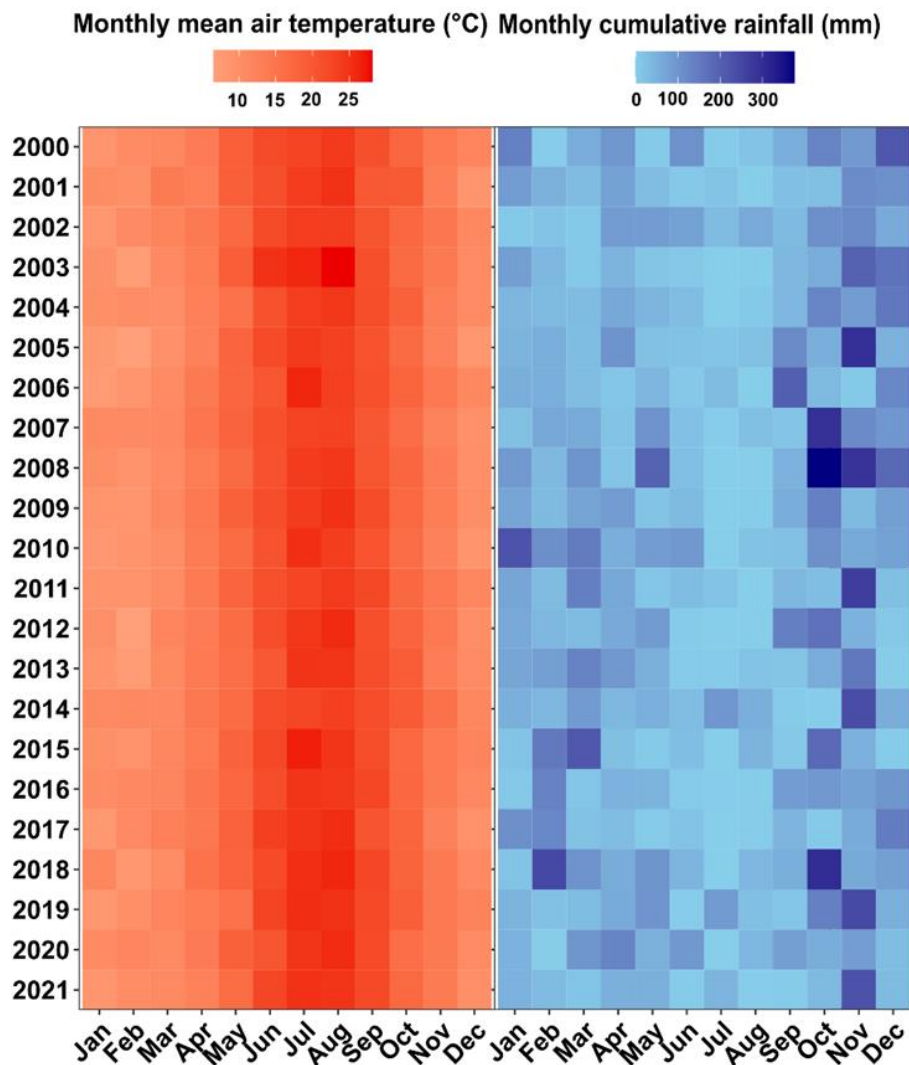


Figure S2 Meteorological conditions at Bastia Airport weather station on monthly basis over the period 2000–2021: heat maps of monthly cumulative rainfall (mm) and of monthly mean air temperature (°C).

ANNEXE III – SUPPLEMENTARY MATERIAL (LIGORINI ET AL., 2023)

Table S1 Floristic list, by year and season, of all phytoplankton taxonomic units identified in each lagoon during microscopy analyses. The presence of a taxonomic unit is identified by an “X” in the corresponding case, while empty cases indicate the absence of the taxonomic entity. “Diat.,” “Dino.” and “Und.” stand for “Diatom”, “Dinoflagellate” and “Undetermined”, respectively.

	Arasu				Santa Giulia				Balistra			
	2020		2021		2020		2021		2020		2021	
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
<i>Chaetoceros</i> sp. 1	X	X										
<i>Chaetoceros</i> sp. 2		X	X	X		X			X	X		X
<i>Cheatoceros peruvianus</i>											X	
<i>Achnanthes</i> sp.	X				X	X	X	X	X	X	X	
<i>Cylindrotheca closterium</i>	X	X	X	X			X			X	X	X
<i>Amphora</i> sp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Cocconeis</i> sp.	X				X		X	X	X	X	X	X
<i>Navicula</i> spp.	X	X	X	X	X	X	X	X	X	X	X	X
<i>Diploneis</i> sp.	X	X	X	X	X	X	X		X		X	X
<i>Gyrosigma/Pleurosigma</i> sp.	X	X		X	X	X	X	X	X	X	X	X
<i>Petronis</i> sp.	X				X		X	X	X			X
<i>Surirella</i> sp.	X		X	X	X	X	X	X	X	X	X	X
<i>Entomoneis</i> sp.	X				X	X	X	X	X	X	X	X
<i>Fragilaria/Synedra</i> sp. 1	X	X	X	X	X	X	X	X		X	X	X
<i>Fragilaria/Synedra</i> sp. 2		X			X	X	X		X	X	X	X
Small centric diatoms	X				X					X		X
Small pennate diatoms	X	X			X				X		X	X
<i>Coscinodiscus granii</i>			X									
<i>Coscinodiscus</i> sp.					X	X						X
<i>Nitzschia</i> sp.			X		X	X	X	X	X	X	X	X
<i>Nitzschia sigmaidea</i>										X		
<i>Nitzschia longissima</i>										X		
<i>Nitzschia scalaris</i>												X
<i>Rhopalodia/Campylodiscus</i> sp.					X							
<i>Melosira</i> sp.				X	X	X		X	X	X	X	X
<i>Lyrella</i> sp.							X	X		X	X	X
<i>Licmophora</i> sp.				X	X		X	X	X	X	X	X
<i>Hantzchia</i> sp.							X					X
<i>Pinnularia</i> sp.							X					
<i>Thalassionema</i> sp.									X			
<i>Grammatophora</i> sp.									X			
<i>Striatella unipunctata</i>										X		
<i>Striatella</i> sp. 1				X	X							
<i>Striatella</i> sp. 2					X							X
<i>Leptocylindrus</i> sp.					X							X
<i>Cerataulina pelagica</i>												X
<i>Bacillaria</i> sp.												X
Diat. Und. 1		X										
Diat. Und. 2	X											
Diat. Und. 3	X											

Table S1 - continued

	Arasu				Santa Giulia				Balistra												
	2020		2021		2020		2021		2020		2021										
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn									
Diat. Und. 4	x																				
Diat. Und. 5	x																				
Diat.Und.6										x											
Diat.Und.7											x										
Diat.Und.8						x															
Diat.Und.9		x																			
Diat.Und.10							x														
Diat.Und.11											x										
<i>Prorocentrum micans</i>	x	x	x	x	x	x	x		x	x	x	x	x	x	x						
<i>Prorocentrum cordatum</i>	x	x	x	x		x	x						x	x							
<i>Prorocentrum lima</i>			x		x	x	x														
<i>Prorocentrum</i> sp.									x												
<i>Gymnodinium</i> sp.	x							x					x								
Gymnodiniales						x								x							
<i>Gymnodinium/Kaarenia/Kryptoperidinium</i> sp.													x								
<i>Kryptoperidinium foliaceum</i>					x	x	x	x		x		x		x	x	x					
<i>Dinophysis</i> sp.	x		x	x						x			x	x	x						
<i>Dinophysis caudata</i>													x	x	x						
<i>Diplopsalis</i> sp.	x	x		x			x			x	x		x			x	x				
<i>Gonyaulax</i> sp.	x			x			x	x					x			x	x	x			
<i>Gonyaulax spinifera</i>								x													
<i>Protooperidinium</i> sp. 1		x											x	x							
<i>Protooperidinium</i> sp. 2		x	x	x			x							x	x			x	x		
<i>Protooperidinium bipes</i>								x													
<i>Protooperidinium brevipes</i>					x	x	x	x		x							x	x			
<i>Protooperidinium crassipes</i>						x															
<i>Protooperidinium divergens</i>																		x	x		
<i>Akashiwo sanguinea</i>			x	x	x	x	x	x			x	x			x			x	x		
<i>Scrippsiella</i> sp.								x								x			x	x	
<i>Scrippsiella trocoïdea</i>														x							
<i>Ceratium furca</i>															x	x				x	
<i>Ceratium fusus</i>																	x				
<i>Alexandrium</i> sp.						x	x	x			x	x		x					x	x	
<i>Gyrodinium</i> sp.						x															
Dino. Und. 1	x																				
Dino. Und. 2		x																			
Dino. Und. 3			x																		
Dino. Und. 4			x																		
Dino. Und. 5				x																	
Dino. Und. 6		x	x	x	x	x	x	x		x	x	x	x		x	x	x	x		x	
Dino. Und. 7											x										
Dino. Und. 8															x						
Dino. Und. 9															x						
Dino. Und. 10																x					
Cyanophyceae	x		x			x	x		x		x		x	x		x			x		x

Table S1 - continued

	Arasu				Santa Giulia				Balistra			
	2020		2021		2020		2021		2020		2021	
	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn	Winter	Spring	Summer	Autumn
<i>Merismopedia</i> sp.	X											
<i>Lyngbya</i> sp.				X	X	X						X
<i>Anabaena</i> sp.				X								
<i>Oscillatoria</i> sp.								X				
Chlorophyceae	X				X				X			
Prasinophyceae	X									X		
Euglenophyceae	X	X	X			X			X	X	X	X
Chrysophyceae Und. 1	X									X	X	
<i>Synura</i> sp.		X	X	X	X	X	X					
<i>Mallomonas</i> sp.				X								
Cryptophyceae	X	X		X	X	X		X	X			X
<i>Rhodosphaera</i> sp.											X	
<i>Apedinella radians</i>				X				X				
Und.1	X											
Und.2	X											
Und.3	X											
Und.4		X										
Und.5		X										
Und.6			X									
Und. 7		X								X		
Und. 8			X									
Und. 9				X								
Und. 10				X								
Und. 11					X							
Und. 12					X							
Und. 13						X						
Und. 14									X			

Monthly analysis of meteorological context for the study period:

At monthly scale, for both stations mean air temperatures followed the seasonal pattern. November 2019 was particularly rainy (cumulative rainfall: 146 mm and 229 mm for La Chiappa and Cap Pertusato stations respectively; Supplementary, [Figure S1c](#)). 2020's winter was especially dry and warm, with cumulative rainfall reaching only 3.4 mm and 2.2 mm and mean air temperature of 14°C and 13°C for La Chiappa and Cap Pertusato stations respectively (Supplementary, [Figure S1c](#)). In 2020, spring rainfall was concentrated in April, which was the rainiest spring month of the year for both stations (cumulative rainfall: 120 mm (La Chiappa) and 150 mm (Cap Pertusato); Supplementary, [Figure S1c](#)). 2021 showed a different pattern than 2020, mainly with more humid and cool winter (February 2021 cumulative rainfall and mean air temperature: 39 mm and 12°C (La Chiappa), 55 mm and 12°C (Cap Pertusato); Supplementary, [Figure S1c](#)), a quite dry spring, but with longer rainy period than 2020 and autumn rainfall

concentrated in November (161 mm (La Chiappa) and 180 mm (Cap Pertusato)); Supplementary, Figure S1c). Such a variability is typical of Mediterranean climate.

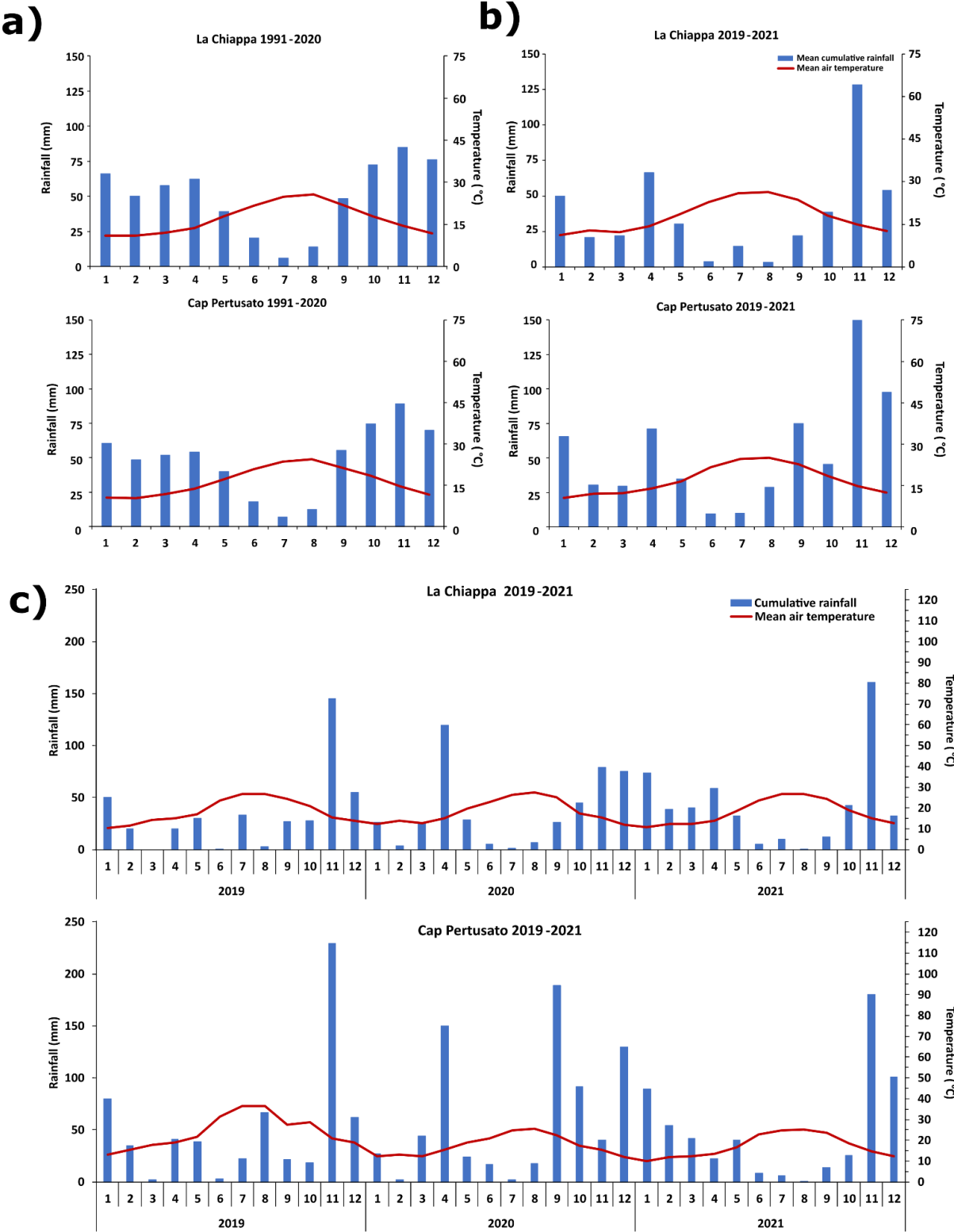


Figure S1 Meteorological context for the two weather stations (La Chiappa and Cap Pertusato). Left scale corresponds to rainfall (mm, blue bars) and right scale to temperature (°C, red line) for the ombrothermic diagrams over a the reference period (1991-2020) and b the study period (2019-2021), and c the representation of monthly mean values for the two sampling years (2020-2021) and antecedent year (2019).

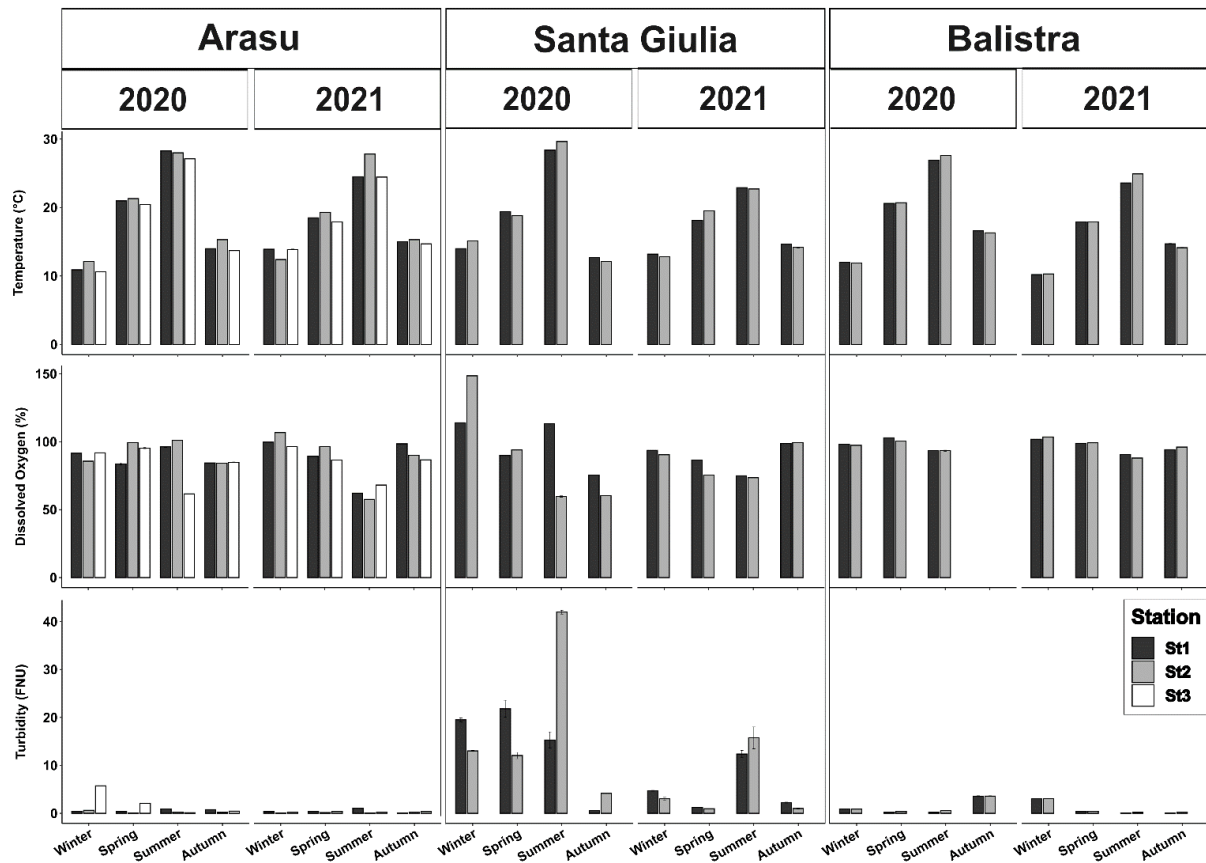


Figure S2 Temperature (°C), dissolved oxygen concentration (% saturation) and turbidity (FNU) seasonal values for the three studied lagoons in 2020 and 2021, with error bars representing Standard Error over the three replicates measured *in situ*.

ANNEXE IV – SUPPLEMENTARY MATERIAL (CHAPITRE V)

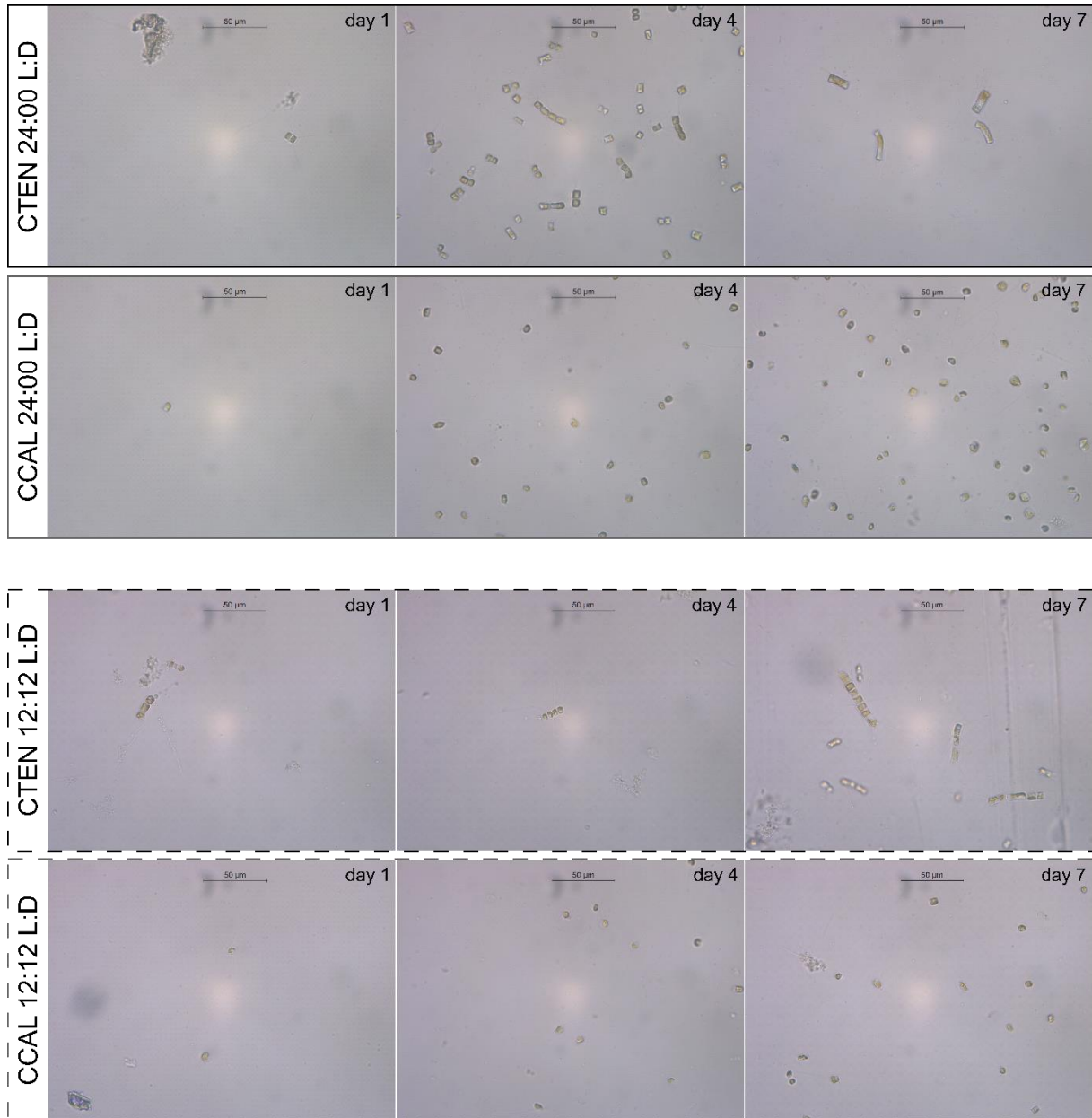


Figure S1 Samples of micrographs taken at day 1, day 4 and day 7, in the CTEN and CCAL cultures under the two photoperiod treatments, showing changes in cell morphology, including cell chain elongation in CTEN during exponential growth phase. Micrographs were used for measurements of cell section area.

Table S1 Evolution of cell concentrations (cell mL⁻¹) in the experiments carried out for setting the concentration of the inoculum, in the CTEN (10 ×10³; 50 ×10³; 100 ×10³; 300 ×10³ cell mL⁻¹) and CCAL (10 ×10³; 50 ×10³; 100 ×10³ cell mL⁻¹) cultures.

Time (day)	CTEN (cell mL ⁻¹)				CCAL (cell mL ⁻¹)		
	CTEN 10	CTEN 50	CTEN 100	CTEN 300	CCAL 10	CCAL 50	CCAL 100
0	1.04E+04	5.00E+04	1.00E+05	2.91E+05	1.00E+04	6.27E+04	1.00E+05
1	3.40E+04	8.00E+04	2.09E+05	9.36E+05	2.67E+04	8.00E+04	1.97E+05
2	8.00E+04	2.73E+05	6.44E+05	2.83E+06	5.93E+04	1.62E+05	4.36E+05
3	1.97E+05	7.29E+05	1.25E+06	4.48E+06	1.19E+05	3.65E+05	9.18E+05
4	4.02E+05	1.87E+06	2.80E+06	4.34E+06	1.33E+05	6.53E+05	2.23E+06
5	9.24E+05	3.67E+06	4.33E+06	4.33E+06	2.81E+05	1.42E+06	5.04E+06
6	1.67E+06	3.95E+06	3.68E+06	4.59E+06	5.76E+05	2.38E+06	8.91E+06
7	3.17E+06	4.37E+06	4.57E+06	3.66E+06	1.35E+06	4.28E+06	1.23E+07
8	3.99E+06	3.81E+06	3.85E+06	3.61E+06	2.77E+06	6.76E+06	1.59E+07
9	4.21E+06	2.55E+06	3.71E+06	2.95E+06	5.86E+06	9.02E+06	1.71E+07
10	3.87E+06	2.00E+06	3.35E+06	2.49E+06	9.29E+06	1.44E+07	2.01E+07
11	3.47E+06		2.36E+06		1.21E+07		2.13E+07
12	2.61E+06		2.02E+06		1.72E+07		2.64E+07
13	2.42E+06		1.75E+06		2.00E+07	2.80E+07	3.14E+07
14	1.92E+06		1.52E+06		2.56E+07		3.04E+07
Exponential k Period (days)	1,15 (0 - 7)	1,38 (1 - 5)	1,37 (0 - 4)	1,64 (0 - 2)	1,01 (0 - 8)	0,98 (1 - 6)	1,17 (1 - 5)

Table S2 Variation in cell concentration, growth rate, cell section area, maximum quantum yield and chl *a* content for CTEN and CCAL cultures under the two photoperiod treatments (24:00 L:D; 12:12 L:D). Data are the mean \pm SD, n = 3.

Photoperiod	Time (days)	Cell concentration ($10^3 \text{ cell mL}^{-1} \pm \text{SD}$)	Growth rate ($\text{div d}^{-1} \pm \text{SD}$)	Cell section area ($\mu\text{m}^2 \pm \text{SD}$)	Fv/Fm ($\pm \text{SD}$)	Chlorophyll <i>a</i> ($\mu\text{g cell}^{-1} \pm \text{SD}$)	
CTEN	24:00 L:D	0	100 \pm 13		59.1 \pm 21.2	0.39 \pm 0.023	0.35 \pm 0.084
		1	136 \pm 30	0.43 \pm 0.4	42.4 \pm 21.9		
		2	1043 \pm 445	2.86 \pm 0.36	33.6 \pm 10.0	0.62 \pm 0.023	0.08 \pm 0.020
		3	2652 \pm 663	1.41 \pm 0.3	34.1 \pm 9.65		
		4	3903 \pm 452	0.58 \pm 0.35	46.3 \pm 16.1	0.55 \pm 0.029	0.11 \pm 0.017
		5	3910 \pm 92	0.01 \pm 0.17	66.1 \pm 34.8		
		6	3528 \pm 128	-0.15 \pm 0.09	78.2 \pm 28.7	0.35 \pm 0.032	0.19 \pm 0.112
		8	3230 \pm 128	-0.13 \pm 0.11	77.9 \pm 42.5		
	12:12 L:D	0	2370 \pm 814	-0.5 \pm 0.42	91.0 \pm 41.8	0.21 \pm 0.042	0.35 \pm 0.108
		0	100 \pm 1		66.1 \pm 19.7	0.41 \pm 0.015	0.32 \pm 0.165
		1	130 \pm 14	0.36 \pm 0.15	53.3 \pm 22.6		
		2	146 \pm 14	0.18 \pm 0.23	47.2 \pm 35.6	0.47 \pm 0.015	0.20 \pm 0.035
		3	214 \pm 26	0.55 \pm 0.04	40.9 \pm 20.7		
		4	403 \pm 56	0.91 \pm 0.12	27.9 \pm 6.55	0.60 \pm 0.007	0.18 \pm 0.008
		5	863 \pm 43	1.11 \pm 0.2	34.7 \pm 11.6		
		6	1868 \pm 431	1.09 \pm 0.39	38.2 \pm 8.81	0.61 \pm 0.040	0.13 \pm 0.035
7	2203 \pm 504	0.24 \pm 0.05	48.9 \pm 16.0				
8	2565 \pm 854	0.19 \pm 0.15		0.50 \pm 0.0134	0.12 \pm 0.026		
CCAL	24:00 L:D	0	117 \pm 9		40.3 \pm 7.85	0.61 \pm 0.062	0.34 \pm 0.074
		1	402 \pm 14	1.78 \pm 0.16	45 \pm 10.4		
		2	2010 \pm 339	2.31 \pm 0.25	43.2 \pm 11.3	0.60 \pm 0.025	0.16 \pm 0.033
		3	7097 \pm 565	1.83 \pm 0.14	37.3 \pm 7.70		
		4	12555 \pm 1110	0.82 \pm 0.01	37.9 \pm 7.89	0.66 \pm 0.030	0.11 \pm 0.093
		5	19313 \pm 2506	0.62 \pm 0.06	38.3 \pm 7.08		
		6	24220 \pm 1682	0.33 \pm 0.1	39.9 \pm 8.05	0.68 \pm 0.017	0.16 \pm 0.123
		7	28600 \pm 3776	0.23 \pm 0.18	39 \pm 9.01		
	12:12 L:D	8	32567 \pm 4004	0.19 \pm 0.02	34.7 \pm 8.66	0.67 \pm 0.016	0.17 \pm 0.080
		0	96 \pm 1		34.5 \pm 8.06	0.56 \pm 0.042	0.26 \pm 0.031
		1	151 \pm 14	0.65 \pm 0.16	33.3 \pm 9.66		
		2	444 \pm 25	1.56 \pm 0.22	34.6 \pm 8.66	0.65 \pm 0.013	0.26 \pm 0.101
		3	1424 \pm 173	1.68 \pm 0.2	36.1 \pm 9.04		
		4	4563 \pm 1690	1.63 \pm 0.34	30 \pm 5.07	0.67 \pm 0.002	0.18 \pm 0.111
		5	8420 \pm 1206	0.93 \pm 0.36	28.8 \pm 5.70		
		6	13230 \pm 2485	0.64 \pm 0.11	37.6 \pm 6.01	0.68 \pm 0.005	0.10 \pm 0.034
7	14950 \pm 1653	0.19 \pm 0.15	32.3 \pm 8.34				
8	18660 \pm 2421	0.32 \pm 0.24		0.71 \pm 0.035	0.19 \pm 0.039		

Table S3 Pigment and lipid concentrations (mg L⁻¹; mean ± SD) in CTEN and CCAL cultures under the two photoperiod treatments (24:00 L:D; 12:12 L:D) on day 4. Results below the detection limits are represented as “< LD”. The sum of the pigments, Omega-3 and Omega-6 are described below the table.

Pigments & Lipids (day 4; mg L ⁻¹ ±SD)		CTEN		CCAL	
		24:00 L:D	12:12 L:D	24:00 L:D	12:12 L:D
Pigment composition	Xanthophyll ⁽¹⁾	0.354 ±0.131	0.078 ±0.006	4.063 ±0.494	1.500 ±0.420
	Fucoxanthin	0.322 ±0.119	0.067 ±0.004	3.612 ±0.460	1.320 ±0.368
	Diadinoxanthin	0.032 ±0.013	0.008 ±0.001	0.442 ±0.037	0.180 ±0.052
	Diatoxanthin	< LD	0.003 ±0.001	0.009 ±0.004	< LD
	Chlorophyllid <i>a</i>	0.631 ±0.459	0.062 ±0.012	< LD	< LD
	β-carotene	0.034 ±0.006	0.004 ±0.001	0.178 ±0.029	0.085 ±0.028
Total lipids	Total	9.653 ±3.452	1.021 ±0.028	61.410 ±14.051	9.122 ±2.181
	SFA	3.137 ±1.024	0.378 ±0.011	21.053 ±6.903	2.086 ±0.439
	MUFA	3.015 ±1.193	0.285 ±0.014	20.535 ±5.816	2.078 ±0.430
	PUFA	3.501 ±1.236	0.357 ±0.008	19.822 ±2.140	4.958 ±1.338
	Omega-6 ⁽²⁾	0.184 ±0.035	0.013 ±0.002	3.030 ±0.956	0.119 ±0.047
	Omega-3 ⁽³⁾	1.845 ±0.739	0.176 ±0.008	9.199 ±1.286	2.213 ±0.696
	EPA	1.463 ±0.592	0.139 ±0.005	7.811 ±1.039	1.859 ±0.618
	DHA	0.268 ±0.103	0.024 ±0.003	0.747 ±0.120	0.163 ±0.028
Polar lipids	Total	3.700 ±0.307	0.624 ±0.014	24.985 ±3.160	8.056 ±1.920
	SFA	1.037 ±0.105	0.16 ±0.004	5.766 ±0.449	1.614 ±0.348
	MUFA	0.887 ±0.138	0.196 ±0.012	5.311 ±0.626	1.718 ±0.351
	PUFA	1.776 ±0.064	0.268 ±0.004	13.908 ±2.106	4.724 ±1.253
	Omega-6 ⁽²⁾	0.115 ±0.005	0.010 ±0.001	2.045 ±0.415	0.112 ±0.040
	Omega-3 ⁽³⁾	0.865 ±0.008	0.141 ±0.006	6.585 ±1.394	2.142 ±0.659
	EPA	0.586 ±0.101	0.116 ±0.001	5.575 ±1.250	1.806 ±0.590
	DHA	0.218 ±0.079	0.020 ±0.003	0.630 ±0.117	0.153 ±0.026
Neutral lipids	Total	5.953 ±3.145	0.396 ±0.029	36.424 ±15.487	1.066 ±0.263
	SFA	2.100 ±0.918	0.219 ±0.015	15.288 ±7.035	0.473 ±0.093
	MUFA	2.128 ±1.056	0.088 ±0.013	15.223 ±6.226	0.359 ±0.085
	PUFA	1.725 ±1.171	0.089 ±0.009	5.913 ±2.228	0.234 ±0.085
	Omega-6 ⁽²⁾	0.069 ±0.029	0.003 ±0.001	0.985 ±0.616	0.007 ±0.007
	Omega-3 ⁽³⁾	0.979 ±0.747	0.035 ±0.008	2.614 ±1.234	0.072 ±0.037
	EPA	0.877 ±0.693	0.023 ±0.004	2.237 ±1.017	0.053 ±0.028
	DHA	0.050 ±0.024	0.004 ±0.005	0.117 ±0.042	0.010 ±0.004

⁽¹⁾ sum of pigments fucoxanthin; diadinoxanthin; diatoxanthin

⁽²⁾ sum of lipids C18:2n-6; C18:3n-6; C20:3n-6; C20:4n-6; C22:4n-6; C22:5n-6

⁽³⁾ sum of lipids C18:4n-3; C20:4n-3; C20:5n-3 (EPA); C22:5n-3; C22:6n-3 (DHA)