Etude de la diversité des nurseries artificielles dans les zones portuaires et de leur connectivité trophique avec les écosystèmes adjacents

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ETUDE DE LA DIVERSITÉ DES NURSERIES ARTIFICIELLES DANS LES ZONES PORTUAIRES ET DE LEUR CONNECTIVITÉ TROPHIQUE AVEC LES ÉCOSYSTÈMES ADJACENTS

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DIVERSITY OF ARTIFICIAL NURSERIES IN PORT AREAS AND THEIR TROPHIC CONNECTIVITY WITH ADJACENT ECOSYSTEMS

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Présentée en vue de l'obtention du grade de Docteur en Sciences de l'Environnement d'Université Côte d'Azur

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A ma fille Albanana
Et à ma femme Mamangue

RESUME

Le développement côtier introduit des habitats artificiels qui impactent la biodiversité et le fonctionnement des écosystèmes. Les solutions d'ingénierie écologique, comme les habitats artificiels à poissons (HAP), peuvent réhabiliter des zones très modifiées, comme les ports, en offrant un abri aux poissons. Les HAP peuvent aussi fournir un substrat aux invertébrés et aux macroalgues, améliorant le fonctionnement de l'écosystème. Leurs effets pourraient aller au-delà des ports et modifier les échanges trophiques avec les habitats adjacents. Cette thèse étudie la biodiversité des invertébrés associés aux HAP et explore les échanges de biomasse entre les ports et les herbiers de *Posidonia oceanica* adjacents le long de la côte méditerranéenne française.

Les objectifs sont : (i) évaluer comment la diversité et la composition des invertébrés benthiques varient avec le temps d'immersion des HAP, (ii) comprendre comment les types d'HAP et le contexte environnemental modifient les assemblages benthiques, et (iii) explorer les échanges de matière organique entre les ports et les herbiers adjacents. J'ai étudié les HAP Biohut® (ECOCEAN), composés d'une cage métallique remplie de coquilles d'huîtres, attachés aux quais ou sous les pontons dans les ports.

Au chapitre 1, j'ai examiné le rôle du temps d'immersion des HAP sur la diversité et la composition des assemblages d'invertébrés dans 3 ports commerciaux. Des variations dans la composition des invertébrés ont été observées entre 6 et 18 mois d'immersion, avec une augmentation de l'abondance, de la richesse et de l'équitabilité au fil du temps. Au chapitre 2, j'ai étudié les variations géographiques et intra-portuaires de la composition et de la diversité des invertébrés. L'étude a révélé des différences dans la composition des taxons entre 2 régions caractérisées par des apports en nutriments différents et des corrélations entre la composition des assemblages et la chlorophylle-a, indicateur de la concentration en nutriments. Les assemblages d'invertébrés variaient aussi selon les zones où les HAP étaient installés, probablement à cause de différences d'accès à la lumière. Au chapitre 3, j'ai étudié la connectivité trophique entre les herbiers de *P. oceanica* et les ports adjacents sur 4 sites : 2 avec des ports équipés en HAP et 2 non équipés. Dans les sites non équipés, les valeurs $\delta^{15}N$ de la matière organique particulaire à l'intérieur du port étaient les plus élevées, suggérant un enrichissement en nutriments d'origine humaine. Ces valeurs diminuaient dans les herbiers selon la distance, indiquant un effet de ces nutriments sur

l’herbier proche de l’entrée du port. Les poissons (*Diplodus* spp.) pouvaient utiliser des ressources venant à la fois de l’herbier et du port de manière similaire sur les 4 sites. Les niches trophiques des poissons capturés dans le port équipé étaient légèrement plus grandes que celles des ports non équipés et se chevauchaient moins avec celles des poissons capturés à l'extérieur. Leurs fèces faisaient également partie de la matière organique sédimentaires des herbiers.

Mon travail a révélé des aspects susceptibles d'améliorer l'utilisation des HAP. La durée d'immersion, les conditions environnementales et les emplacements dans les ports doivent faire l'objet d'une attention particulière. Bien que je n'aie pas trouvé de différences claires dans les échanges entre habitats liés aux HAP, ces derniers semblent jouer un rôle en réduisant l'enrichissement en nutriments. L’importance des poissons dans les échanges entre habitats et le fait que les HAP favorisent leur survie suggèrent que ces HAP pourraient contribuer indirectement à la connectivité trophique.

Mots-clés : habitats artificiels à poissons ; réhabilitation écologique ; ports et marinas ; invertébrés benthiques ; connectivité trophique.

ABSTRACT

Coastal development modifies shorelines by introducing man-made habitats, which significantly impact coastal biodiversity and ecosystem functioning. Ecological engineering solutions, such as artificial fish habitats (AFH), can help rehabilitate extremely modified areas, including ports, by offering shelter for fish. As a side effect, AFH provide a substrate to benthic invertebrates and macroalgae, that could improve ecosystem functioning. The effects of AFH may also extend beyond ports and modify trophic exchange with adjacent habitats via fish feeding hydrodynamics. This thesis investigates the patterns of distribution of invertebrate biodiversity associated with AFH and explores the exchange of biomass between marinas and adjacent *Posidonia oceanica* meadows along the French Mediterranean coast where these habitats are often adjacent.

The objectives are: (1) evaluating how taxonomic diversity and composition of benthic invertebrates vary with AFH immersion time, (2) understanding how AFH types and environmental context modify benthic assemblages, and (3) exploring the exchanges of organic matter between marinas and adjacent meadows. I focused on Biohut® AFH (ECOCEAN), made of a metal cage filled with oyster shells, attached to docks or under pontoons in harbours and marinas.

In chapter 1, I examined the role of immersion time in determining the diversity and composition of invertebrate assemblages colonising AFH in 3 commercial harbours. The findings indicated significant variations in invertebrate composition from 6 to 18 months, with increased abundance, taxonomic richness, and evenness over time. In chapter 2, I focused on the geographical and within-port variability in taxonomic composition and diversity of invertebrates dwelling in AFH. The study revealed differences in taxa composition between 2 large regions, characterised by different nutrient loads and correlations between assemblage composition and chlorophyll-a, a proxy for nutrient concentration. The number of taxa was the highest in the nutrient-enriched region. Additionally, invertebrate assemblages varied according to port habitats where the AFH were placed, possibly due to differences in light availability. In chapter 3, I investigated trophic connectivity between *P. oceanica* meadows and adjacent marinas at 4 sites where both habitats are present. Two marinas were equipped with AFH and the remaining 2 were

not. At the unequipped sites, the $\delta^{15}N$ values of the particulate organic matter within the marina were the highest indicating human-derived nutrient enrichment. The values decreased within the meadow, gradually according to the distance. This suggests a spill of nutrients over the portion of the meadow adjacent to the inlet. Fish relied on resources from both the seagrass meadow and the marina, similarly among the 4 sites, however, the trophic niches of fishes (*Diplodus* spp.) captured within the equipped marina were slightly larger than those within unequipped ones and overlapped less with the trophic niches of the fish captured outside. Fish faeces were also part of the organic matter sedimenting within meadows.

My work has highlighted several aspects that could improve the effectiveness of AFH as ecological engineering solutions. Immersion time, local environmental conditions, and specific locations within ports need particular attention. Although I did not find clear differences in cross-habitat exchange related to AFH, they seemed to play a role in reducing nutrient enrichment. Moreover, since fish play an important role in cross-habitat exchanges and find refuge within AFH, this ecological engineering solution could indirectly contribute to change trophic connectivity.

Keywords: artificial fish habitats; ecological rehabilitation; harbours and marinas; benthic invertebrates; trophic connectivity.

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GENERAL INTRODUCTION AND OBJECTIVES

MARINE DIVERSITY AND ECOSYSTEM SERVICES

« The Earth is blue like an orange ». With these words the French writer Paul Eluard defined our planet in a poetic and surrealistic way, melding the shape, the rarity and the preciousness (at the time Eluard wrote this line, 1929) of an orange and the colour of the Earth planet. Planet Earth is indeed unique due to its physicochemical conditions allowing the existence of liquid water and an atmosphere compatible with life. This is also why we call the Earth planet the "Blue Planet": 70.8% of its surface is covered with oceans and seas. From space, our planet is like a “Blue Marble’ floating in the immensity of the cosmos (Figure 1).

Figure 1. "The Blue Marble" photography of the Earth taken at around 29400km on December 7, 1972. © NASA/Apollo 17 crew.

Globally, the Earth's oceans play an important role in climate and wind regulation by mitigating differences in temperature between regions, through surface circulation and deep ocean currents. They are responsible for nearly all the planet’s precipitation through the evaporation of water from the oceans. They also provide roughly half of the oxygen we breathe through phytoplankton photosynthesis while absorbing between 25 and 35 % per year of the anthropic carbon from the atmosphere and thus mitigate global warming (Behrenfeld *et al.*, 2006; Field *et al.*, 1998; Gruber *et al.*, 2019; Mcleod *et al.*, 2011; Sabine *et al.*, 2004).

The marine environment hosts a high diversity of life forms and ecosystems in a complex web of ecological interactions (see Box 1: The concept of biodiversity). Approximately 250,000 species were described in the marine environment, all taxonomic groups included (Boeuf, 2011; Duarte, 2006; Groombridge and Jenkins, 2000; Reaka-Kudla, 1997) but most species remain to be discovered (Appeltans *et al.*, 2012; Bouchet, 2006; Costello *et al.*, 2010). At the phylum level, 31 out of the 34 phyla of metazoan phyla and 14 out of the 27 photosynthetic phyla are represented in marine environments (Boeuf, 2011; Boudouresque, 2014; Grassle *et al.*, 1991; Morris, 1993; Sala and Knowlton, 2006).

Box 1. The concept of biodiversity

For most people, biodiversity is usually simply defined as species richness. However, this definition is partial and mainly incomplete. During my master's degree, my professor Charles-François Boudouresque once said, "assessing biodiversity using only the number of species is like evaluating a painting based only on the number of colours used". Biodiversity is defined as the variety of life, which includes different facets:

- diversity within species (genetic diversity),
- diversity between species (specific diversity) or at higher taxonomic levels (taxonomic diversity),
- diversity between patches, habitats, ecosystems or landscapes (ecological diversity),
- diversity in the range and the value of functional traits (e.g. diet, feeding behaviour, weight, lifespan, habitats, reproduction strategies) of the species in a given patch, habitat, ecosystem or landscape (functional diversity)
- the relative abundance of individuals among species (heterogeneity diversity).

These different facets of biodiversity are combined with different spatial scales:

- Within a single sample: *point*-diversity
- Within a habitat or an ecosystem of a given region: *alpha*-diversity
- The turnover of species between samples or habitats: *beta*-diversity
- Within all the ecosystems of the given region: *gamma*-diversity
- Within all the ecosystems of a biogeographical province: *epsilon*-diversity

Biodiversity therefore is a multi-faceted concept which encompasses a wide range of scales and metrics used together to measure each of its facets depending on the scope of the study (Boudouresque, 2014; Sala and Knowlton, 2006).

Due to the differences in environmental characteristics (e.g. temperature, salinity, light availability, nutrients), the marine diversity is widely variable throughout ocean basins but also throughout latitudes, where higher diversity is generally found near the equatorial regions than the polar ones (Briggs, 1974; Cousteau, 1991; Clarke, 1992; Angel, 1993; Ormond *et al.*, 1997; Groombridge and Jenkins, 2000). The distribution of species is also determined by the biological and evolutionary interactions that occurred over time (Sanders, 1968; Witman *et al.*, 2004; Appeltans *et al.*, 2012). Some regions are considered biological hotspots, as they host a tremendous number of diverse, rare or endemic ecosystems, communities, and species.

The high taxonomic diversity found in the marine environment provides ecosystem services to humans contributing for instance to sustainable economic growth, food security or protection from meteorological events (see Box 2: Ecosystems services).

Box 2. Ecosystems services

Ecosystems services (ES) define the contributions (goods and services) provided by ecosystems to human well-being (Millennium Ecosystem Assessment, 2005). The ES concept was first developed in the 1970s to raise public awareness of the need to protect biodiversity by questioning how human populations depend on the natural environment, what benefits ecosystems produce, and how to manage, protect, and maintain these services (Balmford *et al.*, 2002; Costanza and Daly, 1992; Randall, 1988; Westman, 1977). According to Costanza *et al.* (1997), 63 % of the world total value of ES is provided by marine ecosystems, which represent $20.9 billions per year.

ES are divided into 3 broadly accepted categories:

- Provisioning services represent the benefits obtained from products extracted or harvested from ecosystems and are available for direct uses (e.g. animal production from fisheries or aquaculture, algal production, biochemicals resources).
- Regulating and supporting services represent the benefits that humans obtain from the ability of ecosystems to regulate natural processes. These services include, for instance, the regulation of climate, water and nutrient cycles, protection against natural disasters, mitigation of pollution effects, and disease control.
- Cultural services represent the non-material benefits obtained from ecosystems and contribute to a range of cultural uses through education, recreation, aesthetics, and spiritual enrichment, among others.

As such, there is a strong interaction between humans and ecosystems: human-induced drivers of changes (e.g. management, human demography, habitat destruction, biological invasion, restoration program) will directly or indirectly impact the ecosystem functioning which will cause changes in ES and, ultimately, affect human well-being (Figure 2).

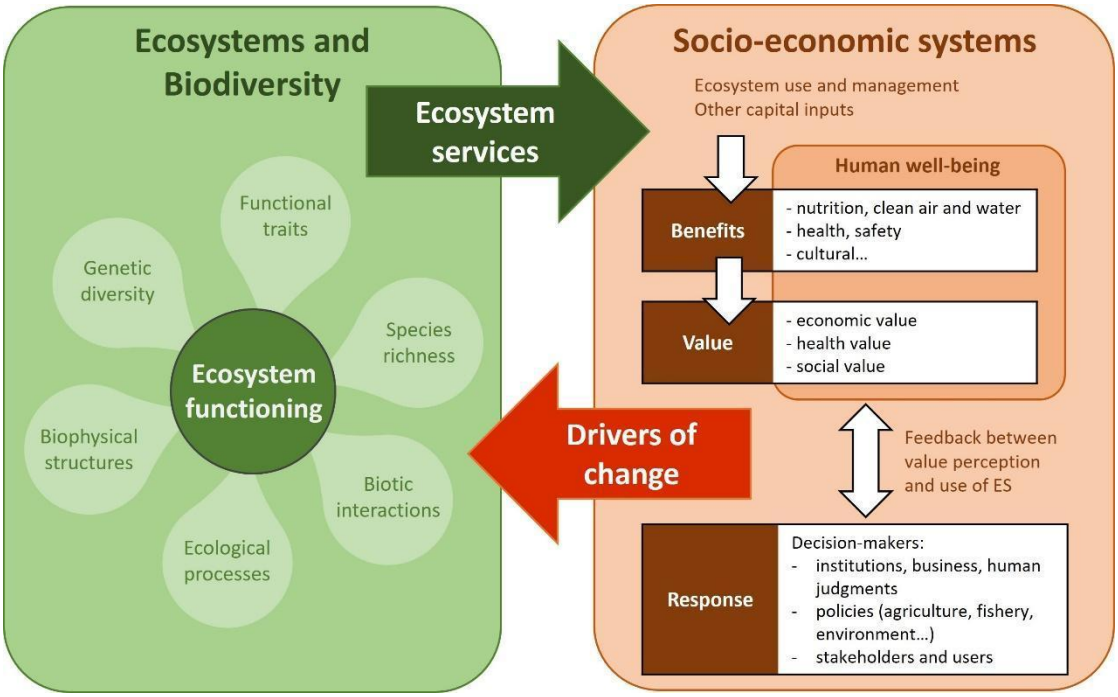

Figure 2. Schematic relationship between Ecosystems/Biodiversity and Socio-economic systems through Ecosystems Services and drivers of changes flows. Modified from DeGroot et al., 2010 and Maes et al., 2016.

COASTAL DEVELOPMENT IN THE MEDITERRANEAN SEA

Coastal ecosystems are among the most productive areas in the world with various habitats (e.g. marine forest, mangroves, seagrass meadows, lagoons) providing food and shelter for many organisms at different stages of development. The rapid increase of the coastal development related to the urbanisation of coastal areas, also called "ocean sprawl" (Duarte *et al.*, 2013; Firth *et al.*, 2016; Morris *et al.*, 2018; Cooper *et al.*, 2020), is causing a progressive replacement of natural coastal habitats with man-made structures and modified the shorelines with less complexity and heterogeneity than the natural habitats (Airoldi and Bulleri, 2011; Bulleri and Chapman, 2010; Chapman and Underwood, 2011). This complexity is important for the settlement and recruitment of several coastal fishes[1] (Cheminée *et al.*, 2021, 2017; Johnson, 2007). In addition, man-made structures can considerably enhance habitat fragmentation, change hydrodynamics and modify ecological connectivity (Bishop *et al.*, 2017; Dafforn *et al.*, 2015; Firth *et al.*, 2014; Perkins *et al.*, 2015), potentially leading to a decline in coastal biodiversity and changes in trophic interactions, ecosystem functioning and services (Airoldi *et al.*, 2005; Hinkel *et al.*, 2014; Jones, 1994).

[1] Fish is paraphyletic group and will be used in this thesis as a synonym of teleost.

In recent years, there has been growing interest in understanding the ecological role of artificial structures in coastal environments and their potential impacts on natural ecosystems. Numerous studies have shown that man-made structures alter different facets of biodiversity leading to a general loss of species and to changes in community structure (Bianchi and Morri, 2000; Hughes *et al.*, 2003; Karl and Trenberth, 2003; Bulleri and Chapman, 2004; Bulleri *et al.*, 2005; Halpern *et al.*, 2008; Bianchi *et al.*, 2012; Boudouresque and Verlaque, 2012). For instance, the replacement of natural rocky and sandy shores, which are considered to play an important role in the settlement, survival and growth of many species, with man-made structures has impacted the life cycle of coastal marine fishes (Gibson, 1994; Able *et al.*, 1999; Pastor *et al.*, 2013). It has also been shown that man-made structures can enhance biological invasions and decrease the resilience of coastal ecosystems or have an impact on fish migrations and other natural dispersion patterns (Bulleri and Chapman, 2010; Airoldi *et al.*, 2015; Shabtay *et al.*, 2018).

Because the Mediterranean coastline is densely populated and represents one of the first tourist destinations in the world (Segreto *et al.*, 2009; Coll *et al.*, 2010; Demeester and Mercier, 2022), the Mediterranean Sea is particularly impacted by the ocean sprawl. The coastal development in this region have greatly intensified over the last decades (Meinesz *et al.*, 1991). For instance, on the French Mediterranean coast, the percentage of artificial coasts has doubled since the 1960s (MEDAM, 2022; Figure 3).

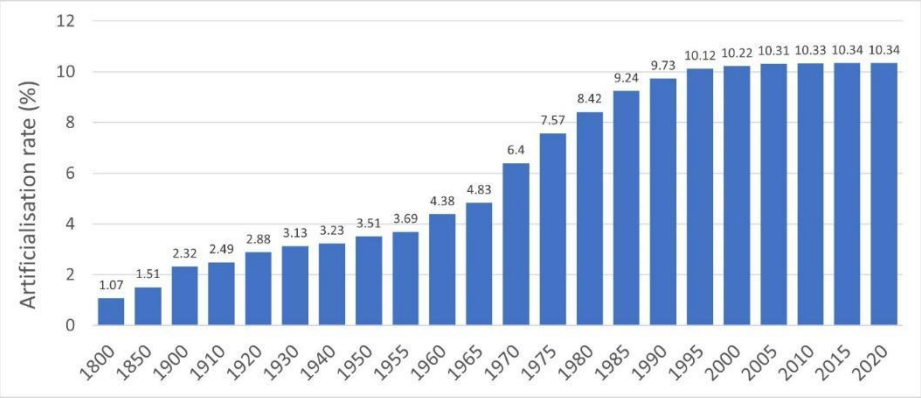

Figure 3. Artificialisation rate of the French Mediterranean coast from 1800 to 2020. Data from www.medam.org

The Mediterranean Sea is a semi-enclosed basin, connected to the Atlantic Ocean by the Strait of Gibraltar (14 km wide) to the West, to the Black Sea by the Strait of Bosporus, and to the Red Sea by the Suez Canal to the East. Its semi-enclosed geomorphology and the alternating warm- and cold-water species entering from the Atlantic through the

Gibraltar strait during the glacial periods have contributed to genetic isolation and speciation (Bianchi and Morri, 2000; Boudouresque, 2004; Coll *et al.*, 2010; Lejeusne *et al.*, 2010).

Nowadays, 8 to 9% of the world's marine specific diversity is found in the Mediterranean Sea (Bianchi *et al.*, 2012; Bianchi and Morri, 2000; Boudouresque, 2004; Coll *et al.*, 2010; Di Martino and Giaccone, 2000), with a notably high number of endemic species (Coll *et al.*, 2010), which includes key-species such as the habitat-forming species phanerogam *Posidonia oceanica*. This marine diversity is mostly concentrated close to the coast (between 0 and 50 metres depth), with about 90% of the known plant species and 75% of the fish species of the Mediterranean (Coll *et al.*, 2010).

ECOLOGICAL ENGINEERING SOLUTIONS

Coastal managers face the challenge of implementing protection and conservation initiatives. When ecosystems are healthy or there is the possibility of introducing effective restoration initiatives, implementing marine protected areas must be a priority. However, when natural habitats are destroyed and replaced with artificial structures, the only initiative that makes sense is to reconcile with nature by creating habitats that, although artificial, may support biodiversity and ecosystem functioning (SER, 2004).

A wide range of ecological engineering solutions can be used to rehabilitate (or reconcile with nature) artificial areas by, for instance, adding habitats that mimic the natural ones to the existing man-made structures (Figure 4; Airoldi *et al.*, 2021, 2005; Bishop *et al.*, 2022; Browne and Chapman, 2014; Chapman and Underwood, 2011; Morris *et al.*, 2019, 2018; Strain *et al.*, 2021).

Artificial fish habitats (AFH) have been deployed in harbours and marinas to provide nursery habitats to coastal fish species (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b). Using oyster shells, plastic, wood, concrete or steel, AFH add complex three-dimensional substrates to seawalls or pontoons and provide a refuge from predators. Previous studies have shown a better survival rate of fish post larvae and juveniles, but also an increase in their richness and abundance in and around such AFH compared to unequipped areas in the ports (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b).

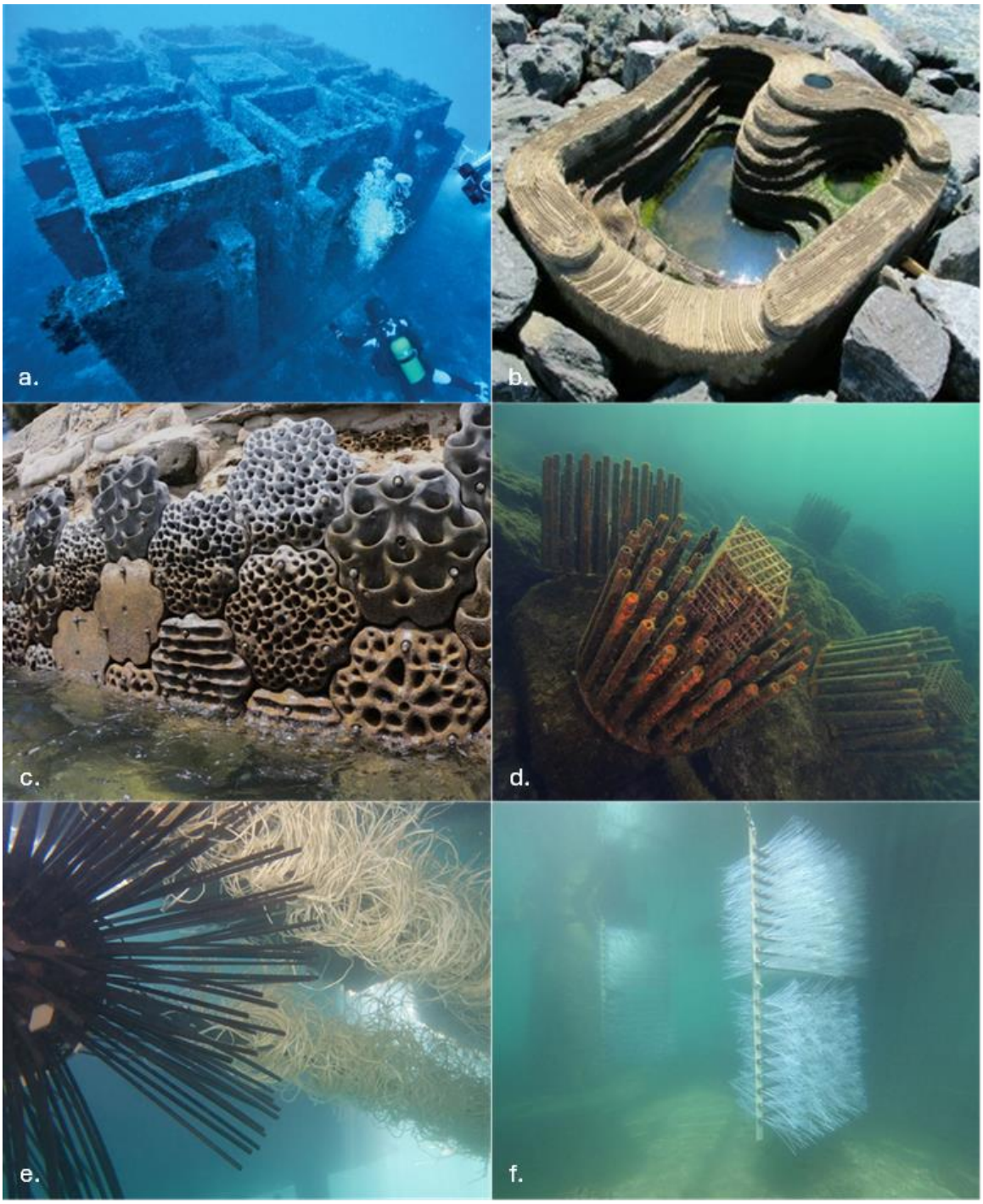

Figure 4. Examples of ecological engineering solutions used in coastal areas (a) Artificials reefs immerged in Marseille (France), © Sandrine Ruitton; (b) Ecocrete® TidePools: Artificial rockpools deployed in Staten Island (USA), © Perkol-Finkel and Sella, 2016; (c) Living seawall panels installed in the Harbour of Sidney (Australia), © Living Seawalls; (d) Dike Biohut® structures deployed against rock armoured breakwaters inside Marseille harbours (France) © ECOCEAN; (e) Roselières© and Oursins© modules deployed under floating pontoons inside Porquerolles marinas (France), © Seaboost; (f) ReFISH® modules installed under pier in Toulon bay (France), © Marinov.

Although the main purpose of the AFH deployed in harbours and marinas is to provide shelter against predators for fish post-larvae and juveniles, they can also be colonised by several invertebrate[2] and macroalgae[3] species. Marine invertebrates are key components of coastal communities and food webs (Chen, 2021; Collier *et al.*, 2016; Kemp *et al.*, 2012). They are essential prey to fishes and seabirds and by feeding on primary producers (e.g. macroalgae) and detritus they mobilise carbon and nutrients up to the food web (Dame *et al.*, 2001; Ehrnsten *et al.*, 2020). Moreover, their bioturbation activity largely contributes to carbon and nutrient mineralisation, whereas their suspension feeding plays a key role in maintaining water clarity (Hily, 1991; Ostroumov, 2005). Many species also represent an important economic resource (Alves *et al.*, 2020; Beseres Pollack *et al.*, 2013; Chen, 2021; Diniz *et al.*, 2014; Spalding *et al.*, 2014). Additionally, when AFH enhance diversity and biomass of benthic species, they might also modify exchanges of material among the habitat where they are installed and the adjacent habitats. This may for instance happen because benthos is food to fishes that then migrate towards other habitats or because excess benthic organic matter growing and decaying on AFH may be transported with water currents.

Information of how AFH are colonised by benthic species and how they might contribute to trophic exchanges between habitats is scant. This information is however crucial for understanding how these measures may rehabilitate by now degraded artificial habitats.

OBJECTIVES

This thesis examines the distribution patterns of invertebrate biodiversity linked to AFH and investigates the biomass exchange between marinas and nearby *Posidonia oceanica* meadows along the French Mediterranean coast. I focus on a particular type of AFH registered under the name Biohut® (ECOCEAN, France; www.ecocean.fr), made of a metal cage filled with oyster shells and surrounded with a protective large mesh grid. These structures are widely deployed in Mediterranean harbours and marinas, attached to vertical seawalls and docks or hung beneath pontoons. My PhD project has been funded by the "Association Nationale de la Recherche et de la Technologie (ANRT)" and by the "Agence

[2] Invertebrates is a paraphyletic group and will refer in the thesis as all animals excluding the chordate subphylum Vertebrata.

[3] Macroalgae is a polyphyletic group but will be used in this thesis as its morphological sense encompassing Chlorophyta (green algae), Phaeophyceae (brown algae) and Rhodophyta (red algae)

de l'Eau Rhône Méditerranée Corse", through a collaboration between ECOCEAN company and ECOSEAS laboratory in order to start understanding the ecological role of Biohut beyond their original role as nursery for fishes.

The specific objectives of my work, declined into 3 papers are: (i) evaluating how taxonomic diversity and community composition of benthic invertebrates varies with AFH immersion time, (ii) understanding how AFH types and environmental context (e.g. nutrient loading) may modify benthic assemblages and (iii) exploring the provenance of organic matter in seagrass meadows (*Posidonia oceanica*) adjacent to marinas equipped or not with AFH and the role of fish feeding.

The results should contribute to a better comprehension of the ecological functioning of AFH deployed in harbours and marinas and provide valuable insights into the management and rehabilitation programs in degraded coastal ecosystems.

The chapters of this thesis, presented hereafter, combine field sampling, laboratory analyses (including stable isotope analysis) and analyses of archived database extracted from monitoring programs. Below, a brief summary of the objectives for each chapter:

- Chapter 1: *Immersion time determines performance of artificial habitats in commercial harbours by changing biodiversity of colonising invertebrate assemblages*. In this chapter I compare the composition of assemblages of invertebrates colonising artificial fish habitats immersed in 3 commercial harbours for different period of time (~6 vs ~18 months) with a particular focus on the variations in total abundance, species richness, species diversity and evenness, and abundance of ecological and economic important species.

- Chapter 2: *Geographical and within ports variability in diversity and taxonomic composition of invertebrates dwelling in artificial fish habitats*. In this chapter, using field sampling and data from monitoring programs, I examine the spatial distribution of invertebrates dwelling in artificial fish habitats across 2 geographical regions characterised by different seawater nutrient concentrations and according to the type of port habitat where they are placed inside the marinas.

- Chapter 3. *Artificial fish habitats and trophic connectivity between marinas and adjacent natural ecosystems.* This chapter is the first step towards better

understanding how the AFH can impact the exchanges of organic material between marinas and adjacent seagrass habitats. Collected samples, including particulate and sedimentary organic matter (POM & SOM), seagrass shoots (and their epiphytes), macroalgae and fishes, were processed for bulk stable isotope analyses of carbon and nitrogen and for fish stomach content to estimate the trophic connectivity.

CHAPTER 1: IMMERSION TIME DETERMINES PERFORMANCE OF ARTIFICIAL HABITATS IN COMMERCIAL HARBOURS BY CHANGING BIODIVERSITY OF COLONISING INVERTEBRATE ASSEMBLAGES

Alix Varenne, Laura E. Richardson, Andrew N. Radford, Francesca Rossi, Gilles Lecaillon, Anaïs Gudefin, Lucas Bérenger, Etienne Abadie, Pierre Boissery, Philippe Lenfant, Stephen D. Simpson. *Diversity* (2023), *15*, 505. doi: 10.3390/d15040505

ABSTRACT

In highly modified coastal environments, such as commercial harbours, the installation of artificial habitats has garnered support as a means of enhancing local biological recruitment and connectivity. The success of these measures depends largely on the patterns of species colonisation. Using post-installation monitoring data, we compare the composition of assemblages of invertebrates colonising artificial habitats that were immersed for different periods (~6 vs ~18 months) in 3 commercial harbours along the French Mediterranean coast. The artificial habitats were colonised by taxonomically diverse invertebrate assemblages of ecological and economic importance, including molluscs, crustaceans and echinoids. Composition differed significantly with the immersion time of the artificial habitats, with total abundance, species richness and evenness significantly higher after ~18 than after ~6 months of immersion, indicating that long periods are necessary to enrich these new habitats with economically and ecologically important species. These results can inform restoration protocols and emphasise the value of post-installation monitoring programs.

Keywords: ecological community development; coastal biodiversity; species composition; artificial structures; coastal restoration

1. INTRODUCTION

Habitat degradation and loss threaten population persistence, biodiversity and the functioning of ecosystems (Cardinale *et al.*, 2012; Ellis *et al.*, 2013; Ellison *et al.*, 2005). Ecosystem managers face the challenge of implementing conservation and restoration initiatives in altered environments (Hobbs *et al.*, 2014) where the effects of climate change exacerbate the impacts of coastal development (Beck *et al.*, 2001; Hughes *et al.*, 2003; Thibaut *et al.*, 2005; Townhill *et al.*, 2017). In systems where it is determined that ecosystem thresholds have been crossed as a result of human impacts and where changes are irreversible, such as on heavily modified coastlines within large grey infrastructures (e.g. ports, harbours, commercial marinas), options for their management as 'novel ecosystems' may be considered to manipulate them and fulfil desired ecological conditions or functions (Hobbs *et al.*, 2014, 2006; Ido and Shimrit, 2015).

The installation of artificial habitats with ecologically-engineered elements has been widely advocated and implemented for replacement of lost or degraded natural habitat, ecological conservation, biodiversity enhancement and improvement of ecosystem services (Bell *et al.*, 2006; Firth *et al.*, 2020; Grove *et al.*, 1991; Morris *et al.*, 2018). Specific goals of artificial habitats may include: supporting local biodiversity and communities of fish or invertebrates of commercial or ecological interest (Baine, 2001; Bell *et al.*, 2009, 2006; Folke *et al.*, 2004; Mercader *et al.*, 2017b, 2017a), building ecosystem resilience and enhancing ecological connectivity (Bouchoucha *et al.*, 2016; Higgins *et al.*, 2019; Hobbs *et al.*, 2014; Sutton and Bushnell, 2007).

Evidence shows the efficacy of these artificial habitats in attracting marine organisms at different development stages, from larvae to adults, although the patterns of colonisation are context-dependent (Bouchoucha *et al.*, 2016; Higgins *et al.*, 2019; Komyakova *et al.*, 2019; Mercader *et al.*, 2018, 2017b). These patterns can depend on processes of community assembly and succession that are determined, among others, by the timing of species colonisation and interactions among species (Palmer *et al.*, 1997; Wiggins *et al.*, 1980; Young *et al.*, 2001). It is therefore anticipated that implementing artificial habitats in degraded ecosystems can facilitate or accelerate successional processes that foster the establishment and maintenance of diverse communities (Hauser *et al.*, 2006; Komyakova *et al.*, 2019; Palmer *et al.*, 1997).

Evaluating the colonisation process of artificial habitats is key for assessing their use in ecologically degraded coastal ecosystems. In this study, we examine the composition (structure and diversity) of invertebrate assemblages colonising artificial habitats after two distinct immersion periods: 5.5–7 months (Year 1), and 17.5–19.5 months (Year 2).

The artificial habitats (Dock Biohut®; ECOCEAN SAS, Montpellier) were designed to provide ecological nursery habitat within commercial harbours and marinas (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b). We use a subset of existing monitoring data from these artificial habitats in three spatially distinct commercial harbours along the French Mediterranean coast where post-installation sampling replication allowed for comparison of colonisation across years. We compare invertebrate assemblages found in artificial habitats in Years 1 and 2, and hypothesise that the species composition of invertebrates would differ across time periods and that abundance and taxonomic diversity would increase with immersion time.

2. MATERIALS AND METHODS

2.1. Study sites

This study uses ecological monitoring data from three large commercial harbours in the Gulf of Lion along the French Mediterranean coast, separated by distances of 29 to 204 km, namely Le Barcarès (42.7980° N, 3.0375° E), Port-Vendres (42.5190° N, 3.1089° E), and Grand Port Maritime de Marseille (43.3448° N, 5.3377° E). Each of these three harbours has >200 vessel moorings and has been operating commercially for >40 years, although the physical and environmental characteristics of each harbour vary across a range of parameters (Table 1).

We extracted this subset of data from a large monitoring database comprising data from Biohuts installed in 21 harbours and marinas across 19 French cities and in Monaco between 2013 and 2017 (Table S1). The subset was selected to allow sufficient replication of artificial habitats within harbours across years.

2.2. Sampling Unit and protocol

Biohuts were composed of two adjoined carbon-steel alloy cages (50 x 80 x 12.5 cm; combined cages depth 25 cm), and attached to the dockside (Figure 1). One cage was filled with empty oyster shells to provide complex substrate and was positioned against the dock (2.5 cm mesh-size); the outward-facing adjoining cage was left empty (5 cm mesh size) to keep out large mobile predatory fish.

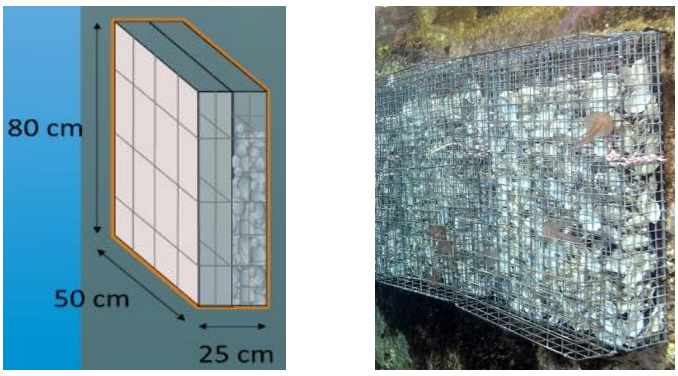

Figure 1. Dimensions (a) and image (b) of Dock Biohut structures, composed of two carbon-steel alloy cages: inner-cage filled with oyster shells (2.5cm mesh), and empty outer-cage (5cm mesh)

In March and June 2013, all the sampled Biohuts were installed in each harbour, submerged just below the surface of the water. Assemblages were sampled on randomly selected Biohuts at least 20 m apart either 5.5–7 (Year 1), or 17.5–19.5 months after installation (Year 2; Table 1). Because of the number of remaining Biohuts available in Year 2, the number of sampled Biohuts were different among years. During Year 1, 30 Biohuts were sampled (9 in Le Bacarès, 12 in Marseille and 9 in Port-Vendres) whereas 16 were sampled in Year 2 (4 in Le Bacarès, 7 in Marseille and 5 in Port-Vendres).

During monitoring, the Biohuts were encased with a PVC net (2 mm mesh) by divers to prevent loss of organisms during removal and lifted from the water onto the adjoining dock. Biohuts were then disassembled, the organisms identified to the lowest taxonomic level possible and counted. The sampling protocol did not allow us to sample for macroalgal cover or biomass and we focused the study on consumers.

Table 1. Characteristics of the three study sites (harbours) and Dock Biohut sampling.

Harbour	Coast type	Distance to Rhone River mouth (km)	Connections	Harbour construction date	Harbour surface area (ha)	Harbour maximum depth (m)	Mean ± SE distance from Biohuts to sea (m)	Mean ± SE depth under Biohuts (m)	Biohuts installation date	Date of sampling (sample size)	
										Year 1	Year 2
Le Barcarès	Sandy	158 (west)	Sea and lagoon	1963	81	2.5	610 ± 112	1.50 ± 0.50	01 Mar 2013	30 Sept – 01 Oct 2013 (n=9)	15 Oct 2014 (n=4)
Port-Vendres	Rocky	167 (west)	Sea	1953	33	10.0	816 ± 133	5.67 ± 1.33	01 Mar 2013	01 – 02 Oct 2013 (n=9)	07 Oct 2014 (n=5)
Grand Port maritime de Marseille	Rocky	42 (east)	Sea	1840	400	14.5	2126 ± 152	8.25 ± 1.84	01 June 2013	14 Nov 2013 (n=12)	26 – 27 Nov 2014 (n=7)

2.3. Data Analysis

We fitted generalised linear mixed models (GLMM) with time period as fixed factor (2 levels: Year 1, Year 2) and harbour as a random factor (R Core Team, 2017) on univariate data. We used this structure to model the biodiversity of invertebrate assemblages (species richness, Shannon diversity, Pielou's evenness), the abundance of specific taxa (Bivalvia, Gastropoda, Malacostraca, Ophiuroidea), and the abundance of commercially exploited taxa that contributed >5% to the total invertebrate abundance (e.g. the palaemonid shrimp *Palaemon* spp.; the variegated scallop *Mimachlamys varia*; FAO, 2022). Mixed-effects models that estimate parameters based on residual maximum likelihood were used due to their capacity to more appropriately handle unbalanced designs (particularly with random effects) than alternative approaches using observed and expected mean squares or error strata (Logan, 2010). Count data of classes and total abundance were fitted using a negative binomial distribution to accommodate alternative exponential distributions of residuals due to evidence of overdispersion (with glmer.nb in *lme4*). Temporal variation in species richness was modelled with a Poisson distribution due to exponential variance but within the assumed bounds of dispersion (glmer in *lme4*). Temporal variation in Shannon diversity and Pielou's evenness was assessed with Gaussian models and a constant variance structure due to heteroscedasticity between time periods. Model assumptions were assessed visually using diagnostic plots of Pearson residuals. Variation in the multivariate taxonomic composition of invertebrate assemblages through time was tested using a two-way PERMANOVA (maximum permutations = 9999) and then visualised with non-metric multidimensional scaling (nMDS) based on a Bray-Curtis dissimilarity matrix of log (x+1) transformed data. We used Monte Carlo sampling to estimate differences due to limited available unique permutations (360) and unconverged permutation versus Monte Carlo P-values (Anderson *et al.*, 2008).

Before running PERMANOVA, homogeneity of residuals was tested using PERMDISP with time period (fixed) and harbour (random) as factors. Similarity percentage analysis (SIMPER) was also performed using Primer v6 with PERMANOVA+ (Anderson *et al.*, 2008; Clarke *et al.*, 2014). The data were *log* (x+1) transformed to quantify, 1) overall similarity across harbours across the time periods; and 2) mean similarity within or dissimilarity between harbours across time periods. SIMPER was also used to identify

those species contributing consistently to similarity or dissimilarity (similarity or dissimilarity/standard deviation ≥ 2).

3. RESULTS

A total of 48 invertebrate taxa, from 39 families, 8 classes, and 5 phyla were recorded in Biohut structures across both survey periods (Table S1, S2). All animals were classified as native to the Mediterranean (Palomares and Pauly, 2023). There were significant differences between Year 1 and Year 2 in total abundance (z (1,42) = 2.36, p = 0.02), species richness (s (1,42) = 2.28, p = 0.02), and Pielou's evenness (s (1,42) = 2.07, p = 0.04), but not Shannon diversity (Table S3, S4). Abundance and species richness were higher in Year 2 than Year 1 (Figure 2).

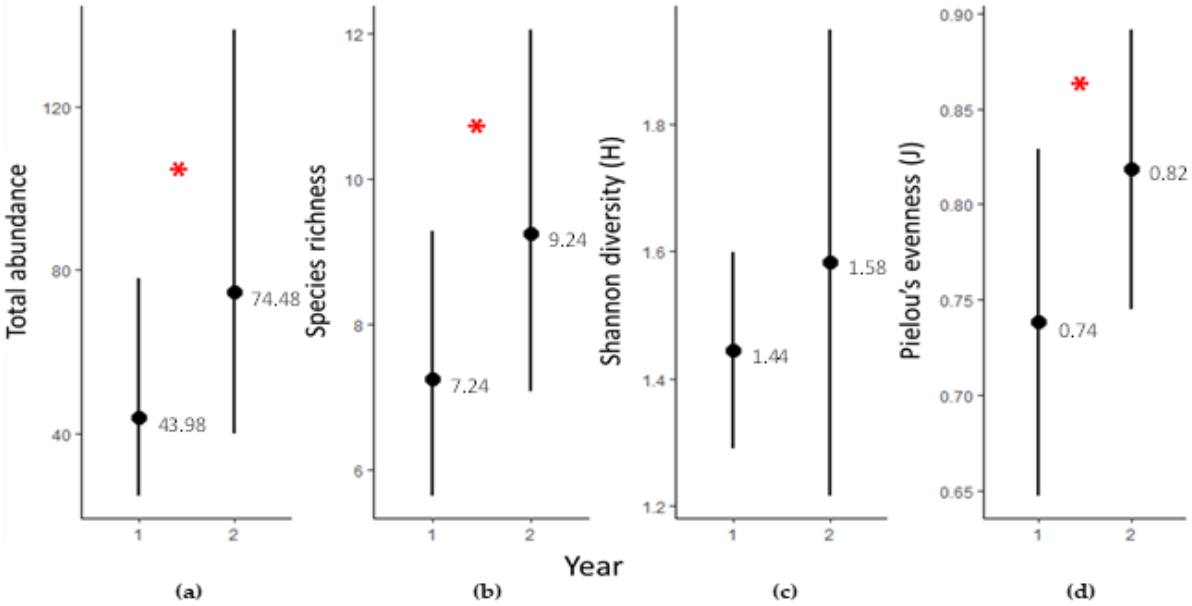

*Figure 2. Temporal variation (fitted values ±95% confidence intervals) in: (a) the total abundance (number of individuals/0.1m3 of artificial structure); (b) species richness (number of taxa/0.1m3 of artificial structure); (c) Shannon diversity; and (d) Pielou's evenness of invertebrate assemblages in artificial Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between time periods of each metric indicated with asterisks (red * indicates p ≤ 0.05).*

The taxonomic composition of invertebrate assemblages varied between Year 1 and Year 2. Non-metric MDS ordination showed distinct clusters between Year 1 and Year 2 (Figure 3). For both Le Bacarès and Port-Vendres, the Year 2 data were closer to each other than for the Year 1. The stress value (respectively 0.07, 0.1 and 0.08) provides a good representation of our data in reduced dimensions. PERMANOVA (F (1,40) = 3.569; p < 0.05) analysis revealed variation in taxonomic composition of invertebrate assemblages from Year 1 to Year 2 (Figure 3). However, PERMDISP analysis showed significant

differences in the mean distance from centroids among the groups (F (5,40) = 11.099; $p < 0.001$), indicating that results from PERMANOVA should be interpreted with caution.

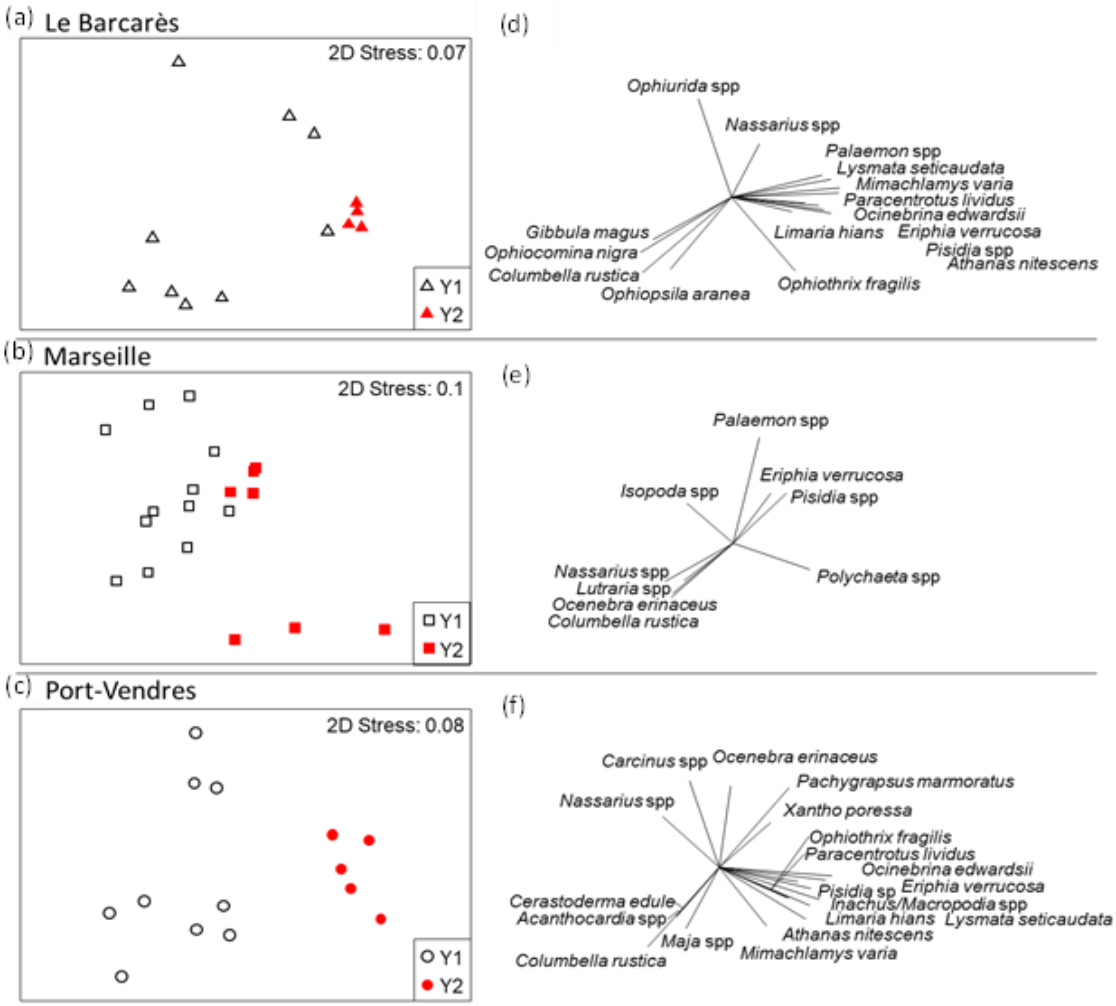

Figure 3. Non-metric multidimensional scaling analyses showing variation in taxonomic composition of invertebrate assemblages among surveyed Dock Biohut structures in each harbour between years (Y1 and Y2) since installation (a-c; log (x+1) transformed data); and the relative contribution of species to variation at each harbour (d-f; >0.5 Pearson correlation).

Changes in assemblage composition between Year 1 and Year 2 caused an overall increase in taxonomic similarity of assemblages across all harbours (average assemblage similarity: Year 1, 28%; Year 2, 37%), with an average 78% dissimilarity in species composition between years. This overall increase was likely driven largely by increased similarity in taxonomic composition of assemblages at La Bacarès (Year 1, 28%; Year 2, 72%) and Port-Vendres (Year 1, 47%; Year 2, 70%), and not Marseille where similarity decreased (Year 1, 39%; Year 2, 31%; Table 2). In Year 1, only the variegated scallop *Mimachlamys varia* contributed consistently to assemblage similarity among Biohuts in Port-Vendres. However, in Year 2, 6 species consistently characterised species assemblages in Le

Barcarès and 8 species in Port-Vendres. In Marseille, no species consistently contributed to assemblage similarity in either year.

Table 2. Similarity Percentage analysis of invertebrate assemblages in surveyed Dock Biohuts through time. Species consistently contributing to the average similarity within (sim/SD>2), and dissimilarity between (diss/SD>2) harbours from Year 1 (Y1) to Year 2 (Y2) identified in one-way SIMPER analysis are shown.

	Le Barcarès	**Port-Vendres**	**Marseille**
Le Barcarès	**Av. Sim:** **Y1**: 28%; no consistent spp. **Y2**: 72%; *Ophiothrix fragilis, Palaemon* spp., *Pisidia* spp., *Mimachlamys varia, Athanas nitescens, Paracentrotus lividus, Lysmata seticaudata, Eriphia verrucosa* **Av. dissim. (Y1 to Y2):** 75%; *Pisidia* spp., *Athanas nitescens, Lysmata seticaudata, Eriphia verrucosa*	**Av. dissim:** **Y1**: 77%; no consistent spp. **Y2** 50%; *Ophiothrix fragilis, Ocinebrina edwardsii, Pisidia* spp., *Pachygrapsus marmoratus, Lysmata seticaudata, Eriphia verrucosa*	**Av. dissim:** **Y1**: 82%; no consistent spp. **Y2**: 69%; *Ophiothrix fragilis, Paracentrotus lividus, Lysmata seticaudata, Eriphia verrucosa*
Port-Vendres		**Av. Sim:** **Y1**: 47%; *Mimachlamys varia* **Y2**: 70%; *Ocinebrina edwardsi, Lysmata seticaudata, Mimachlamys varia, Eriphia verrucosa, Athanas nitescens, Pachygrapsus marmoratus* **Av. Dissim. (Y1 to Y2):** 69%; *Ocinebrina edwardsii, Lysmata seticaudata, Eriphia verrucosa*	**Av. Dissim.:** **Y1**: 71%; no consistent spp. **Y2**: 76%; *Ocinebrina edwardsii, Lysmata seticaudata*
Marseille			**Av. sim:** **Y1**: 39%; no consistent spp. **Y2**: 31%; no consistent spp. Av. dissim. (Y1 to Y2): 75%; no consistent spp.

There was an overall increase in abundance of Malacostraca (z (1,42) = 4.50, $p < 0.0001$), but not Bivalvia, Gastropoda, or Ophiuroidea (Figure 4; Table S3, S4). Of 11 surveyed taxa identified as potentially commercially exploited (FAO, 2022), only two contributed to >5% of the total invertebrate abundance - *Palaemon* spp.(palaemonid shrimp) and *M. varia* - but neither varied in abundance significantly across years (Table S5). The remaining nine species (*Carcinus* spp.; common cockle *Cerastoderma edule*; black squat lobster *Galathea squamifera*; small periwinkle *Melarhaphe neritoides*; European flat oyster *Ostrea edulis*; purple sea urchin *Paracentrotus lividus*; *Periclimenes* spp. shrimp; bristle worm Polychaeta spp.; common cuttlefish *Sepia officinalis*) each accounted for <2% of the total surveyed invertebrate abundance (Table S6).

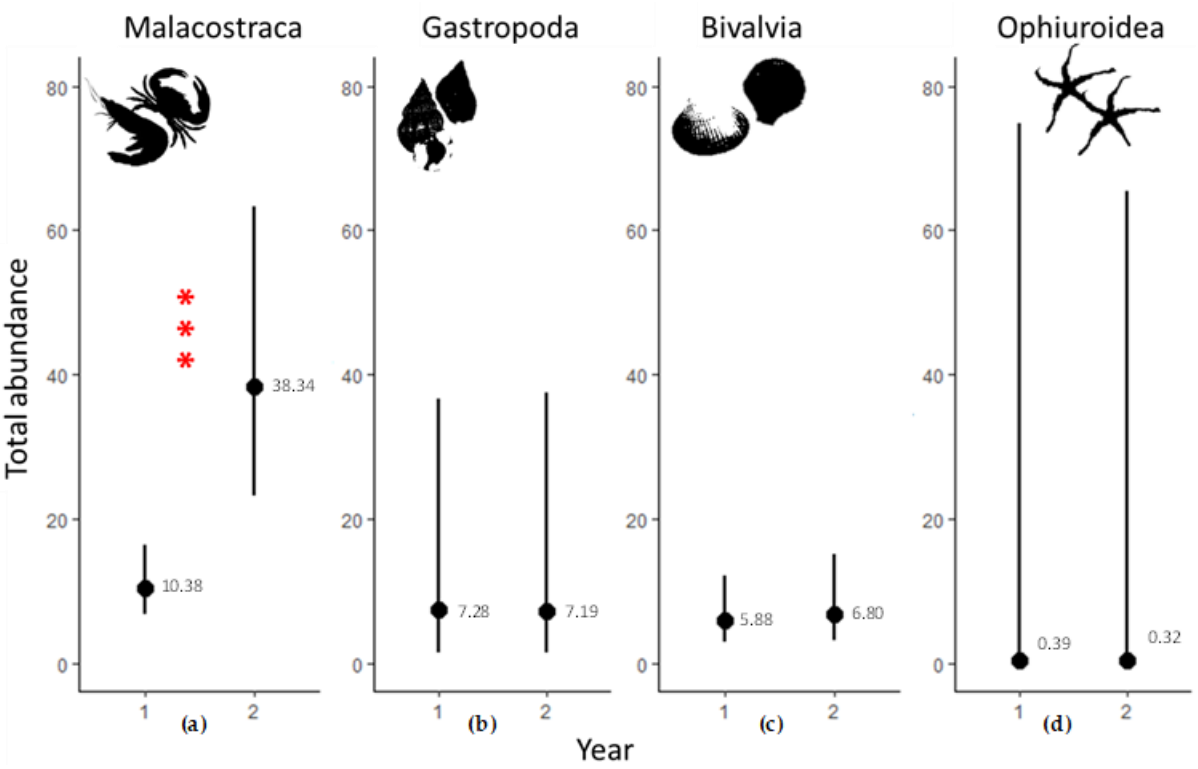

*Figure 4. Temporal variation (fitted values ±95% confidence intervals) in the total abundance (number of individuals/0.1m3 of artificial structure) of (a) Malacostraca; (b) Gastropoda; (c) Bivalvia; and (d) Ophiuroidea in surveyed Dock Biohut structures within Year 1 and Year 2 since installation. Significant differences between time periods indicated with asterisks (red *** $p < 0.001$).*

4. DISCUSSION

Examination of post-installation monitoring data found that artificial habitats (Dock Biohut) hosted taxonomically diverse assemblages of invertebrate species, including molluscs, crustaceans and echinoids of ecological, commercial and social interest. Our analysis aims to complement the already existing studies focused on the fish species associated with artificial habitats (Bell *et al.*, 2009; Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b, 2017a). Communities develop and are structured over time, whereby pioneering species initially colonise areas, with the abundance and composition of colonising assemblages depending on interacting factors including habitat size and connectivity, the proximity of source populations, local hydrodynamics, inter-annual temporal variation in larval supply, and competitive interactions with other species (Caffey, 1985; Higgins *et al.*, 2019; Sale *et al.*, 1984; Weiher and Keddy, 1999; Young *et al.*, 2001).

Community development in restoration or conservation ecology would likely be time-dependent in achieving desired endpoints of biodiversity, productivity and species-specific configurations (Palmer *et al.*, 1997; Suding *et al.*, 2004). The immersion time of artificial

habitats is a known, influential predictor of community composition due to processes of faunal succession (Schneider and Frost, 1996; Wiens, 2014; Wiggins *et al.*, 1980; Young *et al.*, 2001). In our study, the results indicated community change through time, likely due to spatially and temporally variable colonisation by different species (Wiens, 2014; Young *et al.*, 2001). The results showed differences in the colonisation and recruitment of organisms in the Biohuts between Year 1 and Year 2 of immersion, indicating the capacity of artificial habitats to support local biodiversity enhancement via the recruitment of organisms in highly modified harbours.

We found significantly greater total abundance, species richness, species evenness, and abundance of crustaceans in artificial habitats across the three spatially distinct harbours after a longer period of immersion. Multivariate analysis of our data also showed differences in artificial habitats assemblages between Year 1 and Year 2. Indeed, significant variation in composition between the invertebrate assemblages sampled in Year 1 and Year 2 after deployment of the Dock Biohuts indicate processes of community development and highlight the role of habitat soak-time in determining the outcome of artificial habitat installation initiatives (Komyakova *et al.*, 2019; Palmer *et al.*, 1997; Young *et al.*, 2001).

Our analyses revealed an increase in the similarity in composition both within and among assemblages in two of the three spatially distinct harbours between Year 1 and Year 2, and an overall increase in abundance of crustaceans - a group of ecologically important organisms due to their role in food-web dynamics (Szaniawska, 2018) - and their influence on the behaviour of settlement-stage larval organisms (Lillis *et al.*, 2013; Montgomery *et al.*, 2006; Parmentier *et al.*, 2015; Simpson *et al.*, 2005; Stanley *et al.*, 2010). Species composition was highly variable in the first year across all harbours, but in Year 2, assemblage structure became similar within and between Port-Vendres and Le Barcarès, with the dominance of molluscs, crustaceans and echinoderms. These similarities and the differences with Marseille harbour could be explained by the environmental characteristics of Marseille harbour, which is the largest and the deepest harbour of this study and it is not directly influenced by outflow from the Rhone River that delivers organic matter and sediment into the other two study harbours. Furthermore, the Biohuts of the Marseille harbour were positioned a greater distance from the harbour entrance than those of the other two harbours. Finally, the differences in species assemblages could be also due to the local availability of species, e.g. the ecological concept of species pool (Cornell and Harrison,

2014; Shen *et al.*, 2017). We observed an overall increase in abundance of Malacostraca, while the abundance of other predominant classes (gastropods, bivalves and brittle stars) remained consistent, carrying implications for efforts targeting ecological restoration (Palmer *et al.*, 1997; Parmentier *et al.*, 2015; Szaniawska, 2018). Crustaceans are key components of the diets of a range of macroinvertebrates and finfish (Szaniawska, 2018), such that an increase in their abundance may have implications for local food-web dynamics (Leitão *et al.*, 2007). Similarly, crustaceans can create a loud and acoustically complex biophony, producing acoustic cues used by settlement-stage larvae of fish and invertebrates that likely further enhances community development (Lillis *et al.*, 2013; Montgomery *et al.*, 2006; Parmentier *et al.*, 2015; Simpson *et al.*, 2005, 2004; Stanley *et al.*, 2010). For example, the estimated detection distance of snaps of the shrimp, *Athanas nitescens*, characteristic of Biohut invertebrate assemblages in Le Barcarès and Port-Vendres by Year 2, can be up to 40 m (Coquereau *et al.*, 2016). As such, shifts towards greater abundance of crustaceans may have a disproportionate role in the maintenance, development and function of locally diverse ecological communities (Palmer *et al.*, 1997; Szaniawska, 2018), and may point towards opportunities for passive acoustic monitoring of community development where intrusive survey techniques are less desirable (Coquereau *et al.*, 2016; Gervaise *et al.*, 2019; Nedelec *et al.*, 2015).

Our results indicate that provided that the artificial habitats do not simply concentrate organisms, they may enhance local productivity and biodiversity in highly modified areas within relatively short periods of time (Pickering and Whitmarsh, 1997). Similarly, the observed differences in assemblage composition through time suggests that where specific species configurations are desired endpoints for habitat restoration, understanding how local communities are structured over time will likely enable pragmatic management goal setting (Palmer *et al.*, 1997; Young *et al.*, 2001). Many species of crustaceans are also highly valued commercial and recreational fisheries resources (FAO, 2022). Where artificial habitats can enhance rather than relocate local productivity, they may provide opportunities for harvesting species in support of fisheries enhancement initiatives (Bell *et al.*, 2006, 2005; Richardson *et al.*, 2023), for the live-trade of ornamental organisms (Bell *et al.*, 2009) or for aquaculture (Hair *et al.*, 2002).

Artificial habitats can enhance the ecological capacity of highly modified areas of coastline such as large commercial ports and marinas by providing habitats for marine life at different

stages of life-history and migration (Bouchoucha *et al.*, 2016; Hobbs *et al.*, 2014; Ido and Shimrit, 2015; Mercader *et al.*, 2017a). The nursery capacity of artificial habitats in large commercial ports has been shown previously for diverse assemblages of juvenile finfishes, with typically higher abundance and species richness on artificial habitat structures than on adjacent bare surfaces (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b, 2017a). The availability of fine-scale structural complexity, such as is created by caged oyster shells in the focal Biohut structures, can provide refugia and enhance the survival of small-bodied and/or juvenile stage organisms when their risk of mortality is highest (Bouchoucha *et al.*, 2016; Goatley and Bellwood, 2016). Furthermore, the colonisation, abundance and species diversity of macroinvertebrate fauna can be directly associated with availability and structural characteristics of habitats (Attrill *et al.*, 2000; Fabricius *et al.*, 2014; García-Sanz *et al.*, 2012; Hauser *et al.*, 2006; Heck and Orth, 1980; O'Connor, 1991; Warfe and Barmuta, 2006). Investigating existing ecological monitoring data, our results provide insights into the relatively short-term capacity of artificial habitats to attract and maintain diverse assemblages of invertebrates. Moreover, our results highlight the role of habitat duration in community development and changes, and the establishment of biodiversity in highly modified commercial harbours. Our results also suggest that the environmental and physical characteristics of the harbours equipped with artificial habitat structures can also facilitate the colonisation by specific invertebrate assemblages. Furthermore, longer temporal studies comparing the colonisation of artificial habitats against background levels of diversity and productivity would enable greater understanding of their capacity to augment the ecological function of modified systems (Pickering and Whitmarsh, 1997). This includes improving our understanding of their role as ecological steppingstones for enhanced connectivity, and the ecological processes determining positive feedbacks and alternative states across degraded systems (Folke *et al.*, 2004; Suding *et al.*, 2004).

Biodiversity conservation and restoration are widely supported management goals (Brooks *et al.*, 2006; Lewis *et al.*, 2017; Palmer *et al.*, 1997), with species diversity considered important for promoting ecosystem resilience via the maintenance of critical ecosystem functioning during disturbance (due to functional redundancy and response diversity Elmqvist *et al.*, 2003; Walker, 1992). Increasingly, efforts to restore or replace nursery habitats is viewed as a key component of the conservation of biodiversity and management of productive systems (Beck *et al.*, 2001; Hobbs and Norton, 1996). Our results indicate that periods longer than 7 months are necessary to enrich these artificial habitats of

economically and ecologically important species. Finally, given the ecological importance of invertebrates in trophic dynamics and community development (Lillis *et al.*, 2013; Szaniawska, 2018), experimental research considering the influence of variation in invertebrate assemblage composition through time on the recruitment of teleost fishes may aid understanding of the capacity for complementary acoustic ecological enhancement programs (Moeslund *et al.*, 2017; Mukhin *et al.*, 2008; Parmentier *et al.*, 2015).

CHAPTER 2: GEOGRAPHICAL AND WITHIN PORTS VARIABILITY IN DIVERSITY AND TAXONOMIC COMPOSITION OF INVERTEBRATES DWELLING IN ARTIFICIAL FISH HABITATS

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ABSTRACT

Artificial fish habitats unintentionally provide a favourable substrate to benthic invertebrates. This paper examines their spatial distribution (i) across 2 geographical regions separated longitudinally by a large river delta, with different seawater nutrient concentrations and (ii) within ports, according to the port habitat where artificial fish habitats are deployed. We analysed existing datasets and collected new data in autumn 2021. We focused on a particular artificial fish habitat (Biohut) widely deployed in ports along the French Mediterranean coast. Assemblage composition was correlated to seawater chlorophyll-a and the number of taxa was found highest in the nutrient-enriched region situated to the west of the river delta. Different taxa colonised the Biohut hanging under pontoons and those mounted on vertical seawalls. Given the importance of benthic invertebrates for fish nutrition, our results can be useful for optimising the ecological benefits of artificial fish habitats.

Keywords: Ecological engineering; restoration; reconciliation ecology; benthos; harbours.

1. INTRODUCTION

The increasing urban development of coastal areas is expanding the extent of man-made structures along shorelines globally (Bugnot *et al.*, 2021; Komyakova *et al.*, 2022). In several areas, they have replaced natural habitats such as sandy and rocky shores and introduced new artificial habitats (Airoldi *et al.*, 2015, 2005; Bulleri and Chapman, 2010; Cooper *et al.*, 2020; Martin *et al.*, 2005; Shabtay *et al.*, 2018). In general, man-made structures support very different and often impoverished communities in comparison to natural hard bottoms and this is reflected into changes in ecosystem functioning and services (Bulleri, 2005; Bulleri and Chapman, 2010; Dafforn *et al.*, 2015; Firth *et al.*, 2016b; Morris *et al.*, 2018; Moschella *et al.*, 2005). In fact, these structures can rarely mimic the light exposure, the heterogeneity and complexity of the natural seascape (Chapman and Bulleri, 2003; Glasby and Connell, 1999), which provides micro-habitats, food and shelter to invertebrates and fishes (Beck *et al.*, 2001; Cheminée, 2012; Cheminée *et al.*, 2021; Harmelin *et al.*, 1995). Artificial structures can also modify assemblages, by altering water motion (Floerl and Inglis, 2003), loading of nutrients, sediments and pollutants (Piola and Johnston, 2008).

Ecological engineering is used more and more frequently in highly developed coastal areas, such as harbours and marinas, to replace man-made structures with others mimicking key features of natural shores. Their main intent is to ameliorate biodiversity of already damaged ecosystems, approximate the ecological and functional value to that found on natural habitats and, ultimately lead to an improvement in ecosystem services provision (Bilkovic and Mitchell, 2013; Bishop *et al.*, 2017; Chapman and Underwood, 2011; Firth *et al.*, 2014; Morris *et al.*, 2019; O'Shaughnessy *et al.*, 2020). Benthic macroalgae and invertebrates are often among the main colonisers of man-made habitats. Understanding the patterns of colonisation and the mechanisms regulating these patterns is important because these species greatly contribute to the diversity and functioning of coastal ecosystems (Chen, 2021; Collier *et al.*, 2016; Kemp *et al.*, 2012). For instance, they provide secondary natural habitats, are important food sources for fish and mobilise carbon and nutrients up to the food web (Dame *et al.*, 2001; Ehrnsten *et al.*, 2020). Suspension feeders play a key role in maintaining water clarity (Davies *et al.*, 1989; Hily, 1991; Ostroumov, 2005) and some taxa represent an important economic resource (Alves *et al.*, 2020; Caddy, 1989; Dulvy *et al.*, 2003). Ecologically engineered solutions that can ameliorate benthic biodiversity include the addition of artificial rockpools and panels presenting a variety of micro-habitats to existing man-made structures (Airoldi et al., 2021, 2005; Bishop et al., 2022; Dafforn et al., 2015; Firth et al., 2016a; Morris et al., 2019, 2018; Strain et al., 2021).

The installation of artificial fish habitats aimed at mitigating the loss of habitat available to juvenile fishes within harbours and marinas (Bouchoucha *et al.*, 2016; Joubert *et al.*, 2023; Mercader *et al.*, 2018, 2017b; Patranella *et al.*, 2017) can unintentionally provide a suitable substrate for invertebrates and macroalgae (Gauff *et al.*, 2023; Varenne *et al.*, 2023). Given that benthic organisms contribute to coastal ecosystem services and serve as both habitats and food sources for fishes, understanding their composition and diversity in artificial fish habitats can provide valuable insights for ameliorating their effectiveness. To the best of our knowledge, information on the distribution pattern of invertebrates colonising artificial fish habitats in harbours and marinas remains limited to a few studies and specific locations.

Previous studies on colonisation patterns and diversity of invertebrate assemblages on other eco-engineered and traditional man-made structures have shown that diversity and species composition may vary because of differences in habitat orientation, substrate rugosity and habitat complexity (Airoldi and Beck, 2007; Lawrence *et al.*, 2021; Strain *et al.*, 2021,

2018). Increasing complexity or changing the orientation may have a positive effect on the diversity of these structures (Bishop *et al.*, 2022; Drakard *et al.*, 2023; Strain *et al.*, 2021, 2018). For instance, it has been observed that benthic communities colonising ecologically engineered habitats are more resistant to biological invasion than those occupying other man-made structures (Elton, 1958; Firth *et al.*, 2016b; Perkol-Finkel *et al.*, 2018). However, evidence has also shown that patterns can vary locally because of habitat characteristics, but also regionally because of differences, among other things, in seawater nutrients, productivity or temperature (Bracewell *et al.*, 2018; Osman, 2015; Simpson *et al.*, 2017). Remarkably, artificial fish habitats have also been found to increase the likelihood of colonisation by non-indigenous species (NIS), thus potentially resulting in an ecosystem disservice (Gauff *et al.*, 2023). The complexity of the substrate might also facilitate the colonisation of several benthic species, thus providing potential food sources to fishes and stimulating their settlement. Benthic species could also attract fish larvae and juveniles by producing acoustically complex sounds (Lillis *et al.*, 2013; Montgomery *et al.*, 2006; Simpson *et al.*, 2005, 2004; Stanley *et al.*, 2010).

This study aims at understanding the spatial patterns of distribution of invertebrate assemblages colonising artificial fish habitats deployed in marinas and harbours along the Mediterranean coast. The Mediterranean Sea is highly urbanised, and a large percentage of the coastline is occupied by man-made structures, including industrial ports and marinas. A wide range of different eco-engineered artificial fish habitats (e.g. pontoon hanging, dock-mounted, dike, benthic, mourning artificial habitats) made from various materials and substrate (e.g. concrete, steel, wood, plastic, oyster shell) are nowadays present in several ports. In the present paper, we first estimated how species composition and diversity varied among 2 regions characterised by well-known differences in seawater nutrients, due to the geomorphological characteristics of the largest European delta (Rhone River delta). Then, we examined how assemblages varied among the artificial fish habitats when hanged under pontoon or attached to vertical docks. We hypothesized that (i) community structure and diversity would be different among regions, with more individuals in the region characterised by high nutrient inputs because of availability of food sources and (ii) there would be different taxa composition among artificial fish habitats placed on docks and those hanging under pontoons.

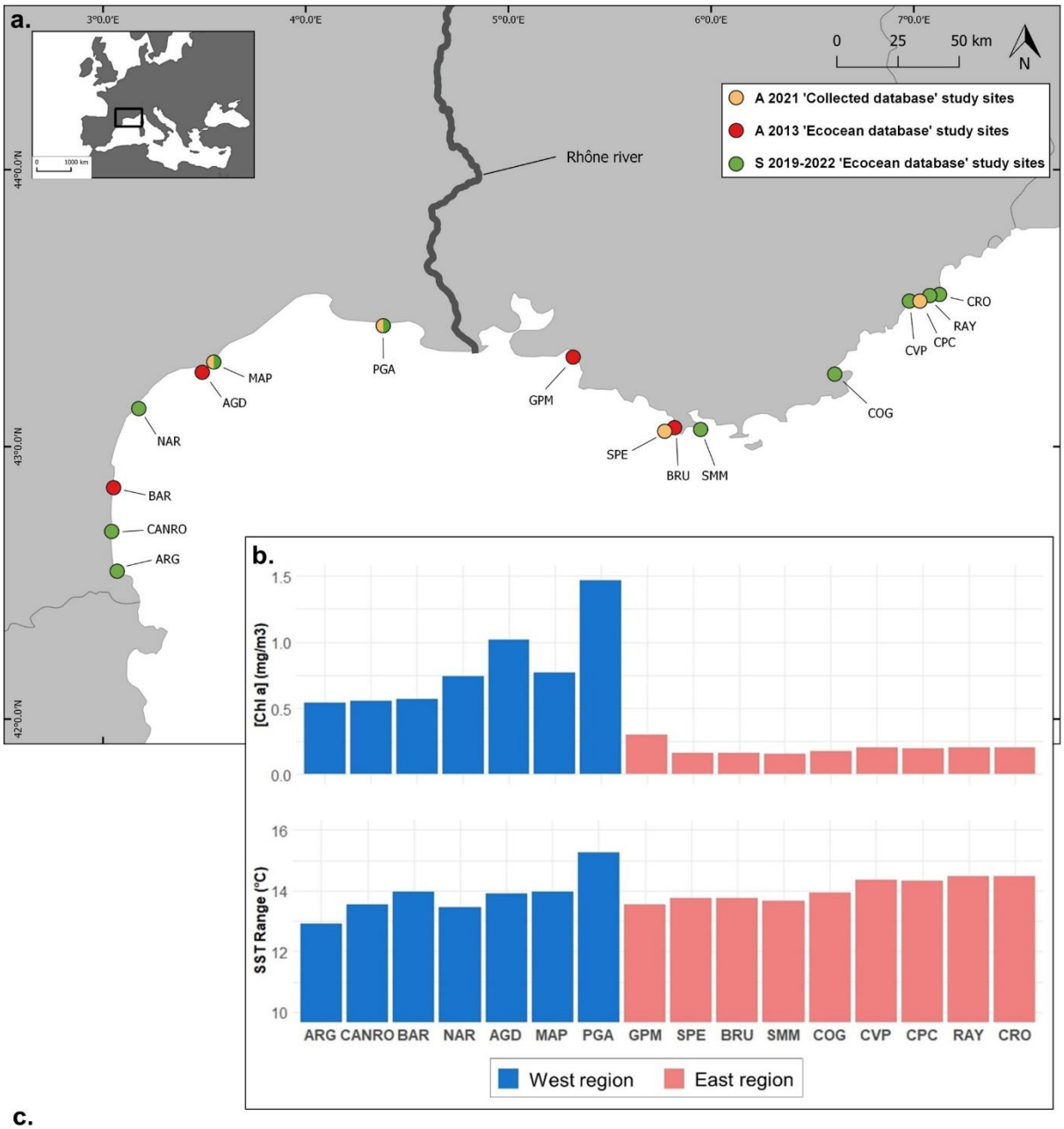
2. MATERIALS AND METHODS

2.1. Study area

The study area was situated along the North-Western French Mediterranean coast, where the large delta of the Rhone River delimits two regions with distinct biogeographical characteristics at the same latitude (Figure 1). The coastline of the region situated to the west of the delta receives significant nutrient (nitrogen, phosphorus, silica, carbon) and sediment inputs from the Rhone River (Cruzado and Velasquez, 1990; Gaudy *et al.*, 2003; Lefevre *et al.*, 1997; Lochet and Leveau, 1990). It is characterised by a wide continental shelf with a prevalence of soft sediments and numerous coastal lagoons. Moreover, strong and transient coastal upwellings, connected to North-westerly winds, brings up to the surface cold and nutrient-rich waters (Millot, 1979). Seawater and sediments exhibit remarkable biological productivity, and the coast is classified among the most eutrophic in the world (Margalef, 1985; Petrenko *et al.*, 2005). The Rhone River has instead no influence on the coast situated to the east side of its delta, bathed by the Ligurian Sea. The nutrient concentration in the seawater and the biological productivity of this marine environment are low (Agostini and Bakun, 2002; Millot, 1999). The morphological characteristics of this area include a narrow continental shelf and small pocket beaches, with marine coastal habitats dominated by the Neptune grass *Posidonia oceanica* meadows and coralligenous reefs. We will refer to the region situated to the west of the delta as "west region" and to the one situated to the east as the "east region".

2.2. Artificial fish habitats

In the present study, we focused on eco-engineered artificial fish habitats registered under the name Biohut® (ECOCEAN, France; www.ecocean.fr), which have been deployed in port habitats in France and abroad since 2013. A Biohut is made of a metal cage filled with oyster shells with a protective large mesh grid. In Mediterranean ports, they are attached to vertical seawalls and docks or hanged beneath pontoons (hereafter dock and pontoon Biohut; Figure 2), and always positioned approximately 20 cm below the high tide surface.



c.

Location	Marina name	Code	Location	Marina name	Code
West region	Port d'Argelès-sur-Mer	ARG	East region	Grand Port Maritime de Marseille	GPM
	Port du Canet-en-Roussillon	CANRO		Port de Saint-Pierre des Embiez	SPE
	Port-Barcarès	BAR		Port du Brusc	BRU
	Port de Narbonne-Plage	NAR		Port de Saint-Mandrier-sur-Mer	SMM
	Port du Cap d'Agde	AGD		Port des Marines de Cogolin	COG
	Port de Marseillan-Plage	MAP		Cannes Vieux-Port	CVP
	Port-Gardian	PGA		Cannes Port-Canto	CPC
				Port Camille Rayon	RAY
				Port Crouton	CRO

Figure 1. (a) Map of the 16 ports considered in the study along the French Mediterranean coastline (Northwestern Mediterranean Sea). Colours are used to differentiate the study sites from the 3 databases, (b) bar plots of concentration in Chlorophyll-a (mg/m3) and Sea Surface Temperature (SST) range (°C) of the ports considered in the study, and (c) list of ports with code name.

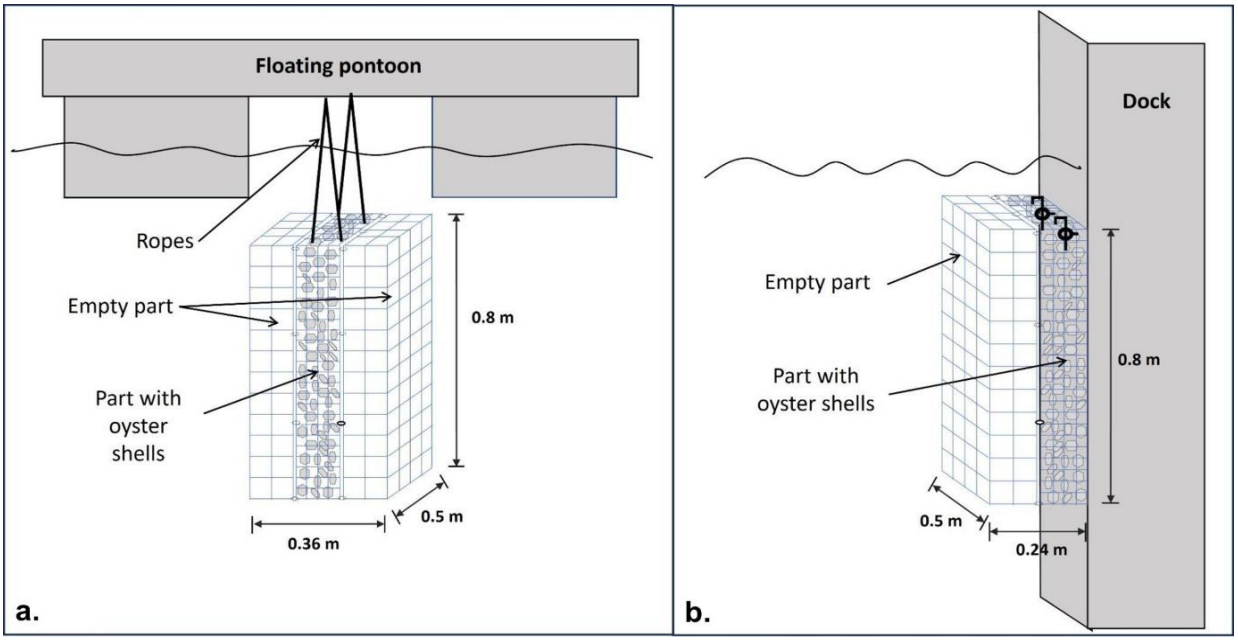


Figure 2. Illustration of the artificial fish habitats considered named Biohut. (a) Biohut deployed under pontoons; (b) Biohut mounted on the vertical wall of docks. The 5 cm-mesh cages, made of iron wire, coated with an alloy of Zn, Al and Mg, exclude large predators. An inner 2.5cm-cage (not shown in the drawing for simplicity) is filed with oyster shells.

2.3. Data collection

In this study, we collected data through field sampling and extracted relevant data from ECOCEAN ongoing post-installation monitoring program, which has been in operation since 2013. Furthermore, using the geographical coordinates of each port of the study, we extracted environmental biogeographical data between January 1st, 2013, and December 31st, 2022, from E.U. Copernicus Marine Service Information, specifically focussing on chlorophyll-a concentration in seawater (Figure 1; doi.org/10.48670/moi-00300). We also extracted the annual mean sea surface temperature range (Figure 1; doi.org/10.48670/moi-00173), but preliminary analyses showed no significant variation in SST among regions or ports within regions nor correlations with benthic assemblages and these data are not considered any further in this study.

2.3.1. Field sampling

From 4th to 12th October 2021, we sampled 4 marinas, 2 in the east and 2 in the west region (Figure 1). The marinas had a comparable size (between ca. 5 ha to 10.5 ha), number of vessel moorings (> 200) and depth (ranging from 2 m to 4 m depth) and they were equipped with a similar number of artificial fish habitats immersed for at least 3 years (Table S1). Due to the difference in the inlet shapes among the marinas, we sampled around the port

entrance (< 300 m from the mouth). For each marina, we randomly selected 3 pontoon Biohut. In the marinas located in the east region, we also sampled 3 dock Biohut for comparing port habitats. There were no dock Biohut of similar characteristics in the west region. This dataset, restrained to the east region, was referred hereafter as "A 2021 reduced" database (Table S2).

During sampling, each Biohut was covered with a 0.5 mm mesh net to avoid loss of material and brought to the surface. After removing the oyster shells from the cage, the large invertebrates were identified, counted and released alive. Remaining organisms were fixed in 70% alcohol and brought to the laboratory for identification. In the laboratory, organisms were sorted and identified to the taxonomic levels of family or species, when possible, using a binocular magnifier and a microscope. Collected data were collated into a database referred hereafter as "A 2021" database (Table S3).

2.3.2. Data extraction from the ECOCEAN archives

The initial ECOCEAN database was built from post-installation monitoring efforts and included information gathered from 72 harbours and marinas sampled from 2013 to 2022, totalling 654 Biohut. We extracted from this database all information regarding invertebrate abundance from dock and pontoon Biohut installed in French Mediterranean ports across the east and west region. The ECOCEAN monitoring protocol consisted in sampling different ports during different seasons and years and there were instances when Biohut were not replicated within ports. Sometimes, their immersion time also varied. Hence, data underwent additional refinement in order to have subsets of data with replicated Biohut of similar type of installation and immersion time, sampled during the same season. To do that, data were separated into an autumn (A) and a spring (S) dataset. The autumn database comprised data sampled during autumn 2013 (from September 23rd to November 14th) from 2 ports per region and a total of 48 Biohut with a comparable immersion time, ranging between 183 and 203 days (hereafter as "A 2013" dataset; Table S3). However, in the west region there were 21 pontoon and 3 dock Biohut across the 2 ports whereas in the east region, the 2 ports had 3 pontoon and 21 dock Biohut (Table S2). We kept this imbalance between the port habitats (pontoon vs. dock Biohut) to ensure a high number of replicated Biohut per port when comparing assemblages among regions. However, in order to compare dock and pontoon Biohut, we extracted data where replicated pontoon and dock

Biohut were present in the same port. The dataset included 1 port per region with 3 dock and 3 pontoon Biohut (hereafter "A 2013 reduced" dataset; Tables S2, S4).

The spring dataset included only pontoon Biohut sampled from 16th April 2019 to 10th June 2022 from 5 ports per region (hereafter S 2019-2022 database; Table S3) with a number of replicated pontoon Biohut ranging between 2 and 3 (Table S2). However, the immersion time was variable between Biohut, ranging from 334 to 735 days.

For all datasets extracted from the ECOCEAN database, the taxonomic resolution was at the levels of family or higher (Tables S3, S4).

2.4. Statistical Analyses

Data were analysed using the software Primer V7 with PERMANOVA+ (Anderson *et al.*, 2008; Clarke *et al.*, 2014). Differences between regions and between pontoon and dock Biohut were tested using permutational analysis of variance (PERMANOVA) for each dataset separately. For differences among regions, we used Region (fixed) and Port (random) nested in Region as factors and chlorophyll-a concentration as a covariate. Port habitat (i.e. dock and pontoon Biohut) was also included as a random factor for the A 2013 dataset and immersion time for the S 2019-2022 dataset. For the differences between port habitat, we used Port (fixed) and Port habitat (fixed) as factors for the A 2013 and A 2021 reduced dataset. *A posteriori* pairwise comparisons were done when there was a significant interaction term. Distance-based multivariate multiple regression (DistLM) analysis was also run between the biological data and chlorophyll-a concentration.

Analyses were run on species composition, total number of taxa and individuals and on the abundance of dominant taxa. When PERMANOVA test on species composition identified significant difference among regions, port habitats or their interaction with ports, we identified the taxa responsible for these differences fitting their abundance with the nMDS axes with Pearson correlation and using the Similarity percentage analysis (SIMPER). The resulting taxa, if different from the dominant ones were also analysed.

Before running the PERMANOVA analyses, the homogeneity of residuals was tested using a PERMDISP test. If the test resulted in significant differences in dispersion, data were 4^{th} root transformed. Univariate analyses were run on Euclidean distance resemblance matrices

and multivariate analyses on Bray-Curtis dissimilarity matrices. The differences in assemblages were visualised with nMDS ordination plots.

3. RESULTS

In autumn 2021 we collected and identified a total of 26,487 organisms (Tables S3, S4) including 10,581 animals to the species level (70 species), 1,450 to the level of genus (10 genera) and 14,440 to the level of family (39 families). Remaining 16 organisms were identified to the level of order (Pantopoda).

The A 2013 database included 3,856 individuals identified to the family level (44 families), 59 to the level of order (Isopoda and Ophiurida) and 2 to the level of class (Polychaeta), whereas the S 2019-2022 database includes 1,909 individuals to the level of family (30 families), 142 to the class level (Bivalvia and Polychaeta), 61 to the order level (Amphipoda, Decapoda and Ophiurida) and 34 to the level of phylum (Annelida and Platyhelminthes; Table S3). Moreover, the A 2013 reduced dataset contains 957 individuals identified in 22 distinct family levels and 1 individual identified to the level of order (Isopoda; Table S4).

3.1. Differences among regions

The taxa composition of benthic assemblages and the total number of individuals did not vary among regions (Figure S1), but there was large variability among ports, especially for the taxa composition (Table 1a-b). DistLM analysis showed a significant regression between taxa composition of invertebrate assemblages and chlorophyll-a concentration, which significantly explained 7.97 % (A 2013), 11.57 % (S 2019-2022) and 28.57 % (A 2021) of the variation in benthic assemblages among ports (Figure 3a; Table S5). The total number of taxonomic groups significantly varied between the 2 regions in the A 2021 database (Table 1c), when a highest taxonomic resolution was used. More taxa were found in the west region (Figure 3b). Although no significant differences were found, the two other databases exhibited a similar trend (Table 1c; Figure 3b).

*Table 1. Results from PERMANOVA analysis for differences among regions in (a) the composition of taxa; (b) the total number of individuals and (c) the number of taxonomic groups for the 3 databases analysed. * p < 0.05; ** p < 0.01; ^ pooling when p > 0.25.*

		(a) Taxa composition		(b) N individuals		(c) N taxa	
A 2021 Pontoon	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
[Chl a]	1	4601.4	1.716	0.320	0.450	0.058	2.223
Region = Re	1	3423.1	1.277	0.304	0.427	0.168	6.392*
Port (Re)	1	2681.5	3.974**	0.712	3.476	0.011	0.375^
Residuals	8	674.76		0.205		0.028	
AW 2013	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
[Chl a]	1	9915.4	0.637	0.301	0.113	0.043	2.122
Port habitat	1	5814.3	0.689	2.519	1.694	0.033	1.630
Region = Re	1	9647.3	1.007	1.611	0.954	0.044	2.137
Port (Re)	1	15149	7.769**	2.672	7.839**	0.001	0.046^
Residuals	43	1949.9		0.341		0.021	
SS 2019-2022	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
[Chl a]	1	5405.5	0.97	0.536	0.793	0.09	0.781
Immersion time	1	7700.2	1.405	0.08	0.214	0.001	0.04
Region = Re	1	4681.2	0.836	0.052	0.193	0.055	0.49
Port (Re)	7	4456.8	6.176**	0.615	1.866	0.092	6.836***
Residuals	15	721.62		0.33		0.014	

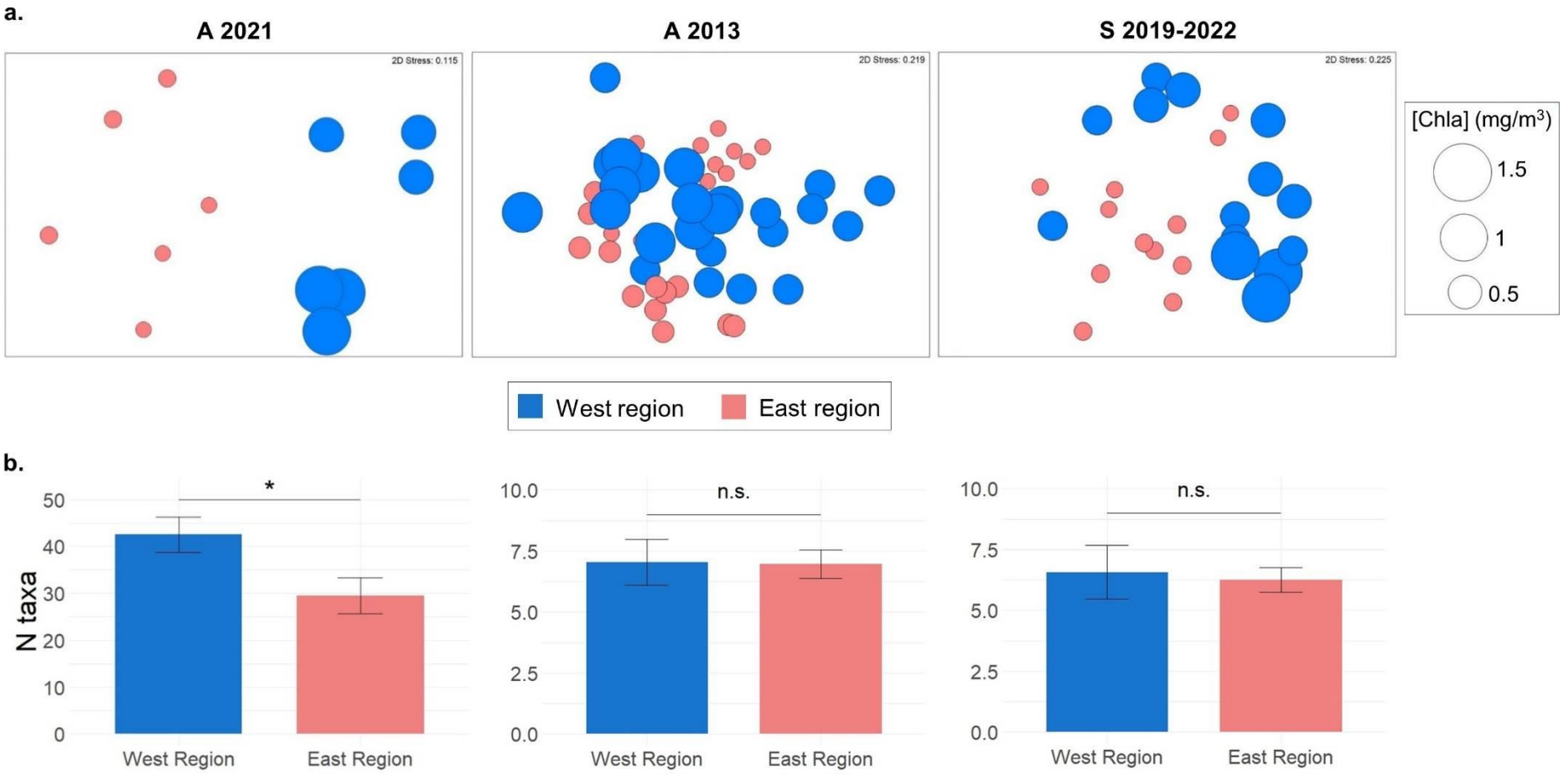


*Figure 3. (a) Non-metric multidimensional scaling ordination (nMDS) plot for the taxonomic composition of invertebrate assemblages and (b) mean (± SE) of number of taxa per region for the 3 datasets analysed (A 2021 (n = 6), A 2013 (n = 24) and S 2019-2022 (West: n = 14; East: n = 12)). n.s. = not significant; * * = p < 0.05. In the nMDS plots the size of the bubbles is proportional to the concentration of chlorophyll a ([Chl a]).*

In the 3 databases, assemblages were dominated by 7 or 8 taxa that made up 70% of total abundance. In the A 2021 database, among the 8 most numerically abundant taxa there were 3 families of amphipods (Melitidae, Corophiidae and Gammaridae), the polychate *Nereis* sp. and the ascidian family Asciididae, which were not dominant in any other database. Remaining 3 taxa were the decapod shrimp *Palaemon serratus*, whose corresponding family level (Palaemonidae) was also abundant in the other databases, the porcellanid crab *Pisidia bluteli*, found at the family level (Porcellanidae) in S 2019-2022, and the mussel *Mytilus galloprovincialis*, found at the level of family (Mytilidae) in A 2013. The family of the bivalve Pectinidae characterised both A 2013 and S 2019-2022 assemblages, whereas 4 families were typical of A 2013 (the echinoderm: Ophiopsilidae, Ophiotrichidae and Ophiodermatidae, and the gastropod: Columbellidae) and 4 other families of S 2019-2022 (the polychate Terebellidae, the decapod Alpheidae and Grapsidae, and the bivalve Limidae). The order Polychaeta was also abundant in S 2019-2022. Four of these taxa were only present in the west region (Ophiopsilidae, Ophiotrichidae and Ophiodermatidae in A 2013; Limidae in S 2019-2022; Table S3). The remaining taxa were further analysed to test differences among regions. Significant differences between regions were found for *P. bluteli* in A 2021 and for Mytilidae in A 2013 (Table S6) where both taxa were more abundant in the west region (Table S3).

Moreover, immersion time explained part of the variability in the abundance of Polychaeta in S 2019-2022 (Table S6). Port habitat (pontoon and dock Biohut) was significant for the abundance of Mytilidae in the A 2013 dataset (Table S6), which included an imbalanced number of dock and pontoon Biohut among regions (Table S2). The specific effect of port habitat was investigated on the reduced dataset, as shown below (see also Data extraction from the ECOCEAN archives for more details).

3.2. Differences between port habitats (Pontoon vs. Dock Biohut)

In the region situated east of the Rhone River, sampled in autumn 2021 (A 2021 reduced dataset), the taxa composition of the benthic assemblages colonising the Biohut significantly differed in the interaction term Port x Port habitat (Table 2a). The *a posteriori* pairwise test showed that there were differences among the assemblages that had colonised the Biohut attached to the docks (dock Biohut) and those suspended under the pontoons

(pontoon Biohut) in both the ports analysed (Table 2b). The nMDS plot showed a clear separation between pontoon and dock Biohut along the horizontal axis (Figure 4a). The analysis of the data extracted for autumn 2013 for the 2 ports, where replicated Biohut of each port habitat were present (reduced A 2013 dataset), showed differences in taxa composition between dock and pontoon Biohut only in the port located in the east region (Le Brusc port; Table 2; Figure 4a).

Table 2. (a) Results from PERMANOVA analysis on the composition of taxa, the total number of individuals and of taxa for differences among dock and pontoon Biohut in each port on the A 2021 and AW 2013 reduced databases. (b) Pairwise test for differences among dock and pontoon Biohut in each port when interaction term was p < 0.05. For pairwise tests we used Monte Carlo permutations because only 10 permutations were possible.
** p < 0.05; ** p-value < 0.01; ^ pooling at p > 0.25.*

a.		**Taxa composition**		**N individuals**		**N taxa**	
A 2021 reduced	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Port	1	3528.2	5.282**	1.084	3.275	0.031	1.191
Port habitat = PH	1	5144.1	7.701**	1.973	5.958	0.043	1.637
Port x PH	1	2729.4	4.086**	5.246	15.842**	0.092	3.491
Residuals	8	667.99		0.331		0.026	
A 2013 reduced	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
Port	1	3992.7	2.929*	0.119	0.508	0.025	1.776
Port habitat = PH	1	992.5	0.728	0.003	0.013	0.001	0.004
Port x PH	1	7552.7	5.54**	0.008	0.031^	0.003	0.192^
Residuals	8	1363.4		0.263		0.015	

b.	**Database**		**t**	
Taxa composition	**A 2021 reduced**	CPC	2.441*	
		SPE	2.411*	
	A 2013 reduced	AGD	1.317	
		BRU	2.324*	
N individuals	**A 2021 reduced**	CPC	6.229*	Pontoon > Dock
		SPE	0.898	

The numbers of individuals and taxa were comparable among dock and pontoon Biohut for both databases analysed, except for one of the ports sampled in autumn 2021, when more individuals were found on the pontoon than the dock Biohut (significant interaction term in Table 2; Figure 4b, S2).

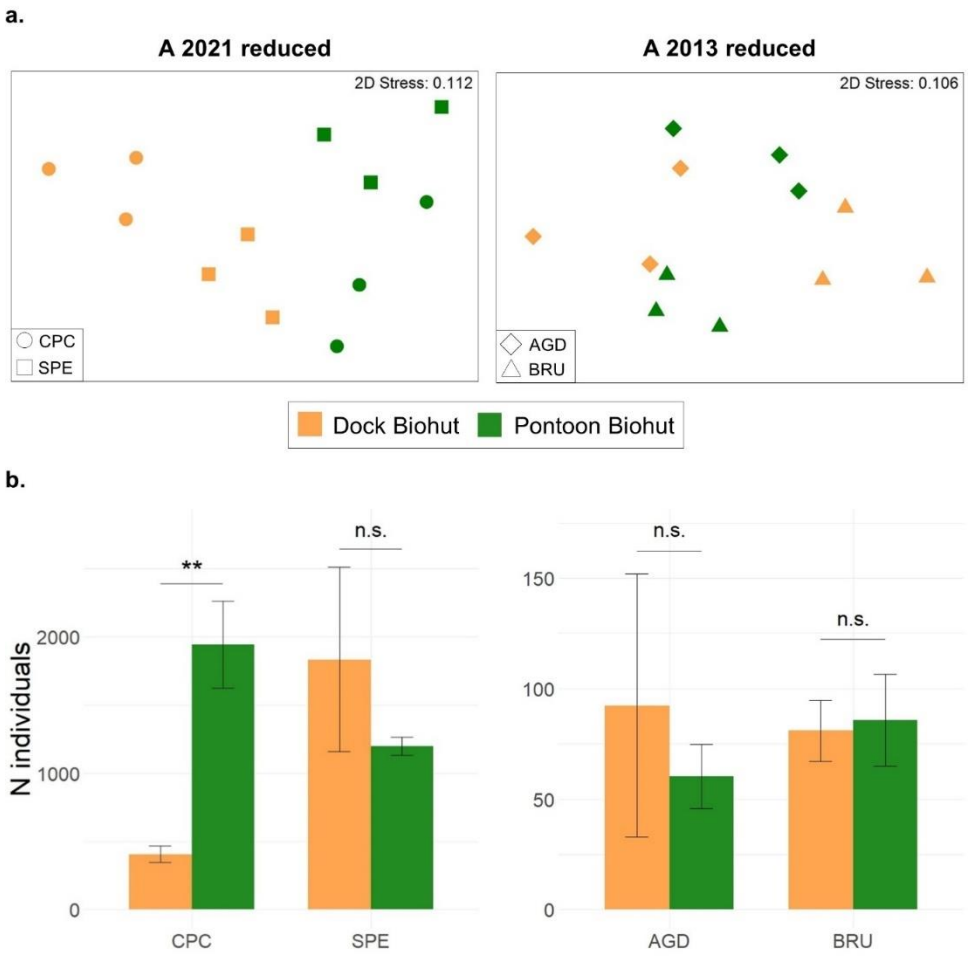


Figure 4. (a) Non-metric multidimensional scaling ordination (nMDS) plot for the taxonomic composition of invertebrate assemblages and (b) mean (± SE, n = 3) of number of individuals within sampled Biohut in habitat (Dock and Pontoon Biohut) and ports. CPC, SPE, AGD and BRU are port code names, see Figure 1 for full names and location.
*n.s. = not significant; ** = p < 0.01.*

In the A 2021 reduced database, 8 out of 90 identified taxa made up 75% of the total abundance. These taxa included 3 amphipod families (Melitidae, Corophiidae and Lysianassidae), the polychate *Nereis* sp., the decapod shrimp *Athanas nitescens*, the ascidian family Asciididae, the isopod family Anthuridae and the mussel *Mytilus galloprovincialis*. Lysianassidae were only present on dock Biohut (Table S4). Other 7 taxa contributed to differences in assemblages between pontoon and dock Biohut (the amphipod Gammaridae, the gastropods *Tritia nitida*, *T. mutabilis* and *Bittium* sp., the decapod shrimp *Alpheus dentipes*, the porcellanid crab *Pisidia bluteli* and the polychate *Platynereis* sp.;

SIMPER analysis and Pearson correlation). Four of these taxa were only present in the dock Biohut (*T. nitida*, *T. mutabilis*, *Bittium* sp. and *A. dentipes*), while Gammaridae were found only on the pontoon Biohut (Table S4). The remaining 2 taxa (*P. bluteli* and *Platynereis* sp.) and the numerically dominant taxa (except Lysianassidae) were further analysed. The PERMANOVA results showed significant differences in the interaction term Port x Port habitat for 4 taxa (Melitidae, Corophiidae, Ascidiidae and *M. galloprovincialis)* and 3 of them showed some differences between pontoon and dock Biohut in one of the ports (Table S7). Melitidae and Ascidiidae were sometimes more abundant on pontoon Biohut, whereas *M. galloprovincialis* on dock Biohut (Figure 5a-c; pairwise *a posteriori* test in Table S7b). Other 3 taxa (*Nereis* sp., *Platynereis* sp. and *P. bluteli*) showed differences between pontoon and dock Biohut consistently among ports (Table S7a). *Pisidia bluteli* was significantly more abundant in dock than pontoon Biohut, whereas the other 2 taxa were most abundant on pontoon Biohut (Figure 5d-f).

In the reduced A 2013 database, 2 out of the 23 taxa identified represented 75% of the total abundance (the shrimp Palaemonidae and the gastropod Columbellidae). Other 4 families (bivalve Cardiidae, and the crabs Grapsidae, Carcinidae and Eriphiidae) were identified as contributing the most to differences in assemblage composition between pontoon and dock Biohut (SIMPER analysis and Pearson correlation). The PERMANOVA results for these taxa showed significant differences in the interaction term Port x Port habitat for the abundance of 2 of these families (Columbellidae and Grapsidae; Table S8a). *A posteriori* test revealed that these taxa differed among Port habitat only in one port, situated in the east region (port of Le Brusc), where Columbellidae were more abundant on the dock Biohut and Grapsidae on the pontoon Biohut (Figure 5g-h; Table S8b).

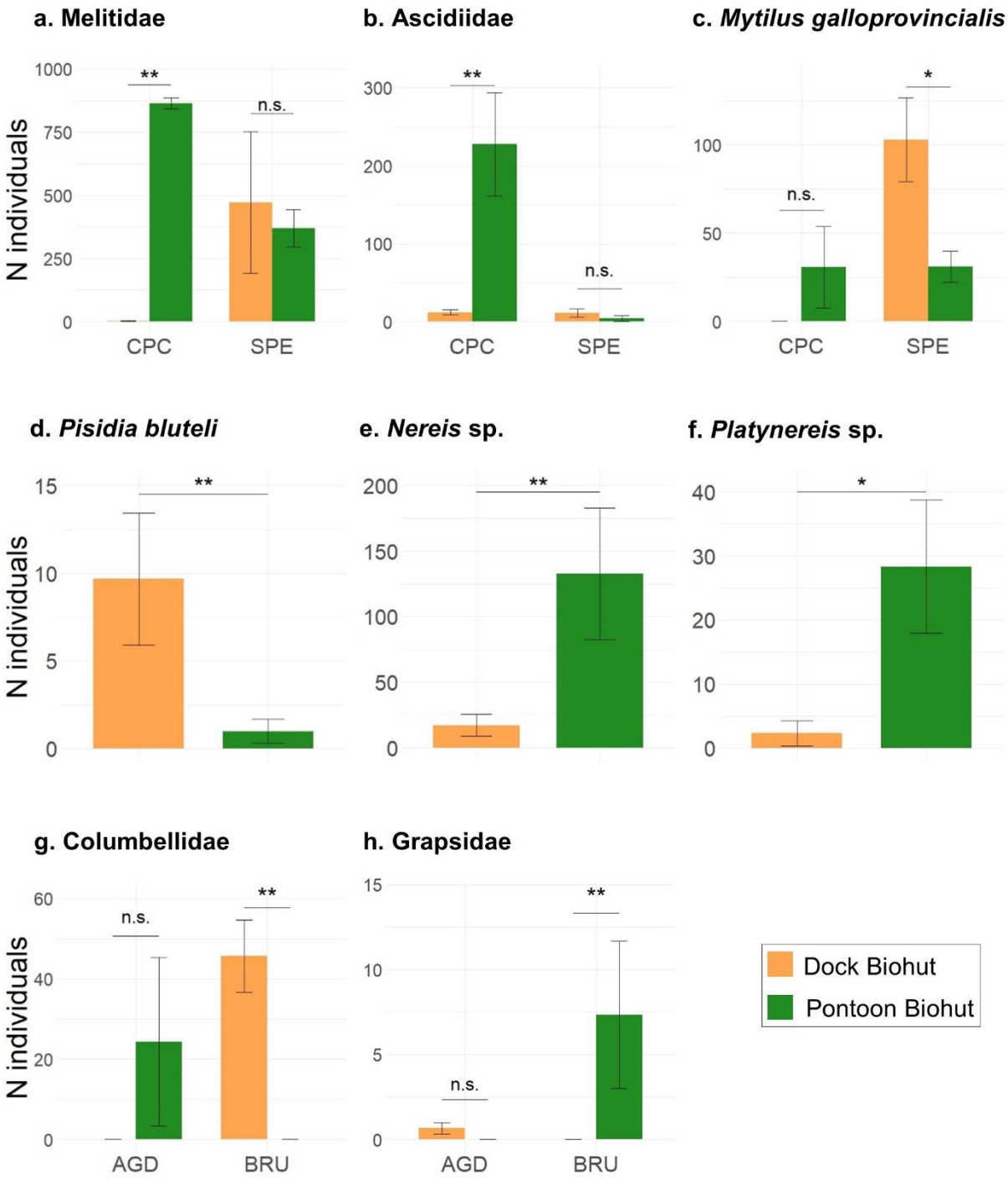


*Figure 5. Mean number of individuals (± SE) for the taxa analysed. (a-f) A 2021 and (g-h) A 2013 reduced databases. CPC, SPE, AGD and BRU are port code names, see Figure 1 for full names and location. n.s. = not significant; * = p < 0.05; ** = p < 0.01*

4. DISCUSSION

The present study analysed 3 spatial scales of variability (among regions, among and within ports) of the invertebrate assemblages dwelling in a specific type of artificial fish habitats made of oyster shells (Biohut® structures described in the material and method section and depicted in Figure 2).

We expected differences among the regions situated to the west and the east of the large delta of the Rhone river (French Mediterranean coast), because these regions have very different environmental conditions, including the supply of nutrients, as illustrated in the material and Methods section and shown in several studies (Agostini and Bakun, 2002; Cruzado and Velasquez, 1990; Lefevre *et al.*, 1997; Lochet and Leveau, 1990; Millot, 1999). Previous studies conducted in natural coastlines have shown a marked difference in macrofauna and fish species according to the environmental differences created by the Rhone river, including the nutrient supply (Bonifácio *et al.*, 2014; Harmelin, 2009; Hermand *et al.*, 2008; Labrune *et al.*, 2012; Salen-Picard *et al.*, 2003; Salen-Picard and Arlhac, 2002). Our study is the first one to have documented a variation in benthic assemblages on artificial fish habitats in the same area.

Although assemblage composition and abundance were found to not vary significantly, taxonomic diversity was highest in the west, most-enriched region, particularly during autumn 2021. Other studies focusing on benthic colonisation of artificial habitats have shown the important role of nutrient supply (Canning-Clode *et al.*, 2008; Jimenez *et al.*, 2017). In particular, Jimenez *et al.* (2017) found differences in benthic assemblages on different shipwrecks exposed to different regimes of temperature and nutrient supply. They found less biodiverse communities under high nutrient supply and suggested that epibenthic communities could be highly impacted by eutrophication caused by anthropogenic activities. Canning-Clode *et al.* (2008) found that fertilization enhanced fouling community diversity on PVC tiles in an oligotrophic system. In our study, not only the regional differences in diversity, but also other findings suggested that nutrient supply could play an important role in structuring benthic assemblages on artificial fish habitats, especially during the autumn sampling campaigns. For instance, the composition of benthic assemblages was partly explained by the differences in seawater chlorophyll-a concentrations (up to 28 % in autumn 2021), which is considered a proxy for nutrient load (Behrenfeld and Falkowski, 1997; Cloern, 1999). Filter feeding taxa, which can benefit from the availability of nutrients in the seawater (Cranford *et al.*, 2011; Hamann and Blanke, 2022; Nicol, 1932; Rubenstein and Koehl, 1977), were among the dominant taxa in the west region and their abundance sometimes correlated with the chlorophyll-a. In particular, the filter feeding crab *Pisidia bluteli* and several families including suspension feeding species (Mytilidae, Ophiopsilidae, Ophiotrichidae and Ophiodermatidae), were almost exclusively found in the west region in autumn 2021 or in 2013 (A 2021 and A 2013

datasets). Furthermore, in autumn 2021, chlorophyll-a significantly explained part of the variability in the abundance of both the crab *P. bluteli*, and the bivalve *Mytilus galloprovincialis.*

In addition to the correlation with chlorophyll-a, we found large variability in taxa composition among ports. This local scale variability is coherent with other studies focusing on invertebrate assemblages colonising man-made structures (Osman, 2015; Simpson *et al.*, 2017). The differences have been explained according to the local availability of species e.g. ecological concept of species pool (Cornell and Harrison, 2014; Shen *et al.*, 2017), as well as by local variations of environmental variables, such as water quality (Kenworthy *et al.*, 2018; Schiff *et al.*, 2007; Toh *et al.*, 2017; Valdor *et al.*, 2019), hydrodynamics (Martin *et al.*, 2005; Nowell and Jumars, 1984) or local anthropogenic activities (Dafforn *et al.*, 2011; Voudrias and Smith, 1986). In our case, these differences could also partly depend on local changes in the nutrient concentration as discussed above.

The subset of data available to test whether the port habitat where the Biohut were placed could regulate invertebrate assemblage composition revealed distinct taxa and assemblages between pontoon and dock Biohut in the ports located on the east, oligotrophic region. One of the possible explanations, could be the differences in light availability. The shadow provided by the floating pontoons, under which the habitats are suspended, reduce the availability of light (Gauff *et al.*, 2023; Lam and Todd, 2013). Shadowing regulates photosynthetic communities, suggesting that we should expect a higher abundance of primary producers on dock Biohut than on pontoon Biohut. Previous observations reported several individuals of the herbivorous fish *Sarpa salpa* feeding on dock Biohut within one of the ports examined in our study (SPE in Figure 1; Couvray *et al.*, 2021). Their voracious feeding behaviour might be the cause of the low macroalgal biomass, but also suggests a greater availability of macroalgae on dock Biohut compared to pontoon Biohut. In addition, on dock Biohut, 4 gastropods taxa (Columbellidae, *Tritia nitida*, *T. mutabilis* and *Bittium* sp.) were among the dominant taxa and frequently found only on these Biohut. These gastropods are micrograzers that can feed on the photosynthetic biofilm growing not only on the metal frame, but also on the oyster shells. Unfortunately, in our study we did not include sampling of macro- or microalgae, since ECOCEAN monitoring program did not include them and during autumn 2021 sampling macroalgal biomass was extremely low, but these observations on herbivores might indicate that dock Biohut may favour primary

production**.** Furthermore, beneath pontoons, both daytime shadowing and artificial light at night have been found to alter fish predation as well as their benthic preys (Bolton *et al.*, 2017). Predation is in fact an ecological process largely affected by light (Cerri, 1983; Czarnecka *et al.*, 2019; Emery, 1973; Hobson, 1979; Rick and Bakker, 2008).

The different communities on dock and pontoon Biohut might also be regulated by differences in the surroundings. The presence of gastropods on dock Biohut might be due to the connection of dock Biohut to the seawall that increases substrate availability and facilitates the movement of crawling species. Pontoon Biohut are, instead, most exposed to waterflow and might enhance larval supply and the recruitment of benthic species with planktonic larvae or of swimming adult species (Breitburg *et al.*, 1995; Koehl, 2007; Leonard *et al.*, 1998; Palardy and Witman, 2011; Powers and Grabowski, 2023; Toh *et al.*, 2017).

The differences among regions were most evident in autumn 2021 when data were collected using a different sampling effort. We reduced the mesh size from 2 to 0.5 mm to collect all macrofauna and examined the samples in the laboratory. Previous campaigns sorted and identified specimens mainly *in situ*. In particular, amphipods (Melitidae, Gammaridae, Corophiidae) were found numerically dominating the assemblage. There were also more individuals of other crustaceans, such as decapods, and overall, more taxa than in the other databases. Amphipods are known to have the ability to rapidly colonise disturbed benthic areas, allowing predators such as fish or other invertebrates to better settle back to perturbed areas (Bonsdorff and Blomqvist, 1993; De la Ossa-Carretero *et al.*, 2016; DeWitt, 1987) and are a crucial link between primary, secondary production, and higher trophic levels, playing a key role in energy flow through food webs (Conlan, 1994; Duffy and Hay, 1991; Marques and Bellan-Santini, 1993; Ritter and Bourne, 2024). In artificial fish habitats, they may represent an important food source for settling fishes and should be monitored.

5. CONCLUSION

In summary, we observed differences in the diversity of invertebrates dwelling in the artificial fish habitats known as Biohut across ports located along a longitudinal gradient marked by differences in seawater nutrient availability. We also identified local-scale differences in taxa composition within ports, influenced by the specific port habitats where

Biohut is deployed. These differences might be attributed to variations in light condition and proximity to other artificial substrates.

The findings of our study can have implications for the management and ecological monitoring of artificial fish habitats in ports and marinas as invertebrates not only serve as food for settling fishes but also provide other important biological cues. For instance, the shrimp *Alpheus dentipes* on pontoon Biohut is also known as snapping shrimp because of the intensity acoustic signal it does using its claws (Versluis *et al.*, 2000) and its sound can affect larval settlement (Lillis *et al.*, 2013; Montgomery *et al.*, 2006; Simpson *et al.*, 2004). We therefore suggest that the effectiveness of these artificial fish habitats could be increased by considering environmental conditions such as seawater characteristics or light availability. A particular care should also be given to the monitoring of these structures, by including the sampling of small invertebrates and primary producers (macroalgae and biofilm), which are at the base of the food web. Although costly and time consuming, investigating the entire food web from end-to-end, might prove important in understanding and predicting the potential benefits of these eco-engineered solutions for coastal restoration.

CHAPTER 3: ARTIFICIAL FISH HABITATS AND TROPHIC CONNECTIVITY BETWEEN MARINAS AND ADJACENT NATURAL ECOSYSTEMS

ABSTRACT

Cross-habitat exchanges of organic matter may play an important role in the functioning of coastal food webs. Information on trophic connectivity between *Posidonia oceanica* meadows and adjacent man-made habitats such as marinas is poorly understood. We explored how marinas could export organic material to the seagrass meadow using stable isotopes. We also asked how artificial fish habitats (AFH) could modify this subsidy. We sampled 4 sites that included a seagrass meadow adjacent to a marina equipped or unequipped with AFH along the Northern-Western Mediterranean Sea. We specifically asked if the proximity to the port could change the health of *P. oceanica* and investigated the differences in isotopic composition of primary producers and detritus from the marina and the seagrass meadow. We then focused on an important and abundant fish genus (*Diplodus*) and investigated where individuals fed and how their faeces contributed to organic matter sedimenting within *Posidonia*. At the unequipped sites, the $\delta^{15}N$ signature of the particulate organic matter (POM), which is an indicator of organic pollution, was highest within the marina and gradually decreased within the seagrass along with the distance from the marina inlet. There was thus a possible spill of nutrients over the seagrass in unequipped ports. Moreover, at the equipped site, fish isotopic niches within the marina and seagrass overlapped less than at the unequipped sites, probably because AFH provided more food. However, there was no evidence of differences between sites in fish faeces contribution to the organic matter sedimenting within the meadow.

1. INTRODUCTION

Coastal marine ecosystems are among the most productive areas in the world. They provide habitats and food for a wide range of organisms, including benthic invertebrates and fish species at different stages of development (Beck *et al.*, 2001; Dahlgren *et al.*, 2006; Seitz *et al.*, 2014; Stoner, 2003). Coastal development replaces natural habitats with man-made structures, which propagate to a series of effects that strongly modify biodiversity, ecosystem functioning and services (Airoldi and Bulleri, 2011; Bulleri and Chapman, 2010; Chapman and Underwood, 2011; Hinkel *et al.*, 2014).

Coastal development also creates a mosaic of natural and artificial substrates across the coastal seascape that can modify ecological connectivity (Bishop *et al.*, 2017; Dafforn *et al.*, 2015; Firth *et al.*, 2014; Perkins *et al.*, 2015). The term “connectivity” was first defined

in relation to environmental science in 1984 (Hillman *et al.*, 2018; Merriam, 1984). Today the term encompasses a variety of fluxes in nature such as the exchange of genes, propagules, larvae, sub-adult, and adult organisms (i.e. population connectivity), or the exchange of energy and nutrients (trophic connectivity). Trophic interactions are common among habitats because the nutrients, detritus, prey and consumers often cross habitat boundaries (Polis and Strong, 1996). Cross-habitat exchanges of materials can be of great importance to effective natural source dynamics both within and between ecosystems (Polis *et al.*, 1997).

Both ports and marinas are extreme examples of coastal development. The natural sandy or rocky shores are replaced with concrete, wood, plastic or steel structures such as docks and pontoons and man-made seawalls, whereas breakwaters and dikes made of concrete, riprap or large boulders are used to protect them from the open sea. These artificial habitats are often colonised by non-native, sometimes invasive species (Airoldi et al., 2015; Bulleri et al., 2006; Bulleri and Airoldi, 2005; Dafforn et al., 2012, 2009; Glasby et al., 2007; Simkanin et al., 2012). Moreover, coastal fishes can be displaced because they are deprived of the habitats where they spend a part of their life-cycle hiding and feeding, such as natural hard and soft substrates, and the habitat-forming species they support (e.g. seagrass meadows; Cheminée *et al.*, 2021, 2017; Johnson, 2007).

Ports and marinas are interspersed with natural shorelines over the coastal seascape and information on the trophic exchange between these areas and adjacent habitats could bring important insights for defining rehabilitation strategies of harbours and marinas and improving restoration in an urban context. Nowadays, the interaction between processes and landscape features is increasingly recognised as an integral aspect of resource management plans (Calabrese and Fagan, 2004).

In an extremely developed area, restoration to natural conditions is impossible, but the functioning might be ameliorated with effective management, based on ecological knowledge. Ecological engineering solutions can be used to improve the biodiversity and ecological functioning in highly modified coastal habitats where man-made structures are dominant (Airoldi et al., 2021, 2005; Bilkovic and Mitchell, 2013; Bishop et al., 2022; Browne and Chapman, 2014; Chapman and Underwood, 2011; Firth et al., 2016a; Morris et al., 2019, 2018; Strain et al., 2021). Artificial fish habitats (AFH) are an example of these solutions and they are used to provide a new habitat to coastal fish species in harbours and

marinas. They are designed to increase the survival rate of early-life stages by providing shelter against predators (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b). As a side effect, AFH are colonised by a range of benthic invertebrates, including non-native species, that modify diversity and increase invertebrate biomass within ports (Gauff *et al.*, 2023; Varenne *et al.*, 2023). These invertebrates may be additional resources of food for consumers occupying high trophic positions, such as invertivorous fishes, which are attracted by AFH. The benthic biomass, including the portion linked to the presence of AFH, may accumulate within the harbour or be washed away, thus providing additional organic matter to adjacent habitats. It can also enter the food web by providing food to fishes that may swim outside the port and facilitate the transport of carbon and nitrogen provided by the AFH to adjacent habitats. However, to our knowledge, such information is largely unknown.

In this paper, we have investigated the trophic exchanges between marinas and adjacent Neptune grass *Posidonia oceanica* meadows in the Mediterranean Sea. *P. oceanica* is endemic of the Mediterranean, where it forms extensive meadows and contributes to support biodiversity, coastal carbon and nutrients cycling and to protect sandy shores from erosion (Boudouresque *et al.*, 2012; Francour, 1997; Gacia and Duarte, 2001; Pergent *et al.*, 1994). This species is threatened by human activities and global change and several restoration measures have been taken so far (Barbier *et al.*, 2011; Borum *et al.*, 2004; Boudouresque *et al.*, 2012; Pergent *et al.*, 2012; Unsworth and Cullen-Unsworth, 2014). *P. oceanica* meadows are often present at the inlet and outside small marinas, and are particularly attractive for coastal species (Bell and Harmelin-Vivien, 1983; Bellan Santini *et al.*, 1994; Boudouresque *et al.*, 2012).

We used stable isotope analysis (SIA) to investigate the trophic relations within and across each habitat (seagrass meadow and marina). Stable isotopes have been used to estimate trophic relationships (Fry, 2006; Michener and Kaufman, 2007; Peterson and Fry, 1987) and study trophic connectivity (e.g. Selleslagh *et al.*, 2015). Carbon stable isotopes (^{13}C) change predictably between diet and consumer, and have been used in ecological studies to trace the flow of sources of organic matter in marine and freshwater ecosystems (Fry and Sherr, 1989; Peterson and Fry, 1987). Nitrogen stable isotopes (^{15}N) can be used to define consumers' trophic position (TP), based on the pathways of energy flow (Post, 2002; Vander Zanden and Rasmussen, 1999).

We first asked if (1) the proximity to the port could change the health of *P. oceanica*. We then hypothesised that if there is a flow of material from the marina to the adjacent meadow, (2) the isotopic compositions of *Posidonia oceanica*, particulate and sedimentary organic matter (POM and SOM respectively) collected within the meadow would vary with the distance from the marina and would be similar to the values measured within the marina at closest distance; (3) the stomach content, isotopic composition and isotopic niches of fishes collected within the marina would be similar to those collected within the meadow, if they relied on the same pool of baseline resources from marinas or seagrass meadows. We focused on 3 fish species belonging to the Sparidae family, *Diplodus annularis*, *D. sargus* and *D. vulgaris*, that are common in marinas, in seagrass meadows and within AFH (Bell and Harmelin-Vivien, 1983; Bouchoucha *et al.*, 2016; Francour, 1997). These species also have a commercial interest for small-scale fishery (FAO, 2024). (4) Eventually, we explored the main food sources for fishes and how fishes could contribute to the organic pool of the sedimentary organic matter within the meadow. We expected that for all hypotheses there would be differences between sites where marinas were equipped with AFH and those unequipped.

2. MATERIAL AND METHODS

2.1. Study sites and sampling design

We sampled along the French coast of the North-Western Mediterranean Sea, where *P. oceanica* is widespread and several marinas have been recently equipped with a particular type of AFH registered under the name Biohut® (ECOCEAN, France; www.ecocean.fr). The study was conducted at 4 sites within an area of 40 km in the North-Western Mediterranean Sea (Figure 1a). Each site was composed of a marina and an adjacent *P. oceanica* meadow.

Two marinas had been equipped with AFH for more than 18 months, while the remaining 2 were unequipped and considered as control. All marinas had comparable size (< 10 ha), vessel moorings (> 200) and a depth ranging from 2 m to 4 m. The adjacent *P. oceanica* meadows were continuous, at similar depths (5-10 m) and had sandy substrates interspersed with rocky shores. In each of the 4 sites we sampled within the marina (hereafter D0), in different port habitats (docks, under pontoons, dikes and within the artificial fish habitats

where present) as well as in the *Posidonia* meadow, immediately outside the marina inlet (300 m; hereafter D1) and 1 km from the port inlet (hereafter D2).

The sampling took place during the first week of October 2022. Within the *Posidonia* meadow, we sampled seagrass leaves and both particulate and sedimentary organic matter (POM and SOM, respectively) at D1 and D2. The POM was sampled using the mussel *Mytilus galloprovincialis* as a proxy, as this species is a well-known suspension feeder (Ceccherelli and Rossi, 1984; Hentschel and Shimeta, 2008). The mussels were collected in Saint Mandrier-sur-Mer, France (43.0830° N, 5.9052° E), a locality close to the study sites. On 11th July, 2022, 5 cages of 20 individuals of *M. galloprovincialis*, were immersed at each distance (D1, D2), and attached to a steel bar above the *P. oceanica* meadows a few metres apart (Figure 1b). The SOM was collected using sediment traps attached to the same steel bars as for the mussel cages, yet placed at the opposite side to avoid collecting potential sediments falling from the cage (Figure 1b). Sediment traps were added to the steel bars on 7th and 8th September, 2022.

During the sampling week of October 2022, we collected both mussels and sediment traps. We collected 5 shoots of *Posidonia oceanica* (POS hereafter), 2 cores (10 cm diameter) of dead leaves (POS DL) and measured the canopy height and shoot density using 50 cm x 50 cm quadrats in proximity to each steel bar. Inside the marinas (D0), POM was sampled using mussel cages suspended under randomly selected floating pontoons, 1 m below the water surface due to restrictions imposed by the port authority, which prohibited the use of steel bars. The sedimentary organic matter was not collected using sediment traps, but by sampling the sediment surface (hereafter SED) because of the same port authority restrictions. In marinas, we also sampled for most spread macroalgae from different port habitats.

From 25th October 2022 and 30th November, 2022, we conducted experimental fishing campaigns to sample fishes both inside (D0) and outside (between D1 and D2) the marinas. We focused on sub-adults (< 200 mm), the most abundant during that period and within these coastal habitats. We could not distinguish among the 3 species of *Diplodus* during the experimental fishing and we collected different numbers of individuals per species and per site. The 3 species are known to have similar diet requirements (Bell and Harmelin-Vivien, 1983; Rosecchi, 1985; Sala and Ballesteros, 1997). We therefore consider the overall genus

for the analyses in order to have enough replication. Samples were stored in cool boxes with ice in the field and preserved frozen at -20°C in the laboratory until further analysis.

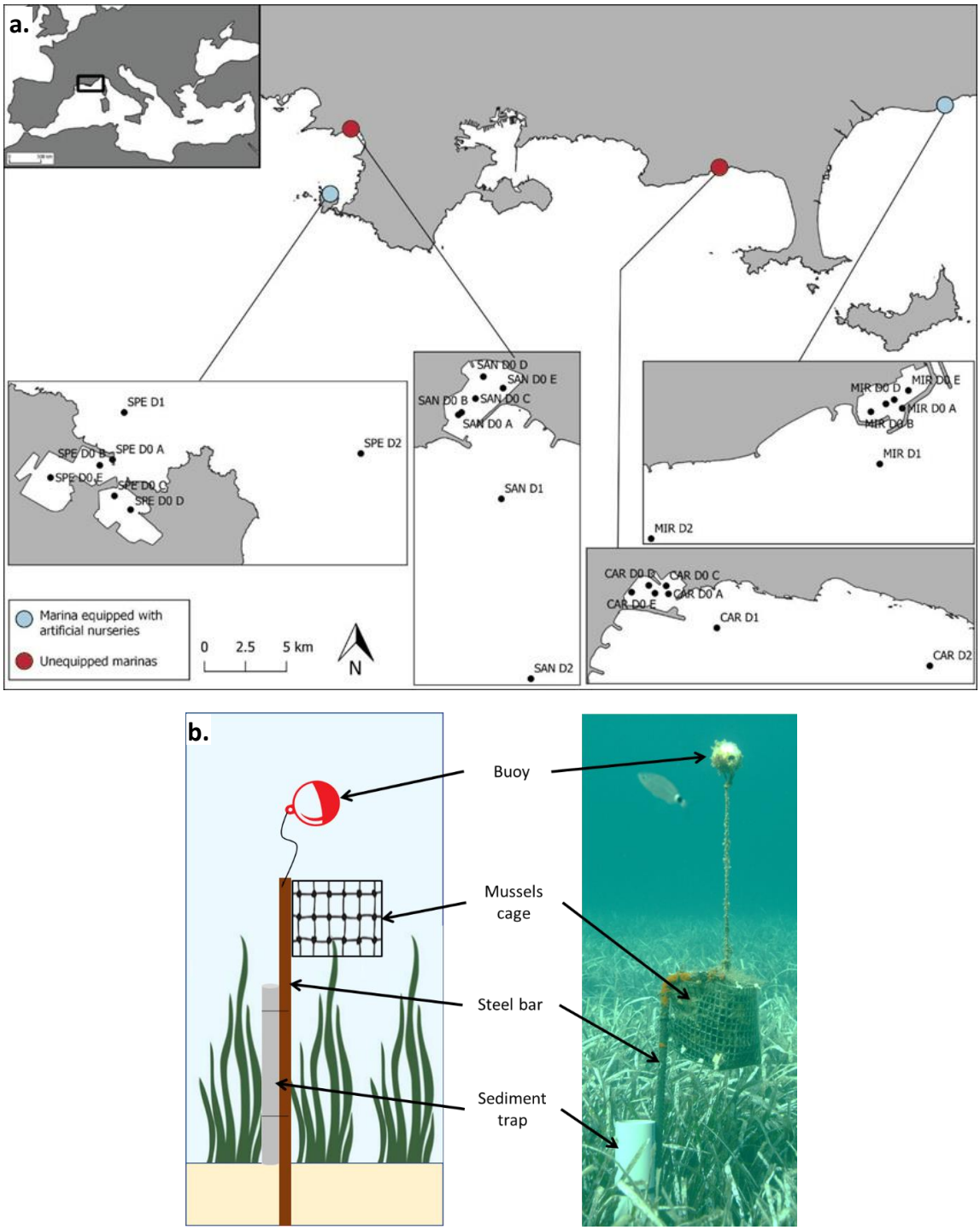


Figure 1. (a) Map of the 4 sites considered in the study and located in the Northwestern Mediterranean Sea (Var, France). Colours are used to differentiate the study sites equipped with artificial fish habitats deployed inside the marinas and the unequipped sites, (b) Illustration of a cage with Mytilus galloprovincialis and a sediment traps, both attached on either side of a same steel bar and placed above a Posidonia meadows canopy.

2.2. Laboratory data analysis

In the laboratory, each seagrass shoot was thawed and analysed for morphological traits. We counted the number of leaves, measured the length and the width of the longest and the shortest leaves and estimated the Leaf Area Index (LAI) by multiplying the mean area of these two leaves by the number of leaves per shoot and by the number of shoots per m^2. We then scraped the longest leaf of each shoot as well as 5 dead leaves using a microscope slide to collect the epiphytes. Each scraped *P. oceanica* leaf and the associated epiphytes were weighed separately as dry weight. The decomposition of the dead leaves was visually estimated and classified into 4 degradation categories from low to high (1-4).

The macroalgae collected in the marinas were thawed, sorted and identified in the laboratory. Macroalgae were grouped into Chlorophyta (GREEN), Phaeophyceae (BROWN) and Rhodophyta (RED). All samples including SOM, POM and macroalgae, as well as scraped leaves and epiphytes were further analysed for stable isotopes.

Each *Diplodus* specimen was thawed, weighed, and its standard length measured. Animals were then dissected for stomach content analyses. The white dorsal muscles and the intestinal contents were also extracted and freeze dried for stable isotope analysis. Fish stomach contents were rinsed with distilled water and identified to the lowest possible taxonomic level under a binocular microscope. Prey items were counted and grouped into 8 different taxa including 4 classes (Bivalvia, Gastropoda, Ostracoda and Polychaeta) and 4 orders (Amphipoda, Decapoda, Isopoda and Tanaidacea).

2.3. Stable isotope analysis

In the *Posidonia* meadows, we analysed the SOM, the POM (mussel tissues), the scraped *Posidonia* leaves and the epiphytes. In the marinas, we analysed the SED, the POM, the macroalgae. All samples were grinded using mortar and pestle and stored at -20°C until analysis. The natural abundances of stable isotopes ratio of carbon ($^{13}C/^{12}C$, expressed as $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) were measured using an isotope ratio mass spectrometer (Delta V Plus Continuous Flow - ThermoFisher Scientific) at the AETE-ISO analytical platform (OREME – Montpellier, France).

For samples likely to contain carbonates (sediments, sedimentary organic matter, *P. oceanica* epiphytes, calcareous macroalgae and fish intestinal contents), sub-samples for

$\delta^{13}C$ analysis were treated with 10 % HCl, while the remaining material for $\delta^{15}N$ analysis remained non-acidified.

Three certified caffeine standards IAEA USGS 61, USGS 62 and USGS 63 were interspersed every 10 to 15 analyses for sample normalisation. Samples and standards were weighed into tin or aluminium cups (for acidified samples) using SARTORIUS CUBIS II balance (precision: 0.001 mg).

Results were normalised to the Vienna Pee Dee Belemnite (V-PDB) standard for $\delta^{13}C$ and to atmospheric nitrogen (N_2) for $\delta^{15}N$, and expressed in per mil (‰) according to the equation:

$$\delta X = \left(\frac{R_{sample}}{R_{standard}} - 1\right) \times 1000$$

Where X represents ^{13}C or ^{15}N and R is the respective isotopic ratio.

Lipid mathematical corrections were performed on $\delta^{13}C$ animal samples as the carbon to nitrogen ratio (C:N), calculated from direct measure of carbon and nitrogen during stable isotopes analysis, was higher than 3.5 for 94 out of 212 samples. Following Post *et al.* (2007) recommendations, all animal sample $\delta^{13}C$ values were thus normalised using this equation:

$$\delta^{13}C_{normalised} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N$$

As only 5 out of the 132 plant samples analysed had a percentage of carbon higher than 40 %, no lipid mathematical corrections were performed (Post *et al.*, 2007).

2.4. Statistical analysis

Data concerning *Posidonia* shoot density and canopy height, leaf morphology (number of leaves, LAI), epiphyte biomass and isotopic values ($\delta^{15}N$ and $\delta^{13}C$) of the leaves, the epiphytes and the SOM were tested with a 2 factors orthogonal model (Site, fixed: 4 levels and Distance, fixed: 2 levels) of permutational analysis of variance (PERMANOVA) using the software Primer V7 with PERMANOVA+ (Anderson *et al.*, 2008; Clarke *et al.*, 2014). As the particulate organic matter (POM) was also sampled inside the marinas (D0) we kept the same model but with 3 levels for the distance factor. *A posteriori* pairwise comparison

for differences between distances among sites and between sites among distances was done when the interaction term was significant. Analyses were performed on Euclidean distance resemblance matrices. Before running the PERMANOVA analyses, the homogeneity of residuals was tested using a PERMDISP test. If the test resulted in significant differences in dispersion, data were 4th root transformed. When the potential sources of organic matter were only sampled inside the marinas, 1 factor model with Site (fixed) as factor was used.

The species composition of fish stomach contents and the $\delta^{15}N$ and $\delta^{13}C$ of their muscle tissue were analysed using the same model, but considering the distances inside vs outside marinas. For prey composition, analyses were performed on Bray-Curtis dissimilarity matrices and the differences were further visualised with nMDS ordination plots.

Stable isotopes dual plots were used to visualise the stable isotope distribution of samples at each of the 4 study sites. When dual plots included, we corrected the baseline data using trophic discrimination factors (TDF). The $\delta^{15}N$ and $\delta^{13}C$ isotope ratios are generally higher in the consumer's tissues than in the bulk of their diet. This enrichment during the process of food digestion and assimilation along the trophic levels is called trophic fractionation and is quantified TDF. The choice for the right TDF is complex and still debated because TDF may vary depending on the environment, lipid extraction, diet, size, age, temperature, and tissue (Ben-David and Schell, 2001; Minagawa and Wada, 1984; Vanderklift and Ponsard, 2003). A generally applied TDF for nitrogen has a value of 3.4 ± 1 ‰ per trophic level, whereas for carbon is 0.4 ± 1.3 ‰ (Minagawa and Wada, 1984; Peterson and Fry, 1987; Post, 2002). In marine organisms TDF for nitrogen have been found to be smaller at low and intermediate trophic levels and to be more variable among organisms occupying the same trophic level for both nitrogen and carbon. Accordingly, in this paper, we have selected a fractionation of 2.32 ± 1.82 ‰ for $\delta^{15}N$ and of 0.35 ± 1.29 ‰ for $\delta^{13}C$, as suggested in Vander Zanden and Rasmussen (2001).

The Standard Ellipse Area (SEA) Layman metric (Layman *et al.*, 2007) was used to estimate the area occupied by the fish isotopic values on the dual plot. This area, also called isotopic niche, can be used to estimate the trophic niche. *Diplodus* spp. niches were estimated separately for the animals captured inside and outside each marina. The SEA were calculated using Stable Isotope Bayesian Ellipses in R (SIBER) packages (Jackson *et al.*, 2011). The SEA were corrected (SEAc) to represent both $\delta^{15}N$ and $\delta^{13}C$ standard deviation and encompass 95 % of the data, reducing the influence of small sample sizes

(Jackson *et al.*, 2011). Additionally, the Bayesian Standard Ellipse Area (SEAb; based on 5.10^5 successive iterations) was used to compare the isotopic niches width among fish sampled inside vs outside the marinas in each site separately. The Bayesian approach provided robust estimates of isotopic niche widths and credible intervals, allowing for detailed and reliable comparisons despite the small sample sizes. The trophic niches were therefore compared by assessing the proportion of lower SEAb calculated for fish sampled inside the marinas compared to the fish sampled outside. If the proportion lower SEAb value is higher than 95%, the trophic niches of the compared groups were considered as different.

3. RESULTS

3.1. Differences between sites and distances from the marina

3.1.1. Posidonia meadows

The PERMANOVA analyses showed significant differences in shoot density, epiphyte biomass and LAI between sites and in their interaction with distance for canopy height (Table 1). However, the *a posteriori* pairwise tests showed no clear patterns of differences between equipped and unequipped marinas and higher canopy height close than far from the port for one site only (SAN in Figure 2b; Figure 2; Tables S1, S2). Epiphyte biomass (mg DW.leaf DW^{-1}) showed a trend of higher biomass in the meadows near the equipped marinas, but this was not corroborated by the PERMANOVA (Table 1, S2, Figure 2c). The dead leaves of *Posidonia oceanica* showed a low level of decomposition (level 1) in the location close to both unequipped marinas (i.e. D1 of SAN and CAR) whereas an intermediate level of decomposition was found in all other locations (level 2) but in D2 of MIR where the dead leaves were more degraded (level 3; Table S1).

*Table 1. Results from PERMANOVA analysis on the P. oceanica characteristics (shoot density, leaf number.shoot^{-1}, canopy height, epiphytes (mgDW.leaf biomass^{-1}), and leaf area index (LAI)) for differences between sites and distances. ^ 4th root transformation; * p < 0.05; ** p < 0.01; *** p < 0.001*

		***Posidonia oceanica* fresh leaves**										***Posidonia oceanica* dead leaves**		
		Shoot density		**n. leaves. shoot^{-1}**		**Canopy height**		**Epiphytes biomass**		**LAI**		**Epiphytes biomass**		
Factors	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**MS^**	**F^**	**MS**	**F**	**df**	**MS^**	**F^**
Site (Si)	3	171830.00	8.19**	1.09	0.70	118760.00	8.64***	0.07	10.79**	7.23	3.07*	3	0.07	11.27***
Distance (Di)	1	74650.00	3.56	2.03	1.31	10433.00	0.76	0.01	0.03	1.39	0.59	1	0.03	4.48
Si x Di	3	57003.00	2.72	1.83	1.18	73115.00	5.32**	0.01	1.78	5.81	2.47	3	0.02	2.95
Residuals	32	20982.00		1.55		13740.00		0.01		2.36		8	0.01	

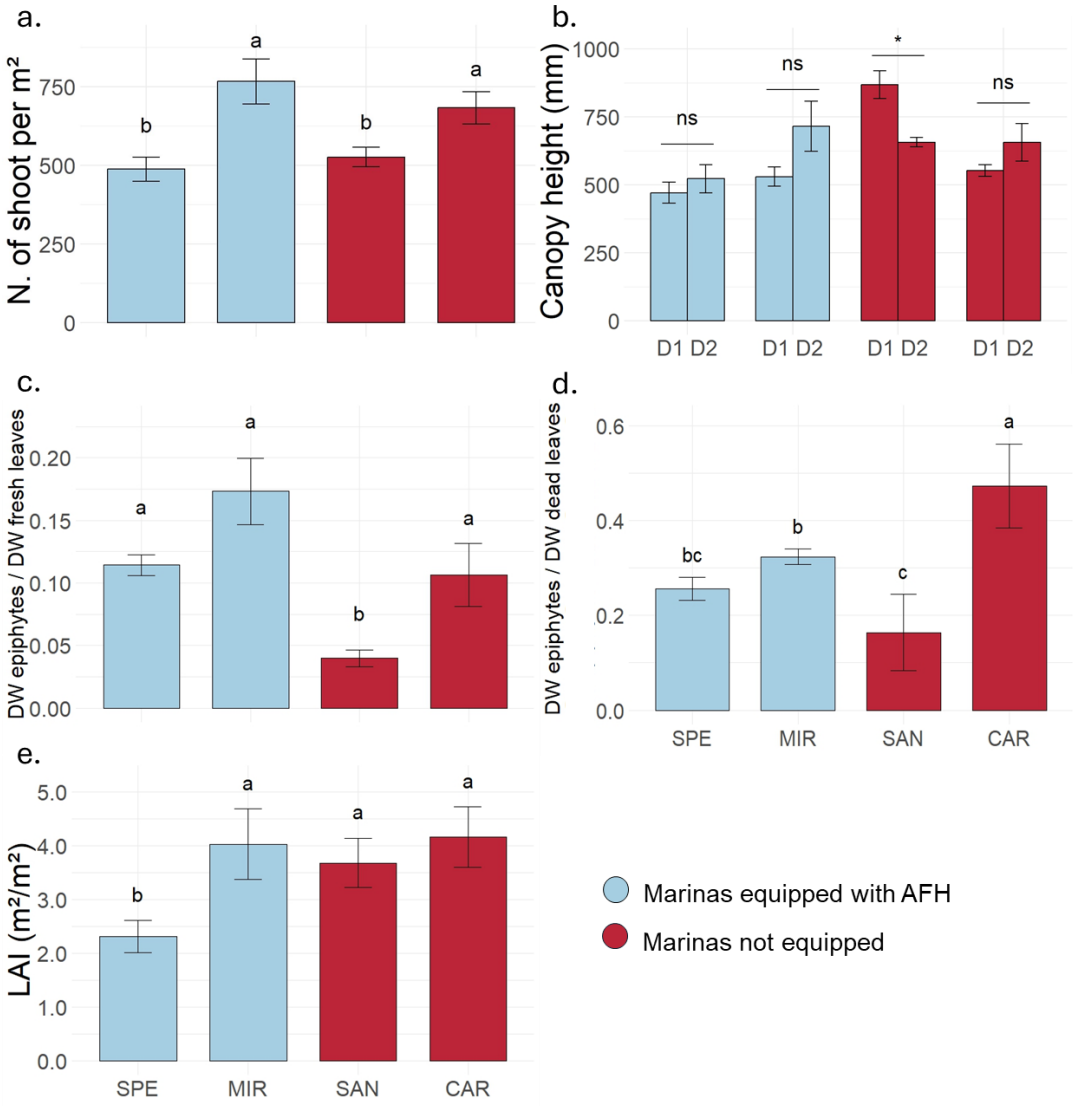


*Figure 2. Mean value (± SE) of Posidonia habitat characteristics at each site (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). Letters are used to show the results of the a posteriori pairwise test between sites when $p < 0.05$; ns = not significant and * = $p < 0.05$ were used to show differences among distances at each site when $p < 0.05$ for the interaction term.*

3.1.2. Isotopic composition of basal food sources

The dual isotope plots for baseline resources (Figure 3) at each site showed that isotopic signatures of *Posidonia oceanica* fresh (POS) and dead leaves (POS DL) always were ^{13}C-enriched (Table S3). The $\delta^{13}C$ values of seagrass epiphytes were more negative than POS and values were comparable to those of the least ^{13}C-enriched basic sources sampled, such as brown algae, POM or the SED sampled inside the marinas (Figure 3). Organic matter (SED, SOM or POM) had the lowest $\delta^{15}N$. The $\delta^{15}N$ of macroalgae sampled in the marinas were highest, especially for the red algae (RED in Figure 3). Epiphytes and POS $\delta^{15}N$ in general occupied intermediate positions between organic matter and macroalgae (Figure 3).

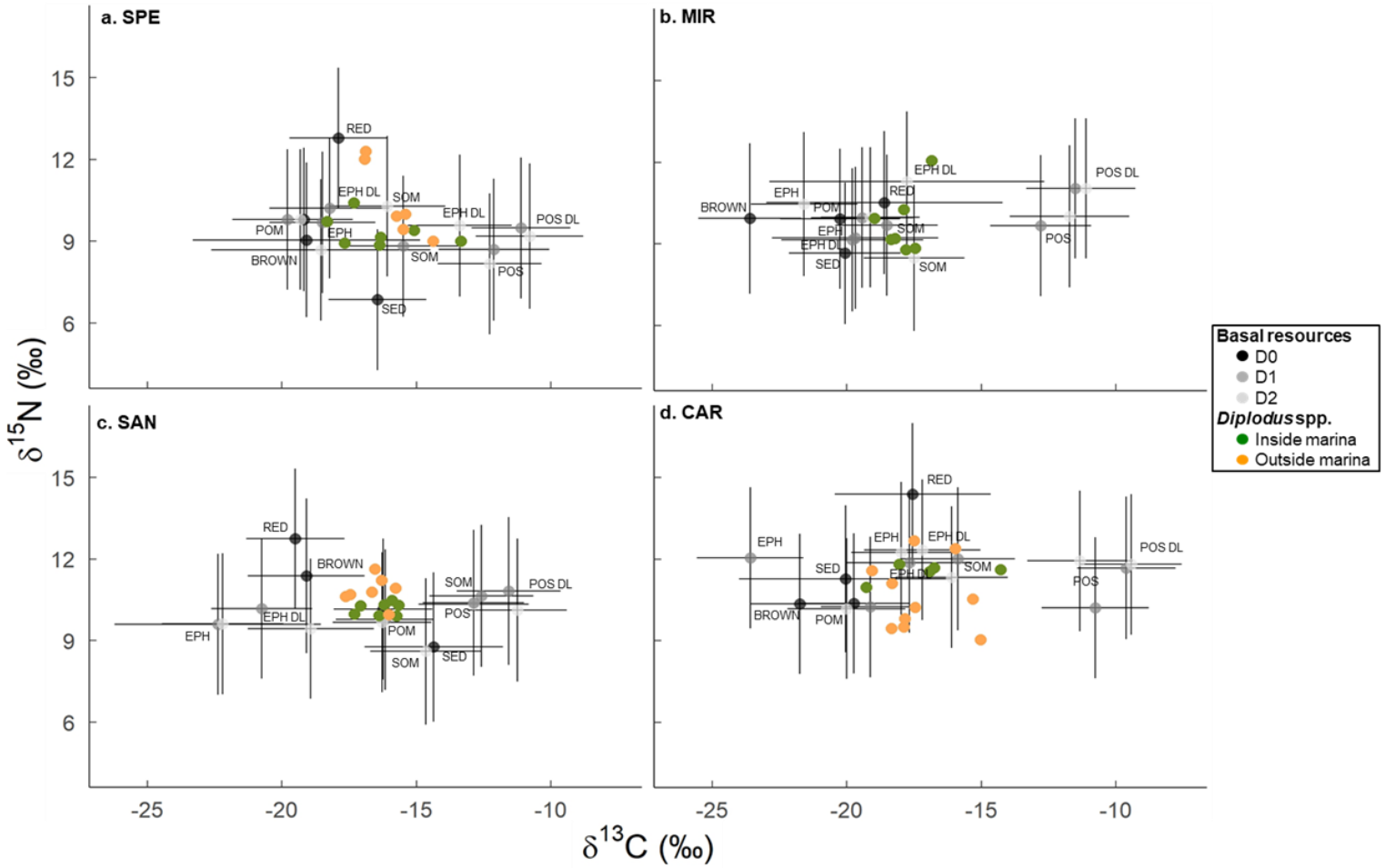


Figure 3. Stable Isotope dual plots of Diplodus spp. sampled inside the marinas (green dots) and outside the marinas (orange dots) with mean (± standard deviation) of each potential sources of organic matter collected inside the marinas (D0; black dots), in the Posidonia meadows habitats immediately outside the port (c.a. 300 m; D1; grey dots) and approximately 1 km far from the port opening (D2; light grey dots). Trophic discrimination factors were applied in all the potential sources. BROWN = Phaeophyceae; RED = Rhodophyta; POS = P. oceanica fresh leaves; POS DL = P. oceanica dead leaves; EPH = Epiphytes of P. oceanica fresh leaves; EPH DL = Epiphytes of P. oceanica dead leaves; SOM = Sedimentary organic matter; and POM = Particulate organic matter.

The PERMANOVA analyses showed significant differences between sites for the $\delta^{13}C$ of POS and POS DL, POM and SED (Table 2) and differences in the interaction term site x distance for the fresh leaf epiphytes (EPH in Table 2) and SOM. No differences were found for EPH DL (Table 2). Differences among sites were due to one of the 2 unequipped sites that was ^{13}C enriched (CAR for *Posidonia* and SAN for sediment; Figure 4, Table S3, S4a). Differences in the interaction term for EPH were due to the ^{15}N depletion or enrichment with distance at one of the equipped or unequipped sites, respectively (Figure 4, Figure 5; Table S4). Those for SOM were due to the ^{15}N depletion or enrichment with distance at one of the unequipped or equipped sites, respectively (Figure 5, Table S4). The $\delta^{15}N$ values of POS DL and SED varied among sites, with the lowest values at one of the equipped sites and the highest value at one of the unequipped (Table 2; Figure 5). The $\delta^{15}N$ values of other baseline sources varied with the interaction site x distance (Table 2, S3, S4; Figure 5). The ^{15}N values for POS and epiphytes (both for fresh and dead leaves) followed a similar pattern, with values decreasing with the distance at one equipped site (SPE in Figure 5) and increasing at the other or at one of the unequipped sites. Overall, the average values across distances showed a similar trend of differences among sites as the one showed by POS DL. The ^{15}N values for SOM increased with distance at one equipped site and decreased at all other sites (Figure 5). Interestingly, the $\delta^{15}N$ values of POM decreased with the distance from the marina only where AFH were absent, although patterns were not always significant (Figure 5; Tables S3, S4).

*Table 2. Results from PERMANOVA analysis on the δ13C and δ15N values of fresh leaves of P. oceanica (POS), epiphytes of P. oceanica fresh leaves (EPH), sedimentary organic matter (SOM), dead leaves of P. oceanica (POS DL), epiphytes of P. oceanica dead leaves (EPH DL), particulate organic matter (POM) and superficial sediments (SED) for differences between sites and distances. * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

		POS		EPH		SOM			POS DL		EPH DL			POM			SED	
δ13C	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**df**	**MS**	**F**	**MS**	**F**	**df**	**MS**	**F**	**df**	**MS**	**F**
Site (Si)	3	5.11	7.35***	24.02	5.56**	30.07	41.63***	3	3.04	17.52**	12.15	2.83	3	38.98	81.32***	3	43.66	9.21**
Distance (Di)	1	0.01	0.01	9.21	2.13	1.29	1.79	1	0.37	2.13	21.07	4.91	2	0.24	0.51			
Si x Di	3	1.32	1.90	26.24	6.07**	3.30	4.57*	3	0.01	0.05	3.37	0.78	6	0.93	1.94			
Residuals	32	0.70		4.32		0.72		8	0.17		4.29		45	0.48		15	4.74	
δ15N	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**	**df**	**MS**	**F**	**MS**	**F**	**df**	**MS**	**F**	**df**	**MS**	**F**
Site (Si)	3	12.87	130.25***	0.74^	124.68***	12.26	39.42***	3	4.14	18.59**	4.65	61.34***	3	0.60	18.11***	3	11.76	21.79***
Distance (Di)	1	0.95	9.60**	0.01^	0.56	2.48	7.96**	1	0.19	0.86	0.39	5.14	2	0.12	3.59*			
Si x Di	3	2.54	25.71***	0.11^	18.11***	3.38	10.87**	3	0.14	0.62	1.79	23.63***	6	0.08	2.39*			
Residuals	32	0.10		0.01^		0.31		8	0.22		0.08		45	0.03		15	0.54	

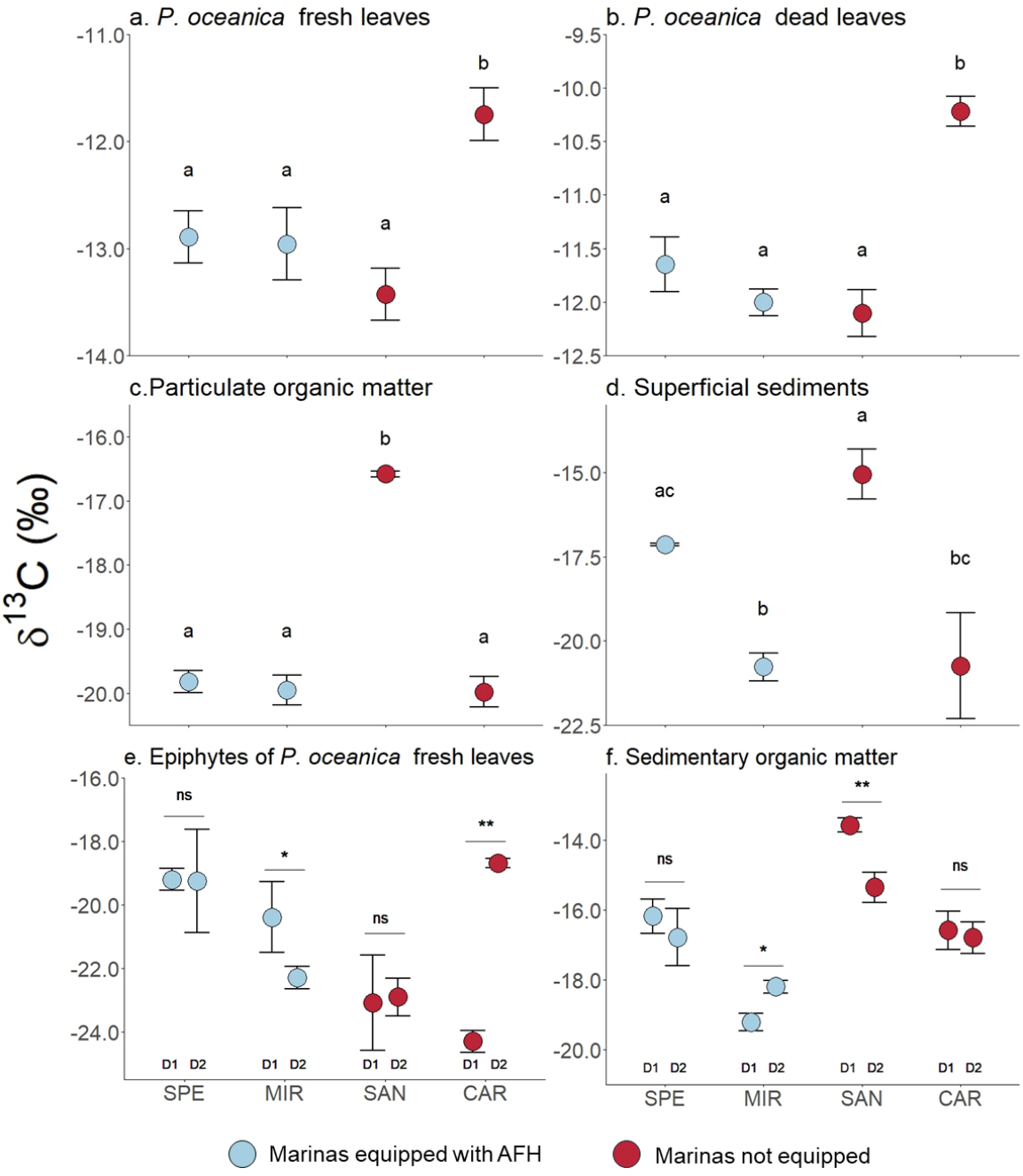


*Figure 4. Mean $\delta^{13}C$ ratio (± SE) for the potential sources of organic matter at each site (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). (a-d) Letters are used to show the results of the a posteriori pairwise test between sites when $p < 0.05$; (e-f) ns = not significant, * = $p < 0.05$ and ** = $p < 0.01$ were used to show differences among distances at each site when $p < 0.05$ for the interaction term.*

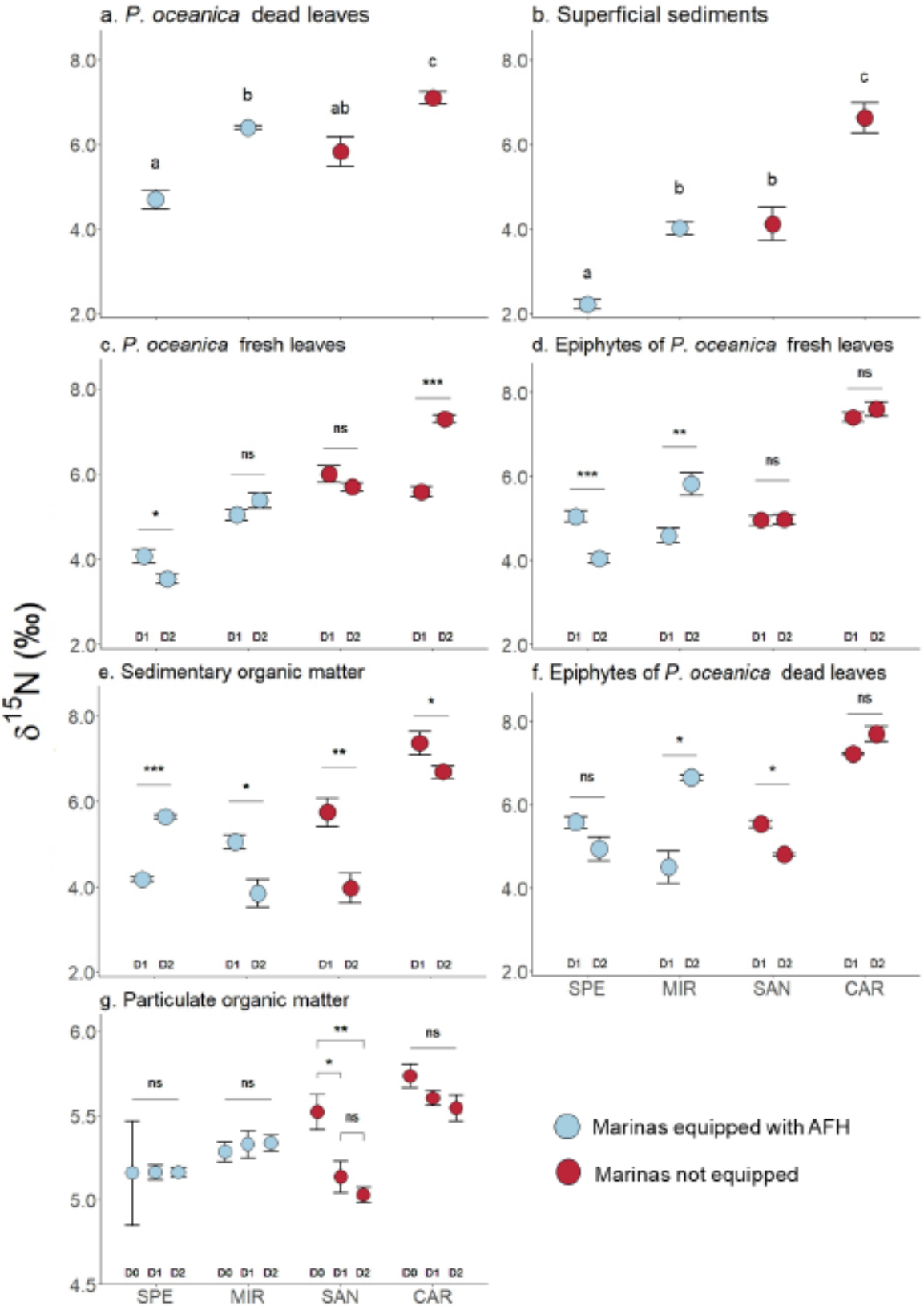


*Figure 5. Mean δ15N ratio (± SE) for the potential sources of organic matter at each site (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). (a-b) Letters are used to show the results of the a posteriori pairwise test between sites when $p < 0.05$; (c-g) ns = not significant, * = $p < 0.05$ and ** = $p < 0.01$ were used to show differences among distances at each site when $p < 0.05$ for the interaction term.*

3.1.3. *Diplodus* spp.

Stable isotopes in muscle tissues and stomach content

A total of 49 individuals of *Diplodus* spp. was collected, with a mean ± SE fish standard length of 118.74 ± 3.21 mm and weight of 59.71 ± 5.06 g (Table S5). Unfortunately, we were unable to obtain fish samples from outside one of the equipped marinas (MIR in Figure 1a). Therefore, this site was not considered any further. Among the 49 fishes, 23 had empty stomachs. For the remaining 26, we collected 248 invertebrates distributed into Gastropoda and Amphipoda (31.05 % and 29.44 % of the total abundance Table S6; Figure S1a), Ostracoda, Polychaeta, and Bivalvia (13.71 %, 10.89 % and 10.48 %, respectively), Isopoda, Decapoda and Tanaidacea (3.63 %, 0.40 % and 0.40 %, respectively). The PERMANOVA analysis showed no significant differences among sites or distance (inside vs outside the marina; Table 3a; Figure S1b). There were also no differences in the $\delta^{13}C$ values of *Diplodus* spp. muscle tissues (Table 3a; Figure 6a). Instead, $\delta^{15}N$ values different for the site x distance interaction (Table 3a). The *a posteriori* pairwise tests showed lowest $\delta^{15}N$ values in the equipped site SPE than in the 2 unequipped ones for the fishes caught inside the marina and differences between marina and seagrass meadow in one of the unequipped sites (Table 3b, S5; Figure 6b).

*Table 3. (a) Results from PERMANOVA analysis on the $\delta^{13}C$ and $\delta^{15}N$ ratio of Diplodus spp. muscle tissues and the composition of taxa identified in the stomach contents for differences between sites and distances; (b) Pairwise test for differences among distances when interaction term was $p < 0.05$. Monte Carlo permutations were used when permutations were limited. SPE = Saint-Pierre des Embiez; SAN = Port of Sanary-sur-mer; CAR = Port of Carqueiranne; [1] = marina equipped with artificial fish habitats; [2] = marina not equipped with artificial fish habitats. * = p < 0.05; ** = p < 0.01; *** = p < 0.001.*

a.		$\delta^{13}C$		$\delta^{15}N$			Stomach content composition	
Factors	df	MS	F	MS	F	df	MS	F
Site (Si)	2	4.01	2.50	4.56	5.84**	2	5899.70	1.61
Distance (Di)	1	0.01	0.01	0.83	1.06	1	3080.80	0.84
Si x Di	2	0.71	0.45	3.61	4.63*	2	2642.30	0.72
Residuals	36	1.60		0.78		20	3661.20	

b.			t	
$\delta^{15}N$	SPE[1]		1.93	
	SAN[2]		3.10*	Outside marina > Inside marina
	CAR[2]		1.53	
	Inside marina	SPE[1] vs SAN[2]	3.59**	
		SPE[1] vs CAR[2]	7.78***	CAR[2] > SAN[2] > SPE[1]
		SAN[2] vs CAR[2]	8.40***	
	Outside marina	SPE[1] vs SAN[2]	0.70	
		SPE[1] vs CAR[2]	0.28	
		SAN[2] vs CAR[2]	0.40	

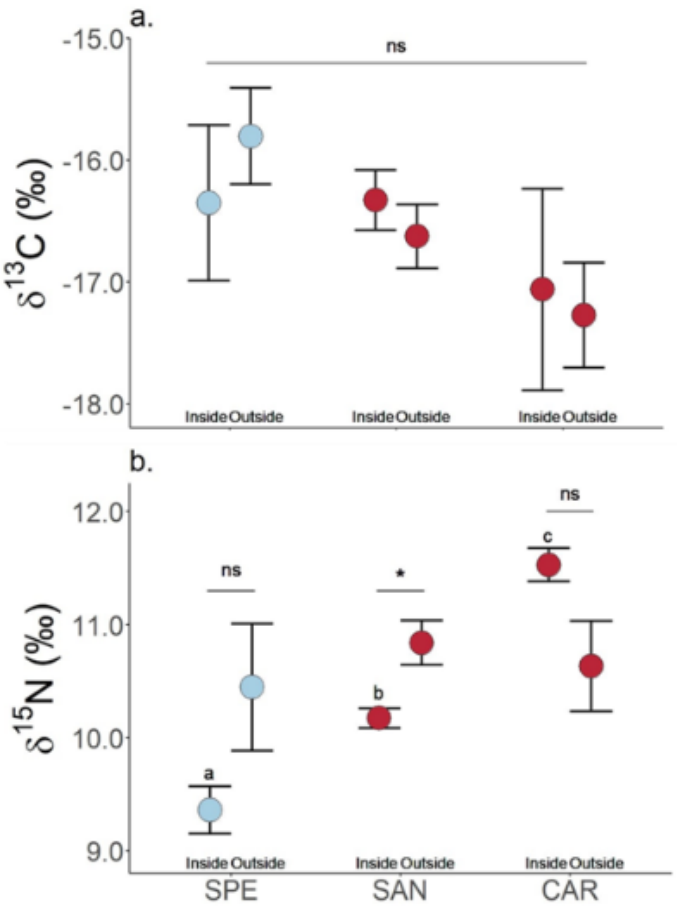


*Figure 6. Mean $\delta^{13}C$ and $\delta^{15}N$ ratio (± SE) for Diplodus spp. muscle tissues at each site (SPE: Saint-Pierre des Embiez; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). Letters are used to show differences between sites for fish sampled inside marinas when $p < 0.05$ while ns = not significant and * = $p < 0.05$ were used to show differences among distances at each site when $p < 0.05$ for the interaction term.*

Isotopic niches

The area occupied by the ellipse showing the variability in $\delta^{13}C$ and $\delta^{15}N$ of *Diplodus* spp. estimated as total area (TA) and as corrected standard ellipse area (SEAc) were slightly smaller in the unequipped than the equipped sites for fishes captured inside the marinas, especially for the SAN site, whereas outside the marina, within the seagrass meadow, the isotopic niche was particularly large at the unequipped site CAR (Table 4a; Figure 7).

There was more overlapping space between the isotopic niches of fishes sampled inside and outside the marinas at the unequipped sites (SAN and CAR; 36.48 % and 24.61 % respectively) than at the equipped site (SPE; 16.93 %; Table 4b; Figure 7a).

Table 4. (a) Isotopic niche data of Diplodus spp. sampled inside and outside the study sites equipped with artificial fish habitats (AFH) deployed inside the marinas (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar) and the unequipped sites (SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). TA = Total area of the convex hulls; SEAc = Standard Ellipse Area (corrected for small sample size); and SEAb = the estimated mean Bayesian standard ellipse area (95 % credible intervals). (b) The proportion of overlap in SEAc for Diplodus spp. collected inside and outside each marina.

a.	Site	Distance	TA	SEAc ‰²	SEAb mean ‰² (CI)
Marinas equipped with Artificial fish habitats	SPE	Inside marina	3.98	3.25	3.23 (1.19 – 5.97)
		Outside marina	1.56	1.64	3.07 (1.01 -5.93)
	MIR	Inside marina	3.11	2.63	2.65 (0.96 – 4.90)
Marinas not equipped	SAN	Inside marina	0.69	0.55	0.54 (0.20 – 1.01)
		Outside marina	1.35	1.36	1.32 (0.49 – 2.46)
	CAR	Inside marina	1.73	2.18	2.18 (0.60 – 4.45)
		Outside marina	10.19	6.06	6.01 (2.69 – 10.17)

b.	SPE	SAN	CAR
Proportion of SEAc overlap	16.93 %	36.48 %	24.61 %

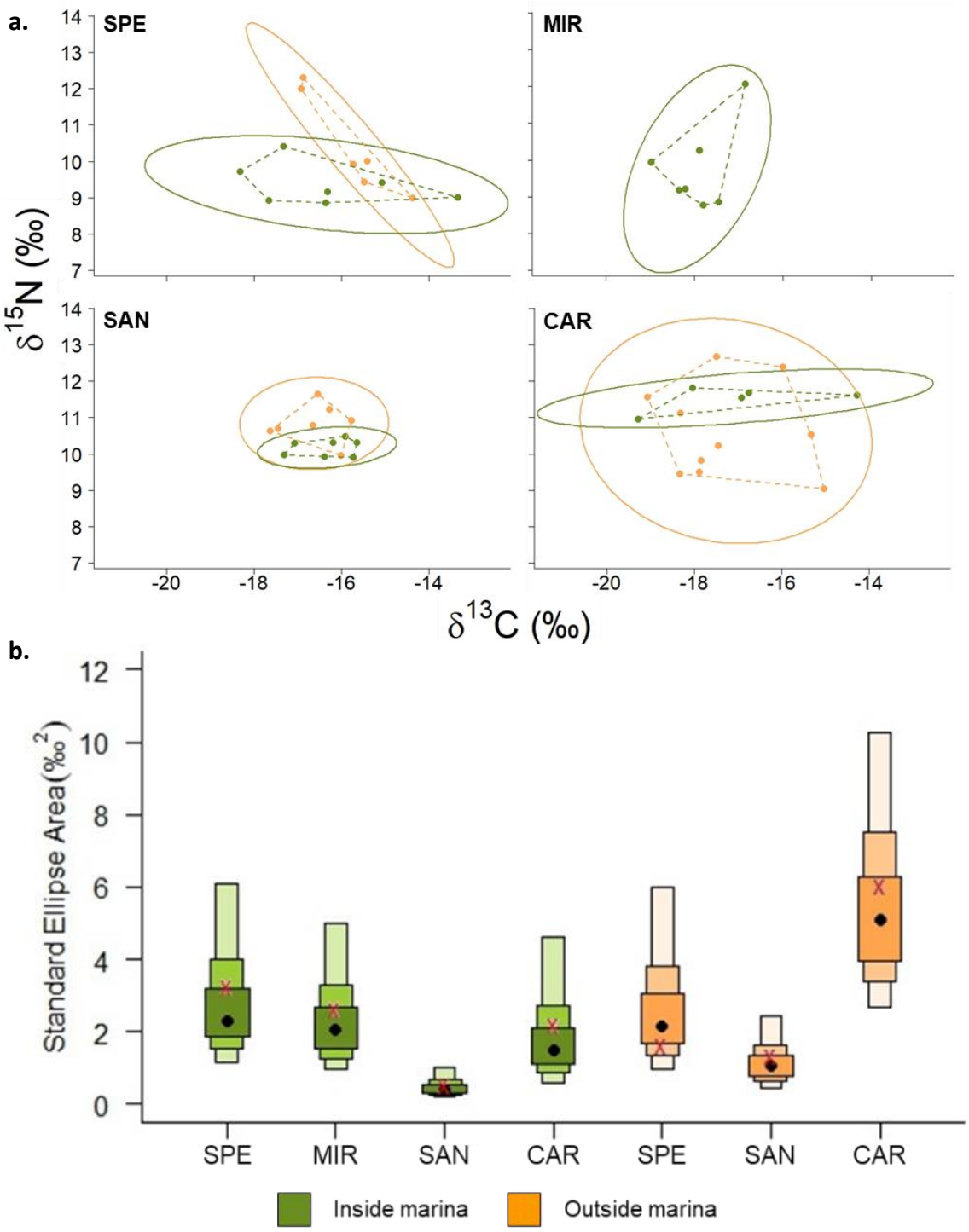


Figure 7. (a) Stable isotope dual plots illustrating the isotopic niche of Diplodus spp. sampled inside (green) and outside (orange) the marinas in the 4 study sites. The solid lines represent the standard ellipse areas corrected for small sample sizes (SEAc) encompassing 95 % of the data; the dashed lines represent the convex hulls area (TA) indicating the trophic space occupied. (b) Density plots of standard ellipse area (SEA) of Diplodus spp. sampled inside (green) and outside (orange) the marinas in the 4 study sites. Mean SEAb is indicated with black dots; SEAc is indicated with red crosses; boxed areas indicate the 50, 75 and 95 % Bayesian credible intervals. Marinas equipped with artificial fish habitats: SPE = Saint-Pierre des Embiez and MIR = Port-Miramar; unequipped marinas: SAN = Port of Sanary-sur-mer and CAR = Port of Carqueiranne.

3.2. Contribution of basal sources to the diet of Diplodus spp.

Fish isotopic values were most of the time within the mean values for baselines, except 1 individual sampled inside the equipped marina (MIR in Figure 3b) and 4 individuals sampled outside the unequipped marina (CAR in Figure 3d) for the $\delta^{15}N$. The values were, however, within the range of variability of the resources (Figure 3b, d). The $\delta^{13}C$ and $\delta^{15}N$ values showed fishes relied mainly on epiphytes (EPH and EPH DL; Figure 3a, d) and particulate and sedimentary organic matter (Figure 3).

3.3. Organic contribution to sedimentary organic matter

Sedimentary organic matter (SOM) sampled within the meadow (D1 and D2) occupied an intermediate position between the $\delta^{13}C$ value of intestinal contents of *Diplodus* spp., and those of *P. oceanica* leaves (Figure 8). In the equipped sites (SPE and MIR) and in one of the unequipped sites (CAR) SOM was close to POM, epiphytes and the intestinal content of fishes, whereas in the remaining site it was close to *P. oceanica* leaves (Figure 8). No consistent patterns were observed neither between the distance where the SOM was collected, nor with the presence of AFH inside the marinas.

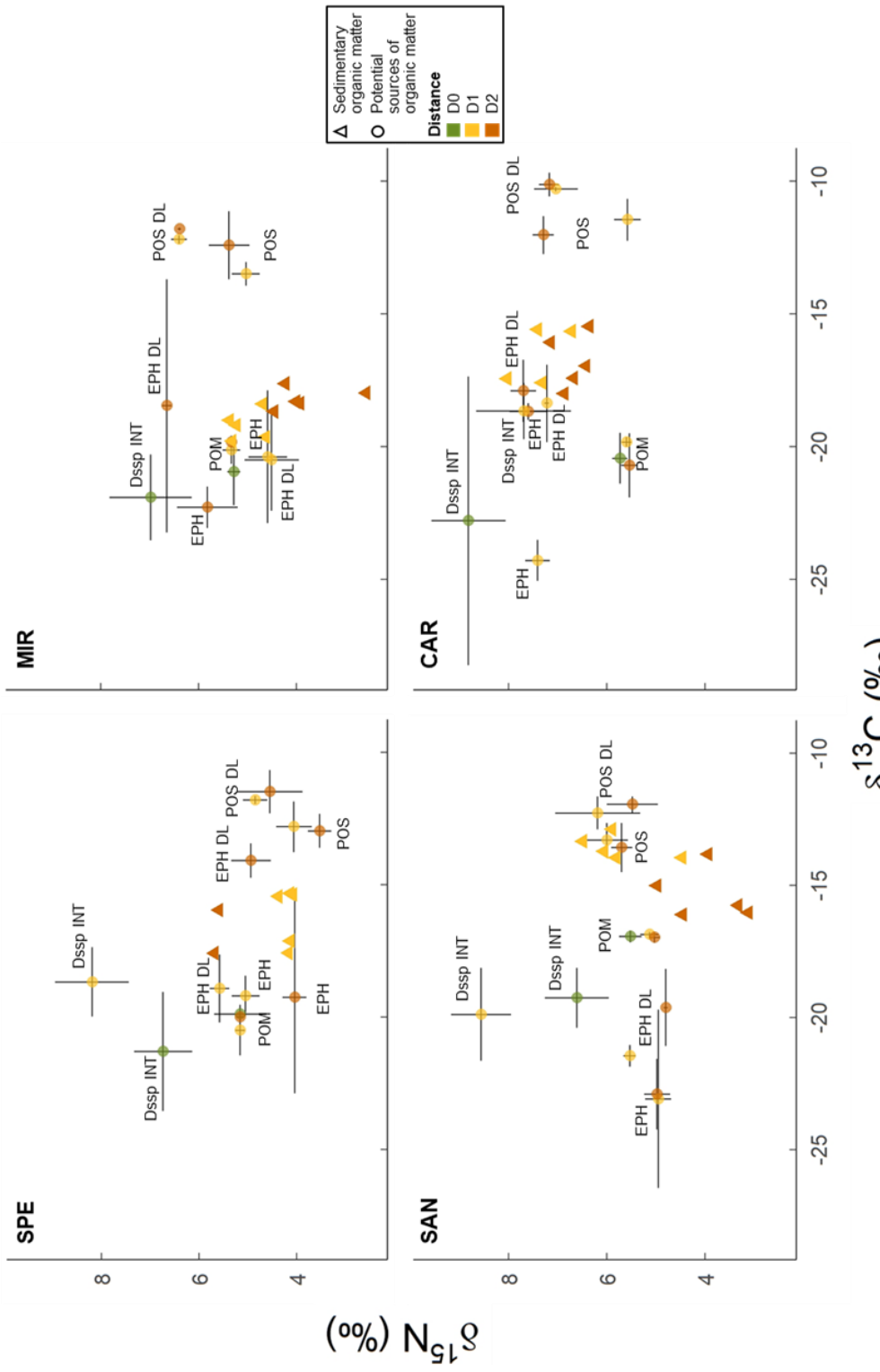


Figure 8. Stable Isotope dual plots of Sedimentary organic matter collected in the Posidonia meadows habitats immediately outside the port (c.a. 300 m; D1) and approximately 1 km far from the port opening (D2) with mean (± standard deviation) of each potential sources of organic matter including fresh and dead leaves of P. oceanica (POS and POS DL), their associated epiphytes (EPH and EPH DL), Particulate organic matter (POM) and the intestinal contents of Diplodus spp. captured inside and outside the marinas.

4. DISCUSSION

We studied trophic connectivity using stable isotopes and expected that values of basal sources from the meadows in proximity to the marina inlet would be closer to those sampled within the marina. We also expected differences between equipped and unequipped sites.

At the unequipped sites, the particulate organic matter was ^{15}N-enriched inside the marina and δ^{15}N values decreased within the meadow at increasing distance from the inlet to reach values similar to the equipped sites at the largest distance from the marina. In addition, the δ^{15}N values in the leaves of *P. oceanica* and epiphytes, and also in the sedimentary organic matter were in general low within the meadow adjacent to the marinas equipped with AFH, although patterns were extremely variable. The observed trend along the distance from the marina are compatible with a possible spillover of POM to the seagrass, since ^{15}N values slightly decrease with distance in the unequipped sites and remained constant in the equipped sites. The high values within unequipped marinas call for an impact of AFH on the POM composition. Marinas are areas particularly exposed to anthropic nitrogen inputs and water pollution through discharge of wastewater from boats, terrestrial runoff or boating maintenance activities (Burgin and Hardiman, 2011; Dolgen *et al.*, 2003). High levels of ^{15}N are often associated with nutrient enrichment (Bergfur *et al.*, 2009; Carmichael *et al.*, 2004; McClelland *et al.*, 1997) and our results might indicate that AFH could partly remove nutrients from the water column. This might be related to the large number of detritivores colonising AFH, most of them being suspension feeders and thus using the particulate organic matter (Varenne *et al.*, submitted; Chapter 2). The likely partial sequestration of the particulate organic matter might decrease the amount of POM exported to the adjacent meadow and be reflected into an increase in its healthy status. We therefore expected a general decline in shoot density, LAI or canopy height in proximity to the marina inlet where AFH were absent. In fact, particulate organic matter in the water column increases turbidity and therefore may have a negative effect on seagrass physiology and on its distribution (Bockel *et al.*, 2024; Boudouresque *et al.*, 2009; Marbà *et al.*, 2014; Waycott *et al.*, 2009). However, only canopy height varied with the distance, and it was lower close than far from the inlet in 3 out of 4 sites, although this was only a trend not corroborated by significant differences, according to the analyses used. Probably more than 4 sites would be necessary to test if this trend indicates a real effect. In addition, both shoot densities and canopy heights were within the range of variability of other meadows in the same region

classified as good status according to the indices used in institutional monitoring programs (Boudouresque *et al.*, 2007; Pergent *et al.*, 1995; Pergent-Martini, 1994). This indicates that marinas, independently on AFH, did not have large effects on the adjacent meadow or that the effect can extend more than 1 km or less than 300 m from the marina inlet (e.g. longer or shorter than our sampling distances).

The biomass of epiphytes within the meadows in proximity to equipped marinas tended to be larger than in the other sites, but this was not statistically significant. At all sites, epiphyte biomass ranged between 3 % and 17% which is in the range described in the literature (Lepoint *et al.*, 1999; Mazzella, 1984; Thelin and Bedhomme, 1983). Nutrient availability can increase epiphytes biomass (Jupp and Spence, 1977; Pergent *et al.*, 1999; Pergent-Martini *et al.*, 1995) up to 40% of the leaves biomass (Gobert *et al.*, 1995; Lepoint *et al.*, 1999; Mazzella, 1995). If the trends observed in our study were related to nutrient enrichment, then one should have observed high biomass values and also the opposite pattern, as ^{15}N-enriched POM, SOM and *P. oceanica leaves* were in unequipped sites. Epiphytes are known to be a source of food for small grazers which can control their biomass (Bell *et al.*, 1984; Chimenz *et al.*, 1989; Scipione *et al.*, 1996; Tomas *et al.*, 2005). The slightly higher epiphyte biomass found outside marinas equipped with AFH could indicate less mesograzers, which might be a result of reduced fish predation. In addition, epiphytes can grow more on old leaves and an additional explanation could be that in equipped sites, because of better environmental conditions plants could better survive and then have more epiphytes. All these hypotheses need to be tested.

Fishes can be an important vehicle for cross-habitat trophic exchanges because of their high mobility. Invertivorous fishes might feed on the invertebrates in the marinas and then move to the seagrass meadow, where they defecate and enrich the meadow of mineralised organic matter. This pattern was found in a seagrass meadow adjacent to artificial reefs in the tropics (Layman and Allgeier, 2020). Previous studies have shown that isotopic signatures of faecal materials from aquaculture waste can be found up to 1 000 m from the fish cages (Sarà *et al.* 2004) but the fish density, the hydrodynamics of the area and the consumption of faecal materials from other organisms widely affect its isotopic contribution to the sediments.

We focused on *Diplodus* spp. because of their site fidelity to both marina and seagrass habitats (Bell and Harmelin-Vivien, 1983; Bouchoucha *et al.*, 2016; Francour, 1997) and

because they are abundant at the study sites. The stomach content analysis showed they fed on molluscs and crustaceans (Amphipoda and Gastropoda), which is in agreement with the literature (Osman and Mahmoud, 2009; Pallaoro *et al.*, 2006). These mesograzers are ubiquitous in coastal waters and can populate marinas (Chou *et al.*, 2023; Saenz-Arias *et al.*, 2022) and seagrass meadows (Bellan-Santini *et al.*, 1986; Boudouresque and Meinesz, 1982), where they may feed on epiphytes and thus control their biomass. They are also abundant on AFH (Gauff *et al.*, 2023; Varenne *et al.*, 2023). The stable isotope analyses on fish muscles showed that fishes captured in the equipped marinas were ^{15}N depleted, which is in agreement with the trend observed for the ^{15}N of POM and might indicate POM can partly support their diet, as also visible in the dual plots of Figure 3, via filter feeders.

In addition, the isotopic niches were overlapping between fishes within marina or seagrass meadow, indicating that they might feed on similar resources and move around from and to the meadow, thereby acting as cross-habitat exchange vehicles. Interestingly, we found that at the equipped site where fishes were collected both within marina and seagrass meadow, niches were slightly larger and overlapped less than at the unequipped sites. This suggests fishes could access more prey items, allowing *Diplodus* spp. to exploit a more diverse range of food resources within the marina and increase their survival (Loxdale *et al.*, 2011) and transport this biomass outside the marina. Availability of more resources within the marina and the presence of AFH to enhance survival might change the role of fishes in exporting organic matter. Juveniles and sub-adult fishes such as those we collected might reside more within marinas with AFH because of better conditions and thus contribute less to export organic matter to the meadow. However, the stable isotope composition of sedimentary organic matter sampled within the seagrass meadow was intermediate between the isotopic composition of fish faeces and *Posidonia* leaves or epiphytes at all sites independently to the presence of AFH.

In summary, it is possible that AFH by supporting suspension feeders could help to reduce nutrient and organic enrichment in the marina and limit the export of this organic matter to the meadow, while offering fishes more diverse prey items, other than enhancing their survival, as shown in other studies (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b). Although we found fishes could contribute to the exchange of material from the marina to the seagrass meadow, we found no evidence that the presence of AFH could modify their contribution. However, the role of AFH in fish survival has been shown and, since fishes

play a role in organic matter export, the increase in survival might indirectly affect cross habitat trophic exchange.

GENERAL DISCUSSION AND CONCLUSION

The aim of my thesis was to investigate the benthic assemblages associated with artificial fish habitats (AFH), which are used to improve the nursery function of man-made coastal structures such as harbours and marinas. While several studies have highlighted that AFH can improve the growth and survival of coastal fishes (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b), how benthic assemblages colonise these structures is poorly known. In particular, this thesis has focused on taxon diversity and composition of benthic invertebrates, how environmental context may affect their distribution and how AFH can contribute to the trophic exchanges between ports and the adjacent habitats, in my case *Posidonia oceanica* meadows. Considering that a specific discussion was detailed in each chapter, here I present a synthesis of the main outputs of this thesis work, the limitations and the perspectives and a general conclusion.

SYNTHESIS OF THE RESULTS

Invertebrates are particularly important in regulating ecosystem functioning, by for instance providing food to high level consumers such as fishes or seabirds and facilitating the movement of carbon and nutrients through the food web (Dame *et al.*, 2001; Ehrnsten *et al.*, 2020). Suspension feeders are also essential for maintaining water clarity (Davies *et al.*, 1989; Hily, 1991; Ostroumov, 2005), and some species are significant economic resources (Alves *et al.*, 2020; Caddy, 1989; Dulvy *et al.*, 2003). In the first 2 chapters I have studied the changes in taxonomic diversity and assemblage distribution of benthic invertebrates following changes in immersion time, type of AFH and biogeographical differences. In the second chapter, I also focused on small taxa such as amphipods that were disregarded in previous monitoring programs.

The first chapter highlighted significant variations in the invertebrate composition between 6 and 18 months after the initial immersion in 3 commercial harbours of the French Mediterranean coast. The results showed an increase in the total abundance, taxonomic richness and Pielou's evenness of invertebrate assemblages dwelling in AFH as well as a greater abundance of ecologically and economically important taxa such as Decapoda. In addition, taxonomic composition was found more similar within and between harbours over time which suggests a convergence in community composition through time of immersion. The second chapter showed regional differences in diversity and assemblage composition, partly explained by differences in seawater chlorophyll-a, a proxy for nutrient concentration. This chapter also showed that invertebrate assemblages varied within ports,

depending on the type of artificial fish habitats (pontoon suspended and dock-mounted AFH). I propose that these differences could be explained by differences in light availability. Both chapters also showed differences among ports, highlighting that local environmental context might play a role in shaping invertebrate communities.

Using stable isotope analysis, the third chapter investigated the trophic connectivity between marinas and adjacent *Posidonia oceanica* meadows and how the exchanges of organic matter could be affected by the presence of AFH inside marinas. Indeed, since several benthic species were filter feeders, we expected that particulate organic matter could be sequestered within equipped marinas, and this could affect the stable isotopic composition of organic matter in the water column and the sediment within ports and seagrass meadows. In addition, due to the function of AFH in attracting fishes by providing refuge and food, we expected that fishes would feed on AFH and transport this material outside the port. I found an isotopic enrichment (^{15}N) of particulate organic matter (POM) within unequipped marinas and also within their adjacent seagrass meadows. In addition, higher ^{15}N values were found in the sedimentary organic matter (SOM) and in the *P. oceanica* leaves located in the seagrass meadows close to unequipped marinas compared to the meadows close to marinas where AFH were present. The ^{15}N enrichment is considered an indicator of human-derived nutrients and this finding suggests that AFH contribute to reducing nutrient enrichment of the water inside the marinas and limit the export to seagrass. I also found evidence that invertivorous fishes may partially rely as POM as food source and that their faeces contribute to the sedimentary organic matter within seagrass meadows. However, no significant differences were detected in relation to the presence of AFH.

So far, my results show that AFH (1) support diverse benthic communities, including filter feeders and other potential prey for invertivorous fishes and (2) might sequester anthropogenic nutrients and limit their export to adjacent seagrass meadows. In addition, fishes seem to play an active role in exporting organic matter from marinas to seagrass meadows. Previous studies have shown the important role of AFH for supporting fish populations (Bouchoucha *et al.*, 2016; Mercader *et al.*, 2017b). Indirectly AFH, by supporting fish communities, could play an important role in cross-habitat exchanges.

LIMITATIONS AND PERSPECTIVES

During this thesis, we used data from both post-monitoring programs and field sampling with an improved taxonomic resolution to evaluate the benthic diversity of invertebrate dwelling in AFH. Although costly and time-consuming, the taxa identification in laboratory has allowed me to consider the importance of small taxa such as Amphipoda, which play a paramount ecological role in coastal ecosystems. Due to the potential presence of cryptic species (species morphologically similar but genetically distinct) and the abundance of small invertebrates (< 2mm), some species identified *in situ* might have been misidentified or overlooked. As species identification is crucial in ecological studies (Austen *et al.*, 2016; Resh and Unzicker, 1975), this could affect the accuracy of biodiversity assessments and ecological analyses.

The biodiversity assessment within AFH reported in the first 2 chapters of the thesis mainly focuses on invertebrates, with limited consideration given to photosynthetic organisms colonising AFH. However, photosynthetic organisms are essential in marine ecosystems, providing primary production and habitat structure (Dayton, 1975; Edwards and Connell, 2012). Their abundance and diversity in AFH can differ according to light availability, water quality, herbivory pressure and can influence the overall ecosystem functioning. Similarly, the impact of fish predation on invertebrate communities dwelling in the AFH was not evaluated. However, fish predation can significantly shape community composition and dynamics (Diehl, 1992; Gilinsky, 1984). Future studies should integrate photosynthetic organisms and fish to provide a more holistic view of the ecological interactions within AFH and their potential effects on the local biodiversity. In addition, environmental factors can profoundly influence marine communities. Incorporating local environmental variables such as salinity, light availability, turbidity or anthropogenic disturbances (e.g. pollution, boat traffic) would improve our knowledge on the environmental context at local scale and its influence on the observed patterns on the biodiversity in AFH.

Previous observations reported several fish species feeding on artificial fish habitats such as the Sparidae species *Sarpa salpa* and *Oblada melanura* (Couvray *et al.*, 2021; ECOCEAN personal communication). Sampling a larger number of fish from varied species would have provided more robust data for evaluating trophic connectivity and the ecological impacts of AFH. In addition, including more basal sources, from different

habitats adjacent to marinas such as rocky bottoms would have provided a more comprehensive understanding of the trophic interactions within the coastal ecosystems.

Finally, the sampling campaigns of the thesis were furthered leveraged through additional studies that extend beyond the primary scope of my research (Appendix D). Through collaborative research, initiatives were developed to investigate some ecological processes associated with the AFH. They include (i) functional diversity of invertebrates species dwelling in AFH deployed under floating pontoons and against docks and the trophic relationships between most abundant species identified; (ii) bio-acoustic monitoring study comparing the sounds produced by AFH and by 1m² of *Posidonia oceanica* meadows; and (iii) *alpha* and *beta*-diversity between seaports and marines reserves using environmental DNA (eDNA) metabarcoding.

GENERAL CONCLUSION

The insights across the three chapters of this thesis highlighted the role of AFH as habitat for taxonomically diverse invertebrate assemblages, which may provide food to AFH-dweller fishes and improve environmental conditions. My results show that ports differ one from another, since I found large variability among ports. However, AFH immersion time, how and where they are attached within ports and the environmental context where ports are situated affect their benthic assemblage diversity and composition. This information should be carefully considered in future implementations of AFH. In addition, my findings suggested that, although AFH did not play an important role in cross-habitat trophic connectivity, fishes were important in transporting organic matter to the seagrass meadow adjacent to marinas. AFH, by supporting fish survival, could indirectly contribute to trophic connectivity. I, therefore, can conclude that AFH might play an important role in ameliorating the ecological conditions of degraded habitats and extend their role beyond to adjacent habitats, at least for seagrass meadows adjacent to marinas. Although I am aware that I cannot infer my conclusion to all ports, I think that the experimental use of AFH as ecological engineering solutions should continue in the light of improving ecological rehabilitation, as recommended by the UN Agenda 2030.

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APPENDICES

APPENDIX A: CHAPTER 1 SUPPLEMENTARY MATERIAL

Table S1. Surveyed species recorded in Biohut structures in Le Barcarès (BA), Port-Vendres (PV), and Grand Port maritime de Marseille (MA) in 2013 and 2014.

Phylum	Class	Family	Species	Location(s) recorded
Annelida	Polychaeta	-	*Polychaeta* spp.	BA, MA
Arthropoda	Malacostraca	Alpheidae	*Athanas nitescens*	BA, MA, PV
Arthropoda	Malacostraca	Carcinidae	*Carcinus* spp.	BA, PV
Arthropoda	Malacostraca	Galatheidae	*Galathea squamifera*	MA
Arthropoda	Malacostraca	Grapsidae	*Pachygrapsus marmoratus*	MA, PV
Arthropoda	Malacostraca	Hippolytidae	*Lysmata seticaudata*	BA, MA, PV
Arthropoda	Malacostraca	Inachidae	*Inachus/Macropodia* spp.	BA, MA, PV
Arthropoda	Malacostraca	-	*Isopoda* spp.	BA, MA, PV
Arthropoda	Malacostraca	Majidae	*Maja crispata*	BA
Arthropoda	Malacostraca	Majidae	*Maja* spp.	MA, PV
Arthropoda	Malacostraca	Eriphiidae	*Eriphia verrucosa*	BA, MA, PV
Arthropoda	Malacostraca	Palaemonidae	*Palaemon* spp.	BA, MA, PV
Arthropoda	Malacostraca	Palaemonidae	*Periclimenes* spp.	MA
Arthropoda	Malacostraca	Porcellanidae	*Pisidia* spp.	BA, MA, PV
Arthropoda	Malacostraca	Xanthidae	*Xantho poressa*	BA, PV
Echinodermata	Echinoidea	Echinidae	*Paracentrotus lividus*	BA, PV
Echinodermata	Ophiuroidea	Amphiuridae	*Amphipholis squamata*	BA
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiocomina nigra*	BA
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiopsila aranea*	BA
Echinodermata	Ophiuroidea	Ophiodermatidae	*Ophioderma longicauda*	BA
Echinodermata	Ophiuroidea	Ophiothricidae	*Ophiothrix fragilis*	BA, PV
Echinodermata	Ophiuroidea	-	*Ophiurida* spp.	BA, PV
Mollusca	Bivalvia	Anomiidae	*Anomia ephippium*	MA, PV
Mollusca	Bivalvia	Cardiidae	*Acanthocardia* spp.	PV
Mollusca	Bivalvia	Cardiidae	*Cerastoderma edule*	BA, MA, PV
Mollusca	Bivalvia	Limidae	*Limaria hians*	BA, MA, PV
Mollusca	Bivalvia	Mactridae	*Lutraria* spp.	BA, MA, PV
Mollusca	Bivalvia	Mytilidae	*Modiolarca subpicta*	BA
Mollusca	Bivalvia	Ostreidae	*Ostrea edulis*	MA
Mollusca	Bivalvia	Pectinidae	*Lissopecten hyalinus*	BA
Mollusca	Bivalvia	Pectinidae	*Mimachlamys varia*	BA, MA, PV
Mollusca	Cephalopoda	Sepiidae	*Sepia officinalis*	PV
Mollusca	Gastropoda	Calliostomatidae	*Calliostoma zizyphinum*	PV
Mollusca	Gastropoda	Cerithiidae	*Bittium reticulatum*	BA, PV
Mollusca	Gastropoda	Columbellidae	*Columbella rustica*	BA, MA, PV
Mollusca	Gastropoda	Facelinidae	*Cratena peregrina*	BA
Mollusca	Gastropoda	Fissurellidae	*Diodora graeca*	PV
Mollusca	Gastropoda	Littorinidae	*Melarhaphe neritoides*	MA
Mollusca	Gastropoda	Muricidae	*Hexaplex trunculus*	BA

Mollusca	Gastropoda	Muricidae	*Ocenebra erinaceus*	BA, MA, PV
Mollusca	Gastropoda	Muricidae	*Ocinebrina edwardsii*	BA, PV
Mollusca	Gastropoda	Muricidae	*Thophonopsis muricatus*	PV
Mollusca	Gastropoda	Nassariidae	*Nassarius incrassatus*	BA, MA, PV
Mollusca	Gastropoda	Nassariidae	*Nassarius* spp.	BA, MA, PV
Mollusca	Gastropoda	Plyceridae	*Polycera quadrilineata*	BA
Mollusca	Gastropoda	Trochidae	*Gibbula magus*	BA, PV
Platyhelminthes	Turbellaria	Discocelidae	*Discocelis tigrina*	MA, PV
Platyhelminthes	Turbellaria	Eurylepidae	*Pseudoceros maximus*	MA

Table S2. Invertebrate species surveyed between 2013 and 2017 in artificial structures (Dock Biohut: D; Pontoon Biohut, P) installed within 21 harbours, in 19 cities in France and Monaco during monitoring (total = 115 spp.).

Phylum	Class	Family	Species	Biohut type
Annelida	Echiura	Bonelliidae	*Bonellia viridis*	D, P
Annelida	Polychaeta	Arenicolidae	*Arenicola* spp.	P
Annelida	Polychaeta	Eunicidae	*Leodice harassii*	P
Annelida	Polychaeta	Eunicidae	*Leodice torquata*	P
Annelida	Polychaeta	Hesionidae	*Hesione pantherina*	D, P
Annelida	Polychaeta	Nereidae	*Nereis* spp.	P
Annelida	Polychaeta	-	*Polychaeta* spp.	D, P
Arthropoda	Malacostraca	Alpheidae	*Alpheus macrocheles*	D, P
Arthropoda	Malacostraca	Alpheidae	*Athanas nitescens*	D, P
Arthropoda	Malacostraca	-	*Brachyura* spp.	P
Arthropoda	Malacostraca	Carcinidae	*Carcinus aestuarii*	D, P
Arthropoda	Malacostraca	Carcinidae	*Carcinus* spp.	D, P
Arthropoda	Malacostraca	Dromiidae	*Dromia personata*	D, P
Arthropoda	Malacostraca	Galatheidae	*Galathea* spp.	P
Arthropoda	Malacostraca	Galatheidae	*Galathea squamifera*	D
Arthropoda	Malacostraca	Gammaridae	*Gammarus* spp.	P
Arthropoda	Malacostraca	Grapsidae	*Pachygrapsus marmoratus*	D, P
Arthropoda	Malacostraca	Hippolytidae	*Hippolyte* spp.	P
Arthropoda	Malacostraca	Hippolytidae	*Lysmata seticaudata*	D, P
Arthropoda	Malacostraca	Inachidae	*Inachus/Macropodia* spp.	D, P
Arthropoda	Malacostraca	-	*Isopoda* spp.	D, P
Arthropoda	Malacostraca	Leucosiidae	*Ebalia* spp.	D
Arthropoda	Malacostraca	Majidae	*Macropodia* spp.	P
Arthropoda	Malacostraca	Majidae	*Maja crispata*	D
Arthropoda	Malacostraca	Majidae	*Maja* spp.	D, P
Arthropoda	Malacostraca	-	*Malacostraca* spp.	P
Arthropoda	Malacostraca	Eriphiidae	*Eriphia verrucosa*	D, P
Arthropoda	Malacostraca	Mysidacea	*Mysidacea* spp.	P

Arthropoda	Malacostraca	Paguridae	*Pagurus anachoretus*	D
Arthropoda	Malacostraca	Palaemonidae	*Palaemon* spp.	D, P
Arthropoda	Malacostraca	Palaemonidae	*Periclimenes* spp.	D
Arthropoda	Malacostraca	Polybiidae	*Liocarcinus* spp.	D
Arthropoda	Malacostraca	Porcellanidae	*Pisidia longicornis*	P
Arthropoda	Malacostraca	Porcellanidae	*Pisidia longimana*	P
Arthropoda	Malacostraca	Porcellanidae	*Pisidia* spp.	D, P
Arthropoda	Malacostraca	Porcellanidae	*Porcellana platycheles*	P
Arthropoda	Malacostraca	Processidae	*Processa* spp.	D, P
Arthropoda	Malacostraca	Sphaeromatidae	*Sphaeromatidae* spp.	P
Arthropoda	Malacostraca	Xanthidae	*Xantho poressa*	D
Echinodermata	Asteroidea	Asteriidae	*Marthasterias glacialis*	D
Echinodermata	Asteroidea	Asterinidae	*Asterina gibbosa*	D, P
Echinodermata	Asteroidea	Astropectinidae	*Astropecten irregularis*	D
Echinodermata	Crinoidea	Antedonidae	*Antedon* spp.	P
Echinodermata	Echinoidea	Echinidae	*Gracilechinus acutus*	P
Echinodermata	Echinoidea	Echinidae	*Paracentrotus lividus*	D, P
Echinodermata	Holothuroidea	Holothuroiidea	*Holothuria forskali*	P
Echinodermata	Holothuroidea	Holothuroiidea	*Holothuria* spp.	D, P
Echinodermata	Ophiuroidea	Amphiuridae	*Amphipholis squamata*	D, P
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiocomina nigra*	D
Echinodermata	Ophiuroidea	Ophiocomidae	*Ophiopsila aranea*	D, P
Echinodermata	Ophiuroidea	Ophiodermatidae	*Ophioderma longicauda*	D, P
Echinodermata	Ophiuroidea	Ophiothricidae	*Ophiothrix fragilis*	D, P
Echinodermata	Ophiuroidea	-	*Ophiurida* spp.	D
Mollusca	Bivalvia	Anomiidae	*Anomia ephippium*	D, P
Mollusca	Bivalvia	Arcidae	*Arca noae*	D, P
Mollusca	Bivalvia	-	*Bivalvia* spp.	P
Mollusca	Bivalvia	Cardiidae	*Acanthocardia* spp.	D, P
Mollusca	Bivalvia	Cardiidae	*Cerastoderma edule*	D, P
Mollusca	Bivalvia	Cardiidae	*Cerastoderma glaucum*	P
Mollusca	Bivalvia	Cardiidae	*Parvicardium scriptum*	D, P
Mollusca	Bivalvia	Donacidae	*Donax* spp.	D, P
Mollusca	Bivalvia	Limidae	*Lima lima*	P
Mollusca	Bivalvia	Limidae	*Limaria hians*	D, P
Mollusca	Bivalvia	Mactridae	*Lutraria* spp.	D, P
Mollusca	Bivalvia	Mytilidae	*Modiolarca subpicta*	D, P
Mollusca	Bivalvia	Ostreidae	*Ostrea edulis*	D, P
Mollusca	Bivalvia	Ostreidae	*Ostreidae* spp.	P
Mollusca	Bivalvia	Pectinidae	*Lissopecten hyalinus*	D
Mollusca	Bivalvia	Pectinidae	*Mimachlamys varia*	D, P
Mollusca	Bivalvia	Thraciidae	*Thracia* spp.	P
Mollusca	Bivalvia	Veneridae	*Chamalea gallina*	P
Mollusca	Bivalvia	Verenidae	*Callista chione*	P
Mollusca	Cephalopoda	Sepiidae	*Sepia officinalis*	D
Mollusca	Gastropoda	Buccinidae	*Buccinum humphreysianum*	D
Mollusca	Gastropoda	Calliostomatidae	*Calliostoma zizyphinum*	D, P

Mollusca	Gastropoda	Cerithiidae	*Bittium reticulatum*	D, P
Mollusca	Gastropoda	Cerithiidae	*Cerithium vulgatum*	D
Mollusca	Gastropoda	Columbellidae	*Columbella rustica*	D, P
Mollusca	Gastropoda	Doridiidae	*Doris verrucosa*	D
Mollusca	Gastropoda	Epitonidae	*Epitonium clathrus*	P
Mollusca	Gastropoda	Facelinidae	*Cratena peregrina*	D, P
Mollusca	Gastropoda	Fissurellidae	*Diodora graeca*	D
Mollusca	Gastropoda	Flabellinidae	*Flabellina* spp.	P
Mollusca	Gastropoda	-	*Gastropoda* spp.	D
Mollusca	Gastropoda	Goniodorididae	*Goniodoris castanea*	P
Mollusca	Gastropoda	Haliotidae	*Haliotis tuberculata*	D
Mollusca	Gastropoda	Haminoeidae	*Haminoea* spp.	D
Mollusca	Gastropoda	Hydrobiidae	*Peringia ulvae*	P
Mollusca	Gastropoda	Littorinidae	*Melarhaphe neritoides*	D
Mollusca	Gastropoda	Muricidae	*Bolinus brandaris*	D
Mollusca	Gastropoda	Muricidae	*Hexaplex trunculus*	D
Mollusca	Gastropoda	Muricidae	*Ocenebra erinaceus*	D
Mollusca	Gastropoda	Muricidae	*Ocinebrina edwardsii*	D, P
Mollusca	Gastropoda	Muricidae	*Thophonopsis muricatus*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius corniculum*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius incrassatus*	D, P
Mollusca	Gastropoda	Nassariidae	*Nassarius* spp.	D, P
Mollusca	Gastropoda	Nassariidae	*Tritia* spp.	D, P
Mollusca	Gastropoda	Naticidae	*Euspira* spp.	D
Mollusca	Gastropoda	Patellidae	*Patella* spp.	D, P
Mollusca	Gastropoda	Plyceridae	*Polycera hedgpethi*	D, P
Mollusca	Gastropoda	Plyceridae	*Polycera quadrilineata*	D, P
Mollusca	Gastropoda	Trochidae	*Gibbula magus*	D, P
Mollusca	Gastropoda	Trochidae	*Gibbula umbilicalis*	D, P
Mollusca	Gastropoda	Trochidae	*Jujubinus gravinae*	D
Mollusca	Gastropoda	Trochidae	*Jujubinus striatus*	D, P
Mollusca	Gastropoda	Trochidae	*Trochidae* spp.	D
Mollusca	Gastropoda	Turritellidae	*Turritella communis*	D
Platyhelminthes	Turbellaria	Discocelidae	*Discocelis tigrina*	D, P
Platyhelminthes	Turbellaria	Euryleptidae	*Oligocladus sanguinolentus*	P
Platyhelminthes	Turbellaria	Euryleptidae	*Prostheceraeus moseleyi*	P
Platyhelminthes	Turbellaria	Euryleptidae	*Pseudoceros maximus*	D, P
Platyhelminthes	Turbellaria	Pseudocerotidae	*Thysanozoon brocchii*	D, P
Platyhelminthes	Turbellaria	Stylocomoplanidae	*Comoplana agilis*	P

Table S3. Temporal comparisons (with 95% confidence intervals: CI) of invertebrate assemblages in Dock Biohut across harbours (random factor) in Year 1 to Year 2 (linear mixed effects models). Significant metrics shown in bold.

Response	Contrast	Lower CI	Upper CI	Test stat	*df*	*p*
Total abundance	**1.69**	**1.08**	**2.66**	**2.36**	**1,42**	**0.02**
Species richness	**1.28**	**1.03**	**1.58**	**2.28**	**1,42**	**0.02**
Shannon (H)	0.14	-0.26	0.54	0.70	1,42	0.48
Pielou's evenness (J)	**0.08**	**0.002**	**0.16**	**2.07**	**1,40**	**0.04**
Malacostraca abundance	**3.69**	**2.06**	**6.63**	**4.50**	**1,42**	**<0.0001**
Bivalvia abundance	1.16	0.60	2.24	0.45	1,42	0.66
Gastropoda abundance	0.99	0.54	1.80	-0.04	1,42	0.97
Ophiuroidea abundance	0.84	0.27	2.66	-0.31	1,42	0.76

Table S4. Mean ± SE total abundance, biodiversity, and abundance of classes of invertebrates surveyed within Biohut structures in year 1 and year 2 since installation.

	Year 1	Year 2
Total abundance	46.30 ± 7.93	75.38 ± 11.25
Species richness	7.20 ± 0.42	9.13 ± 1.15
Shannon diversity (H)	1.44 ± 0.08	1.58 ± 0.18
Pielou's evenness (J)	0.74 ± 0.03	0.82 ± 0.02
Malacostraca abundance	10.97 ± 1.90	39.00 ± 5.81
Bivalvia abundance	6.33 ± 1.53	8.13 ± 2.07
Gastropoda abundance	13.70 ± 3.83	17.50 ± 6.16
Ophiuroidea abundance	14.73 ± 7.15	7.50 ± 3.79

Table S5. Temporal comparisons (with 95% confidence intervals: CI) of potentially exploited species surveyed contributing >5% of the total abundance of invertebrate assemblages in surveyed Biohuts in Year 1 and Year 2 (linear mixed effects models) [30].

Response	Contrast	Lower CI	Upper CI	Test stat	*df*	*p*
***Palaemon* spp. abundance**	1.81	0.81	4.07	1.49	1,42	0.14
***Mimachlamys varia* abundance**	1.10	0.52	2.31	0.25	1,42	0.80

Table S6. Mean ± SE total abundance of commercially exploitable species in surveyed Dock Biohut structures in Year 1 and Year 2 [30].

	Year 1	**Year 2**
***Carcinus* spp.**	0.47 ± 0.23	0.00 ± 0.00
Cerastoderma edule	0.17 ± 0.07	0.00 ± 0.00
Galathea squamifera	0.13 ± 0.08	0.19 ± 0.14
Melarhaphe neritoides	0.03 ± 0.03	0.00 ± 0.00
Mimachlamys varia	5.63 ± 1.50	6.63 ± 1.70
Ostrea edulis	0.03 ± 0.03	0.00 ± 0.00
***Palaemon* spp.**	4.60 ± 1.50	7.81 ± 2.00
Paracentrotus lividus	0.30 ± 0.16	2.63 ± 1.06
***Periclimenes* spp.**	0.00 ± 0.00	0.75 ± 0.44
***Polychaeta* spp.**	0.00 ± 0.00	0.56 ± 0.30
Sepia officinalis	0.07 ± 0.05	0.00 ± 0.00

APPENDIX B: CHAPTER 2 SUPPLEMENTARY MATERIAL

Table S1. (a) Location (west and east region in relation to the Rhone delta) and size (area, depth and boat capacity) of the 4 marinas sampled during autumn 2021 (A 2021 database), (b) Biohut installation date and number per type in each of these marinas. MAP: Marseillan-Plage, PGA: Port-Gardian, SPE: Saint-Pierre des Embiez and CPC: Cannes Port-Canto.

a. Marinas					b. Biohut installed		
Region	**Name**	**Area (ha)**	**Depth (m)**	**Boats capacity**	**Installation date**	**N. dock Biohut**	**N. pontoon Biohut**
West	MAP	5.5	2	200	03/2017	4	47
	PGA	5	3	375	11/2017	4	44
East	SPE	7	3	750	12/2017	16	45
	CPC	10.5	4	553	06/2018	13	22

Table S2. Number of pontoon and dock Biohut considered in each port and their location (west and east region in relation to the Rhone delta) for all databases analysed.

Databases	Region	Ports	N. of Pontoon Biohut sampled	N. of Dock Biohut sampled
A 2021	West	MAP	3	-
		PGA	3	-
	East	SPE	3	-
		CPC	3	-
A 2013	West	BAR	12	-
		AGD	9	3
	East	GPM	-	12
		BRU	3	9
S 2019-2022	West	ARG	3	-
		CANRO	3	-
		NAR	3	-
		MAP	2	-
		PGA	3	-
	East	SMM	2	-
		COG	3	-
		CVP	2	-
		RAY	2	-
		CRO	3	-
A 2021 reduced	East	SPE	3	3
		CPC	3	3
A 2013 reduced	West	AGD	3	3
	East	BRU	3	3

Table S3. Mean number of individuals per Biohut (± SE) for each taxon in the two regions (west and east of the Rhone delta) from A 2013, S 2019-2022 and A 2021 databases. n indicate number of Biohut.

Phylum Class Order Family Specie	Taxa	A 2013		S 2019-2022		A 2021	
		West region (n = 24)	East region (n = 24)	West region (n = 14)	East region (n = 12)	West region (n = 6)	East region (n = 6)
Total		109.83 ± 30.03	53.38 ± 9.8	76 ± 30.95	90.17 ± 27.05	1,724 ± 251.21	1,570.5 ± 220.83
Annelida	Annelida	-	-	0.21 ± 0.15	1.67 ± 1.32	-	-
Polychaeta	Polychaeta	0.08 ± 0.08	-	7.71 ± 4.57	2.67 ± 1.9	-	-
Echiuroidea							
Bonelliidae	Bonelliidae	0.42 ± 0.24	-	0.07 ± 0.07	-	-	-
Bonellia viridis	*B. viridis*	-	-	-	-	-	60 ± 40.41
Eunicida							
Eunicidae	Eunicidae	-	-	0.36 ± 0.36	0.83 ± 0.37	3.67 ± 1.50	7 ± 4.49
Eunice pennata	*E. pennata*	-	-	-	-	0.33 ± 0.33	-
Eunice sp.	*Eunice* sp.	-	-	-	-	0.33 ± 0.33	-
Eunice vittata	*E. vittata*	-	-	-	-	0.33 ± 0.33	0.67 ± 0.67
Marphysa sp.	*Marphysa* sp.	-	-	-	-	1.67 ± 1.67	0.33 ± 0.33
Lumbrineridae	Lumbrineridae	-	-	-	-	0.33 ± 0.33	-
Phyllodocida							
Hesionidae	Hesionidae	-	-	-	-	2 ± 2	0.67 ± 0.67
Nephtyidae	Nephtyidae	-	-	1.36 ± 1.01	-	28.33 ± 12.82	8 ± 5.39
Nereididae	Nereididae	-	-	0.43 ± 0.25	0.75 ± 0.46	-	-
Nereis sp.	*Nereis* sp.	-	-	-	-	13 ± 4.7	132.67 ± 50.11
Platynereis sp.	*Platynereis* sp.	-	-	-	-	2.33 ± 1.96	28.33 ± 10.36
Phyllodocidae	Phyllodocidae	-	-	0.07 ± 0.07	0.08 ± 0.08	9.67 ± 6.68	10 ± 4.59
Polynoidae	Polynoidae	-	-	0.57 ± 0.43	-	11.33 ± 2.72	2.33 ± 1.58
Syllidae	Syllidae	-	-	-	-	1.33 ± 1.33	4 ± 2.58
Sabellida							
Sabellidae	Sabellidae	-	-	-	-	0.33 ± 0.33	-
Laonome kroyeri	*L. kroyeri*	-	-	-	-	5.33 ± 5.33	-
Sabella spallanzanii	*S. spallanzanii*	-	-	-	-	9.33 ± 5.72	-
Serpulidae	Serpulidae	-	-	-	-	26 ± 13.38	16 ± 7.83

Hydroides sp.	*Hydroides* sp.	-	-	-	-	0.67 ± 0.67	-
Serpula vermicularis	*S. vermicularis*	-	-	-	-	3.33 ± 2.35	5 ± 2.91
Spirobranchus lamarcki	*S. lamarcki*	-	-	-	-	0.67 ± 0.67	-
Terebellida							
Cirratulidae	Cirratulidae	-	-	-	-	6.67 ± 2.51	6.33 ± 2.28
Aphelochaeta filiformis	*A. filiformis*	-	-	-	-	0.33 ± 0.33	-
Cirriformia tentaculata	*C. tentaculata*	-	-	-	-	0.33 ± 0.33	-
Terebellidae	Terebellidae	-	-	2.5 ± 2.5	18 ± 10.91	10.33 ± 3.7	7 ± 4.25
Amphitrite sp.	*Amphitrite* sp.	-	-	-	-	10 ± 5.06	-
Capitellida							
Capitellidae	Capitellidae	-	-	-	-	47 ± 25.76	3 ± 3
Sipuncula							
Sipunculidae	Sipunculidae	-	-	-	-	9.33 ± 5.88	10.67 ± 7.71
Arthropoda							
Malacostraca							
Amphipoda	Amphipoda	-	-	1.43 ± 1.16	-	-	-
Ampeliscidae	Ampeliscidae	-	-	-	-	0.33 ± 0.33	-
Caprellidae	Caprellidae	-	-	-	-	31.33 ± 10.57	-
Cheluridae	Cheluridae	-	-	-	-	0.33 ± 0.33	-
Colomastigidae	Colomastigidae	-	-	-	-	7 ± 2.91	8.33 ± 3.32
Corophiidae	Corophiidae	-	-	-	-	216.67 ± 106.88	140.67 ± 33.94
Dexaminidae	Dexaminidae	-	-	-	-	11 ± 2.91	1 ± 0.68
Gammaridae	Gammaridae	-	-	-	-	38 ± 11.22	48.33 ± 17.91
Isaeidea	Isaeidae	-	-	-	-	-	0.67 ± 0.67
Ischyroceridae	Ischyroceridae	-	-	-	-	10.33 ± 6.94	-
Leucothoidae	Leucothoidae	-	-	-	-	20.67 ± 5.08	-
Lysianassidae	Lysianassidae	-	-	-	-	6.33 ± 6.33	0.67 ± 0.67
Melitidae	Melitidae	-	-	-	-	27 ± 9.22	617 ± 115.68
Talitridae	Talitridae	-	-	-	-	3.33 ± 2.17	-
Decapoda	Decapoda	-	-	-	3 ± 2.03	-	-
Alpheidae	Alpheidae	0.38 ± 0.27	2.13 ± 0.64	2.36 ± 1.64	7.92 ± 3.61	-	-
Alpheus dentipes	*A. dentipes*	-	-	-	-	13 ± 6.17	-
Alpheus macrocheles	*A. macrocheles*	-	-	-	-	51.17 ± 31.57	2 ± 1.03
Athanas nitescens	*A. nitescens*	-	-	-	-	4 ± 3.61	58.33 ± 30.25
Carcinidae	Carcinidae	2.63 ± 0.97	0.42 ± 0.21	0.07 ± 0.07	-	-	-
Carcinus aestuarii	*C. aestuarii*	-	-	-	-	0.33 ± 0.33	-
Dromiidae	Dromiidae	-	0.46 ± 0.23	-	-	-	-
Epialtidae							
Herbstia condyliata	*H. condyliata*	-	-	-	-	0.33 ± 0.33	0.5 ± 0.5

Eriphiidae	Eriphiidae	1.33 ± 0.68	1.17 ± 0.35	1.93 ± 0.87	-	-	-
Eriphia verrucosa	*E. verrucosa*	-	-	-	-	1 ± 0.26	2.67 ± 1.78
Galatheidae	Galatheidae	-	0.21 ± 0.1	-	-	-	-
Grapsidae	Grapsidae	0.25 ± 0.17	1.33 ± 0.67	6.07 ± 3.25	9.33 ± 5.45	-	-
Pachygrapsus marmoratus	*P. marmoratus*	-	-	-	-	3.33 ± 2.12	22.83 ± 11.61
Lysmatidae	Lysmatidae	0.63 ± 0.33	0.08 ± 0.06	0.14 ± 0.14	0.75 ± 0.66	-	-
Lysmata seticaudata	*L. seticaudata*	-	-	-	-	8.17 ± 4.58	0.67 ± 0.42
Majidae	Majidae	0.08 ± 0.08	0.04 ± 0.04	-	-	-	-
Eurynome aspera	*E. aspera*	-	-	-	-	0.33 ± 0.33	-
Palaemonidae	Palaemonidae	19.54 ± 8.6	21.29 ± 5.46	16.93 ± 3.76	14.92 ± 6.24	-	-
Palaemon elegans	*P. elegans*	-	-	-	-	18.33 ± 5.96	20.33 ± 9.76
Palaemon serratus	*P. serratus*	-	-	-	-	74.33 ± 17.01	27.67 ± 11.96
Pilumnidae	Pilumnidae	-	-	0.29 ± 0.29	1.92 ± 1.29	-	-
Pilumnus hirtellus	*P. hirtellus*	-	-	-	-	13.33 ± 8.04	7.33 ± 3.53
Pilumnus villosissimus	*P. villosissimus*	-	-	-	-	0.33 ± 0.33	1 ± 0.68
Pirimelidae							
Sirpus zariquieyi	*S. zariquieyi*	-	-	-	-	-	0.33 ± 0.33
Polybiidae	Polybiidae	-	0.04 ± 0.04	-	-	-	-
Porcellanidae	Porcellanidae	-	0.46 ± 0.2	5.21 ± 3.1	22.08 ± 20.76	-	-
Pisidia bluteli	*P. bluteli*	-	-	-	-	580.67 ± 158.26	1 ± 0.68
Porcellana platycheles	*P. platycheles*	-	-	-	-	8.33 ± 6.8	0.33 ± 0.33
Processidae	Processidae	-	-	0.07 ± 0.07	-	-	-
Xanthidae	Xanthidae	-	-	0.07 ± 0.07	-	-	-
Xantho hydrophilus	*X. hydrophilus*	-	-	-	-	0.33 ± 0.33	-
Xantho pilipes	*X. pilipes*	-	-	-	-	-	-
Xantho poressa	*X. poressa*	-	-	-	-	0.67 ± 0.67	3.33 ± 2.23
Isopoda	Isopoda	0.46 ± 0.22	0.33 ± 0.12	-	-	-	-
Anthuridae	Anthuridae	-	-	-	-	6 ± 2.19	55 ± 36.13
Cirolanidae	Cirolanidae	-	-	-	-	-	0.33 ± 0.33
Cymothoidae	Cymothoidae	-	-	0.43 ± 0.43	-	-	-
Gnathiidae	Gnathiidae	-	-	-	-	0.67 ± 0.67	2.67 ± 1.98
Hognathidae							
Cleantis prismatica	*C. prismatica*	-	-	-	-	0.33 ± 0.33	-
Idoteidae	Idoteidae	-	-	0.07 ± 0.07	-	9.67 ± 4.24	-
Joeropsididae	Joeropsididae	-	-	-	-	9.67 ± 4.72	-
Sphaeromatidae	Sphaeromatidae	-	-	0.07 ± 0.07	-	-	1.67 ± 1.67
Tanaidacea							
Tanaididae	Tanaididae	-	-	-	-	0.33 ± 0.33	3.67 ± 3.67
Pycnogonida							

Pantopoda	Pantopoda	-	-	-	-	-	1 ± 1
Thecostraca							
Balanomorpha							
Balanidae	Balanidae	-	-	-	-	2.67 ± 1.98	2.67 ± 2.67
Chordata							
Ascidiacea							
Phlebobranchia							
Ascidiidae	Ascidiidae	-	-	-	-	9.33 ± 5.05	115.67 ± 58.09
Stolidobranchia							
Pyuridae							
Microcosmus sabatieri	*M. sabatieri*	-	-	-	-	1.33 ± 1.33	-
Echinodermata							
Asteroidea							
Paxillosida							
Astropectinidae	Astropectinidae	-	0.04 ± 0.04	-	-	-	-
Valvatida							
Asterinidae	Asterinidae	0.04 ± 0.04	-	-	-	-	-
Crinoidea							
Comatulida							
Antedonidae							
Antedon mediterranea	*A. mediterranea*	-	-	-	-	4.67 ± 4.67	-
Echinoidea							
Camarodonta							
Parechinidae	Parechinidae	0.67 ± 0.3	-	0.07 ± 0.07	0.08 ± 0.08	-	-
Paracentrotus lividus	*P. lividus*	-	-	-	-	1 ± 0.63	-
Holothuroidea							
Holothuriida							
Holothuriidae	Holothuriidae	-	-	-	-	4.33 ± 2.85	0.33 ± 0.33
Ophiuroidea							
Amphilepidida							
Amphiuridae	Amphiuridae	2.08 ± 2.08	-	-	-	-	-
Amphipholis squamata	*A. squamata*	-	-	-	-	48 ± 12.45	-
Ophiopsilidae	Ophiopsilidae	11.33 ± 5.59	-	-	-	-	-
Ophiotrichidae	Ophiotrichidae	26.5 ± 14.54	-	0.07 ± 0.07	-	-	-

Ophiothrix fragilis	*O. fragilis*	-	-	-	-	4.17 ± 2.2	-
Ophiacanthida							
Ophiodermatidae	Ophiodermatidae	8.17 ± 5.48	-	-	-	-	-
Ophiotomidae	Ophiotomidae	3.13 ± 1.94	-	-	-	-	-
Ophiurida	Ophiurida	1.67 ± 1.21	-	0.36 ± 0.25	-	-	-
Mollusca							
Bivalvia	Bivalvia	-	-	-	0.17 ± 0.11	-	-
Adapedonta							
Hiatellidae							
Hiatella arctica	*H. arctica*	-	-	-	-	2 ± 2	-
Arcida							
Arcidae							
Arca noae	*A. noae*	-	-	-	-	2.33 ± 2.33	-
Barbatia barbata	*B. barbata*	-	-	-	-	2 ± 1.37	27.33 ± 15.55
Tetrarca tetragona	*T. tetragona*	-	-	-	-	0.33 ± 0.33	1.33 ± 0.67
Noetiidae							
Striarca lactea	*S. lactea*	-	-	-	-	5.33 ± 4.58	19.33 ± 11.06
Cardiida							
Cardiidae	Cardiidae	3.17 ± 1.3	0.25 ± 0.11	0.14 ± 0.14	3.42 ± 0.86	-	-
Cerastoderma sp.	*Cerastoderma* sp.	-	-	-	-	0.33 ± 0.33	2.33 ± 1.5
Donacidae							
Donax trunculus	*D. trunculus*	-	-	-	-	0.67 ± 0.67	0.33 ± 0.33
Tellinidae							
Peronaea planata	*P. planata*	-	-	-	-	0.33 ± 0.33	0.33 ± 0.33
Gastrochaenida							
Gastrochaenidae							
Rocellaria dubia	*R. dubia*	-	-	-	-	-	0.33 ± 0.33
Limida							
Limidae	Limidae	-	0.08 ± 0.06	17.43 ± 14.59	-	-	-
Lima lima	*L. lima*	-	-	-	-	-	0.67 ± 0.67
Limaria hians	*L. hians*	-	-	-	-	3.17 ± 2.79	0.67 ± 0.42
Limaria tuberculata	*L. tuberculata*	-	-	-	-	17 ± 9.19	-
Myida							
Pholadidae							
Barnea candida	*B. candida*	-	-	-	-	-	0.33 ± 0.33

Mytilida								
Mytilidae	Mytilidae	8.42 ± 4.25	0.17 ± 0.08	-	-	-	-
Modiolus barbatus	*M. barbatus*	-	-	-	-	0.67 ± 0.42	15 ± 9.66
Musculus costulatus	*M. costulatus*	-	-	-	-	1.67 ± 1.09	1.67 ± 1.31
Musculus subpictus	*M. subpictus*	-	-	-	-	-	-
Mytilus galloprovincialis	*M. galloprovincialis*	-	-	-	-	182 ± 37.54	30.83 ± 11.08
Ostreida							
Ostreidae	Ostreidae	0.04 ± 0.04	0.04 ± 0.04	-	-	-	-
Ostrea edulis	*O. edulis*	-	-	-	-	0.67 ± 0.42	4.33 ± 1.74
Pectinida							
Anomiidae	Anomiidae	-	0.13 ± 0.13	-	-	-	-
Anomia ephippium	*A. ephippium*	-	-	-	-	3 ± 1.24	10.67 ± 9.87
Pectinidae	Pectinidae	3.17 ± 0.9	1.75 ± 0.61	5 ± 2.18	0.67 ± 0.45	-	-
Mimachlamys varia	*M. varia*	-	-	-	-	30.67 ± 12.8	2.33 ± 0.95
Talochlamys multistriata	*T. multistriata*	-	-	-	-	2.33 ± 1.5	-
Venerida							
Chamidae							
Chama gryphoides	*C. gryphoides*	-	-	-	-	2.67 ± 1.61	1.67 ± 1.67
Mactridae	Mactridae	0.04 ± 0.04	0.21 ± 0.1	-	-	-	-
Veneridae							
Irus irus	*I. irus*	-	-	-	-	0.33 ± 0.33	-
Gastropoda							
Archaeogastropoda							
Patellidae							
Patella caerulea	*P. caerulea*	-	-	-	-	2.33 ± 1.31	0.67 ± 0.67
Caenogastropoda							
Cerithiidae	Cerithiidae	0.38 ± 0.33	1.71 ± 1.04	-	-	-	-
Epitoniidae	Epitoniidae	-	0.04 ± 0.04	-	-	-	-
Littorinimorpha							
Hydrobiidae	Hydrobiidae	0.29 ± 0.29	-	-	-	-	-
Littorinidae	Littorinidae	-	0.04 ± 0.04	-	-	-	-
Naticidae	Naticidae	-	0.04 ± 0.04	-	-	-	-
Neogastropoda							
Buccinidae	Buccinidae	-	0.04 ± 0.04	-	-	-	-
Columbellidae	Columbellidae	12.42 ± 5.97	16.79 ± 6.57	-	-	-	-
Columbella rustica	*C. rustica*	-	-	-	-	1.67 ± 0.8	-
Muricidae	Muricidae	0.38 ± 0.19	0.42 ± 0.22	-	-	-	-

Nassariidae	Nassariidae	0.88 ± 0.71	1.46 ± 0.63	-	-	-	-
Nudibranchia							
Facelinidae	Facelinidae	0.04 ± 0.04	-	-	-	-	-
Flabellinidae	Flabellinidae	0.04 ± 0.04	-	-	-	-	-
Goniodorididae	Goniodorididae	0.04 ± 0.04	-	-	-	-	-
Polyceridae	Polyceridae	0.17 ± 0.13	-	0.07 ± 0.07	-	-	-
Trochida							
Calliostomatidae	Calliostomatidae	-	0.42 ± 0.18	-	-	-	-
Phasianellidae							
Tricolia tenuis	*T. tenuis*	-	-	-	-	-	0.33 ± 0.33
Trochidae	Trochidae	0.58 ± 0.28	1.17 ± 0.61	-	-	-	-
Clanculus cruciatus	*C. cruciatus*	-	-	-	-	0.33 ± 0.33	-
Polyplacophora							
Chitonida							
Chitonidae	Chitonidae	-	-	-	-	0.67 ± 0.67	-
Tonicellidae							
Lepidochitona cinerea	*L. cinerea*	-	-	-	-	0.33 ± 0.33	-
Platyhelminthes	Platyhelminthes	-	-	0.21 ± 0.21	0.67 ± 0.51	-	-
Polycladida							
Discocelididae	Discocelididae	0.38 ± 0.16	0.13 ± 0.13	1.57 ± 0.78	1.08 ± 0.79	-	-
Discocelis tigrina	*D. tigrina*	-	-	-	-	4.33 ± 2.03	-
Euryleptidae	Euryleptidae	-	-	2.64 ± 1.8	-	-	-
Leptoplanidae	Leptoplanidae	-	-	-	0.08 ± 0.08	-	-
Pseudocerotidae	Pseudocerotidae	0.04 ± 0.04	0.5 ± 0.22	-	0.08 ± 0.08	-	-

Table S4. Mean number of individuals (± SE, n = 3) for each taxon sampled on Dock and Pontoon Biohut in each port from A 2013 and A 2021 reduced dataset. AGD: Agde (west region), BRU: Le Brusc (east region), SPE: Saint-Pierre des Embiez (east region) and CPC: Cannes Port-Canto (east region).

Phylum Class Order Family Specie	Taxa	A 2013 reduced				A 2021 reduced			
		AGD		BRU		SPE		CPC	
		Pontoon Biohut	Dock Biohut	Pontoon Biohut	Dock Biohut	Pontoon Biohut	Dock Biohut	Pontoon Biohut	Dock Biohut
Total		60.33 ± 14.5	92.33 ± 59.51	85.67 ± 20.85	81 ± 13.75	1,198.33 ± 66.52	1834 ± 676.57	1,942.67 ± 317.63	406 ± 60.18
Annelida									
Polychaeta									
Amphinomida									
Amphinomidae	Amphinomidae	-	-	-	-	-	3.33 ± 1.76	-	-
Echiuroidea									
Bonelliidae	Bonelliidae	0.33 ± 0.33	-	-	-	-	-	-	-
Bonellia viridis	*B. viridis*	-	-	-	-	1.33 ± 1.33	-	118.67 ± 68.71	5.33 ± 2.4
Eunicida									
Dorvilleidae	Dorvilleidae	-	-	-	-	-	0.67 ± 0.67	-	-
Eunicidae	Eunicidae	-	-	-	-	-	1.33 ± 0.67	14 ± 7.21	4 ± 1.15
Eunice sp.	*Eunice* sp.	-	-	-	-	-	1.33 ± 0.67	-	-
Eunice vittata	*E. vittata*	-	-	-	-	1.33 ± 1.33	-	-	-
Marphysa sp.	*Marphysa* sp.	-	-	-	-	0.67 ± 0.67	2.67 ± 2.67	-	-
Phyllodocida									
Hesionidae	Hesionidae	-	-	-	-	1.33 ± 1.33	2.67 ± 2.67	-	-
Nephtyidae	Nephtyidae	-	-	-	-	-	1.33 ± 0.67	16 ± 9.02	0.67 ± 0.67
Nereis sp.	*Nereis* sp.	-	-	-	-	214 ± 74.57	31.33 ± 12.13	51.33 ± 19.4	3.33 ± 0.67
Platynereis sp.	*Platynereis* sp.	-	-	-	-	39.33 ± 20.08	4.67 ± 3.71	17.33 ± 3.53	-
Phyllodocidae	Phyllodocidae	-	-	-	-	4 ± 2	3.33 ± 1.76	16 ± 8.08	4.67 ± 1.33
Polynoidae	Polynoidae	-	-	-	-	0.67 ± 0.67	2.67 ± 2.67	4 ± 3.06	0.67 ± 0.67

Syllidae	Syllidae	-	-	-	-	8 ± 4.16	-	-	-
Sabellida									
Sabellidae	Sabellidae	-	-	-	-	-	26 ± 26	-	-
Serpulidae	Serpulidae	-	-	-	-	4.67 ± 2.4	2.67 ± 0.67	27.33 ± 13.13	3.33 ± 1.76
Serpula vermicularis	*S. vermicularis*	-	-	-	-	10 ± 4.16	-	-	-
Terebellida									
Cirratulidae	Cirratulidae	-	-	-	-	5.33 ± 2.91	-	7.3 ± 4.06	4 ± 2
Terebellidae	Terebellidae	-	-	-	-	-	11.33 ± 4.67	14 ± 6.43	0.67 ± 0.67
Capitellida									
Capitellidae	Capitellidae	-	-	-	-	-	-	6 ± 6	-
Sipuncula									
Sipunculidae	Sipunculidae	-	-	-	-	1.33 ± 1.33	-	20 ± 14.42	2.67 ± 1.76
Arthropoda									
Malacostraca									
Amphipoda									
Caprellidae	Caprellidae	-	-	-	-	-	2 ± 2	-	-
Colomastigidae	Colomastigidae	-	-	-	-	9.33 ± 6.36	8 ± 3.06	7.33 ± 3.71	2 ± 2
Corophiidae	Corophiidae	-	-	-	-	147.33 ± 47.14	377.33 ± 158.34	134 ± 59.09	32.67 ± 11.22
Dexaminidae	Dexaminidae	-	-	-	-	2 ± 1.15	8.67 ± 8.67	-	-
Gammaridae	Gammaridae	-	-	-	-	74.67 ± 29.36	-	22 ± 7.02	
Isaeidea	Isaeidae	-	-	-	-	1.33 ± 1.33	-	-	-
Lysianassidae	Lysianassidae	-	-	-	-	-	373.33 ± 154.16	-	-
Melitidae	Melitidae	-	-	-	-	370 ± 73.71	471.33 ± 280.62	864 ± 21.63	2 ± 2
Decapoda									
Alpheidae	Alpheidae	-	-	2.67 ± 2.19	-	-	-	-	-
Alpheus dentipes	*A. dentipes*	-	-	-	-	-	2.67 ± 2.67	-	14.67 ± 1.76
Alpheus macrocheles	*A. macrocheles*	-	-	-	-	2.67 ± 1.76	6.67 ± 4.81	1.33 ± 1.33	11.33 ± 3.71
Athanas nitescens	*A. nitescens*	-	-	-	-	73.33 ± 65.50	18.67 ± 5.33	43.33 ± 7.69	139 ± 35.7
Carcinidae	Carcinidae	3.67 ± 0.88	2.33 ± 2.33	-	1 ± 1	-	-	-	-
Diogenidae									
Clibanarius erythropus	*C. erythropus*	-	-	-	-	-	6 ± 2	-	6.67 ± 3.53
Dromiidae	Dromiidae	-	-	0.33 ± 0.33	1.67 ± 1.67	-	-	-	-
Herbstia condyliata	*H. condyliata*	-	-	-	-	1 ± 1	-	-	-
Eriphiidae	Eriphiidae	4.67 ± 4.67	0.67 ± 0.33	0.67 ± 0.33	2 ± 1.53	-	-	-	-
Eriphia verrucosa	*E. verrucosa*	-	-	-	-	5.33 ± 2.96	-	-	-

Grapsidae	Grapsidae	-	0.67 ± 0.33	7.3 ± 4.33	-	-		-	-
Pachygrapsus marmoratus	*P. marmoratus*	-	-	-	-	45.67 ± 12.33	23.33 ± 8.35	-	1.33 ± 1.33
Lysmatidae	Lysmatidae	-	0.67 ± 0.67	-	-	-	-	-	-
Lysmata seticaudata	*L. seticaudata*	-	-	-	-	0.67 ± 0.67	6.67 ± 6.67	0.67 ± 0.67	11.33 ± 3.53
Palaemonidae	Palaemonidae	15.33 ± 6.98	78 ± 60.45	70 ± 22.68	18 ± 7.81	-	-	-	-
Palaemon elegans	*P. elegans*	-	-	-	-	40 ± 9.45	17.33 ± 1.76	0.67 ± 0.67	4 ± 4
Palaemon serratus	*P. serratus*	-	-	-	-	52 ± 11.02	2.67 ± 1.33	3.33 ± 1.33	9.67 ± 9.67
Pilumnidae									
Pilumnus hirtellus	*P. hirtellus*	-	-	-	-	10 ± 5.77	5.33 ± 0.67	4.67 ± 4.67	8 ± 3.06
Pilumnus villosissimus	*P. villosissimus*	-	-	-	-	0.67 ± 0.67	0.67 ± 0.67	1.33 ± 1.33	-
Pirimelidae									
Sirpus zariquieyi	*S. zariquieyi*	-	-	-	-	-	-	0.67 ± 0.67	-
Porcellanidae									
Pisidia bluteli	*P. bluteli*	-	-	-	-	1.33 ± 1.33	2 ± 0	0.67 ± 0.67	17.33 ± 3.53
Porcellana platycheles	*P. platycheles*	-	-	-	-	0.67 ± 0.67	-	-	0.67 ± 0.67
Xanthidae									
Xantho pilipes	*X. pilipes*	-	-	-	-	-	-	-	0.67 ± 0.67
Xantho poressa	*X. poressa*	-	-	-	-	6.67 ± 3.71	1.33 ± 1.33	-	-
Isopoda	Isopoda	-	0.33 ± 0.33	-	-	-	-	-	-
Anthuridae	Anthuridae	-	-	-	-	8 ± 6.11	98 ± 31.64	102 ± 65.43	16.67 ± 7.86
Cirolanidae	Cirolanidae	-	-	-	-	-	-	0.67 ± 0.67	0.67 ± 0.67
Gnathiidae	Gnathiidae	-	-	-	-	-	-	5.33 ± 3.53	-
Joeropsididae	Joeropsididae	-	-	-	-	-	14 ± 14	-	1.33 ± 1.33
Sphaeromatidae	Sphaeromatidae	-	-	-	-	-	-	3.33 ± 3.33	2 ± 1.15
Tanaidacea									
Tanaididae	Tanaididae	-	-	-	-	-	12.67 ± 1.33	7.33 ± 7.33	-
Pycnogonida									
Pantopoda	Pantopoda	-	-	-	-	-	3.33 ± 3.33	2 ± 2	-
Thecostraca									
Balanomorpha									
Balanidae	Balanidae	-	-	-	-	-	-	5.33 ± 5.33	-
Chordata									
Ascidiacea									
Phlebobranchia									

Ascidiidae	Ascidiidae	-	-	-	-	4 ± 4	11.33 ± 5.46	227.33 ± 66.24	12 ± 3.06
Echinodermata									
Asteroidea									
Paxillosida									
Astropectinidae	Astropectinidae	-	-	-	0.33 ± 0.33	-	-	-	-
Holothuroidea									
Holothuriida									
Holothuriidae	Holothuriidae	-	-	-	-	-	-	0.67 ± 0.67	-
Mollusca									
Bivalvia									
Arcida									
Arcidae									
Barbatia barbata	*B. barbata*	-	-	-	-	4.67 ± 3.71	11.33 ± 7.33	50 ± 26.1	0.67 ± 0.67
Tetrarca tetragona	*T. tetragona*	-	-	-	-	0.67 ± 0.67	5.33 ± 4.37	2 ± 1.15	
Noetiidae									
Striarca lactea	*S. lactea*	-	-	-	-	3.33 ± 1.76	8.67 ± 6.77	35.33 ± 18.77	0.67 ± 0.67
Cardiida									
Cardiidae	Cardiidae	8 ± 7.02	7 ± 4.58	1 ± 0.58	-	-	-	-	-
Acanthocardia aculeata	*A. aculeata*	-	-	-	-	-	1.33 ± 0.67	-	-
Cerastoderma sp.	*Cerastoderma* sp.	-	-	-	-	-	27.33 ± 18.56	4.67 ± 2.4	0.67 ± 0.67
Donacidae									
Donax trunculus	*D. trunculus*	-	-	-	-	0.67 ± 0.67	1.33 ± 1.33	-	-
Tellinidae									
Macomangulus tenuis	*M. tenuis*	-	-	-	-	-	8 ± 7.02	-	-
Peronaea planata	*P. planata*	-	-	-	-	-	-	0.67 ± 0.67	-
Gastrochaenida									
Gastrochaenidae									
Rocellaria dubia	*R. dubia*	-	-	-	-	-	-	0.67 ± 0.67	-
Limida									
Limidae									
Lima lima	*L. lima*	-	-	-	-	-	-	1.33 ± 1.33	-
Limaria hians	*L. hians*	-	-	-	-	0.67 ± 0.67	0.67 ± 0.67	0.67 ± 0.67	-
Limaria tuberculata	*L. tuberculata*	-	-	-	-	-	5.33 ± 1.76	-	-
Myida									

Pholadidae									
Barnea candida	*B. candida*	-	-	-	-	0.67 ± 0.67	0.67 ± 0.67	-	-
Mytilida									
Mytilidae	Mytilidae	-	1.67 ± 0.88	0.67 ± 0.33	-	-	-	-	-
Modiolus barbatus	*M. barbatus*	-	-	-	-	-	0.67 ± 0.67	30 ± 15.53	-
Musculus costulatus	*M. costulatus*	-	-	-	-	-	8.67 ± 4.67	3.33 ± 2.4	-
Musculus subpictus	*M. subpictus*	-	-	-	-	-	0.67 ± 0.67	-	-
Mytilus galloprovincialis	*M. galloprovincialis*	-	-	-	-	31 ± 8.89	102.67 ± 23.6	30.67 ± 23.13	-
Ostreida									
Ostreidae									
Ostrea edulis	*O. edulis*	-	-	-	-	4 ± 3.06	1.33 ± 0.67	4.67 ± 2.4	-
Pectinida									
Anomiidae									
Anomia ephippium	*A. ephippium*	-	-	-	-	0.67 ± 0.67	6.67 ± 4.81	20.67 ± 19.68	-
Pectinidae	Pectinidae	2.67 ± 2.67	-	1.33 ± 1.33	-	-	-	-	-
Aequipecten opercularis	*A. opercularis*	-	-	-	-	-	0.67 ± 0.67	-	-
Mimachlamys varia	*M. varia*	-	-	-	-	2 ± 1.15	26 ± 6	2.67 ± 1.76	-
Talochlamys multistriata	*T. multistriata*	-	-	-	-	-	0.67 ± 0.67	-	-
Venerida									
Chamidae									
Chama gryphoides	*C. gryphoides*	-	-	-	-	-	0.67 ± 0.67	3.33 ± 3.33	0.67 ± 0.67
Mactridae	Mactridae	-	-	-	0.33 ± 0.33	-	-	-	-
Gastropoda									
Archaeogastropoda									
Patellidae									
Patella caerulea	*P. caerulea*	-	-	-	-	-	-	1.33 ± 1.33	-
Caenogastropoda									
Cerithiidae	Cerithiidae	-	-	0.33 ± 0.33	5 ± 3.21	-	-	-	-
Bittium sp.	*Bittium* sp.	-	-	-	-	-	4 ± 2	-	18.67 ± 7.69
Epitoniidae	Epitoniidae	-	-	0.33 ± 0.33	-	-	-	-	-
Littorinimorpha									
Littorinidae									
Melarhaphe neritoides	*M. neritoides*	-	-	-	-	-	-	-	0.67 ± 0.67
Neogastropoda									
Columbellidae	Columbellidae	24.33 ± 20.93	0.33 ± 0.33	-	45.67 ± 8.99	-	-	-	-

Columbella rustica	*C. rustica*	-	-	-	-	-	5.33 ± 0.67	-	2 ± 1.15
Fasciolariidae									
Fusinus sp.	*Fusinus* sp.	-	-	-	-	-	2.67 ± 0.67	-	2 ± 2
Muricidae	Muricidae	1 ± 0.58	-	-	-	-	-	-	-
Hexaplex trunculus	*H. trunculus*	-	-	-	-	-	-	-	1.33 ± 0.67
Nassariidae	Nassariidae	-	-	-	1.67 ± 0.88	-	-	-	-
Tritia mutabilis	*T. mutabilis*	-	-	-	-	-	10 ± 1.15	-	18 ± 13.32
Tritia nitida	*T. nitida*	-	-	-	-	-	16.67 ± 1.33	-	33.33 ± 17.37
Trochida									
Calliostomatidae	Calliostomatidae	-	-	-	1.33 ± 0.67	-	-	-	-
Calliostoma sp.	*Calliostoma* sp.	-	-	-	-	-	-	-	0.67 ± 0.67
Phasianellidae									
Tricolia tenuis	*T. tenuis*	-	-	-	-	-	-	0.67 ± 0.67	-
Trochidae	Trochidae	-	-	-	3.67 ± 3.67	-	-	-	-
Clanculus cruciatus	*C. cruciatus*	-	-	-	-	-	8 ± 3.06	-	3.33 ± 2.4
Platyhelminthes									
Polycladida									
Discocelididae	Discocelididae	0.33 ± 0.33	1 ± 1	-	-	-	-	-	-
Pseudocerotidae	Pseudocerotidae	-	-	1 ± 1	0.33 ± 0.33	-	-	-	-

Table S5. Results of the Distance-based multivariate multiple regression (DistLM) marginal test between seawater chlorophyll a concentration ([Chl a]) and taxa composition, number of individuals and species for the 3 databases analysed.

* $p < 0.01$. % indicates the percentage of variation of the assemblages explained by [Chl a].

		Taxa composition		N individuals		N taxa	
	res. df	**F**	**%**	**F**	**%**	**F**	**%**
A 2021	10	4.000*	28.57	1.207	10.77	1.444	12.62
A 2013	46	3.985*	7.97	0.646	1.38	2.043	4.25
S 2019-2022	24	3.139*	11.57	1.555	6.08	2.118	8.11

Table S6. Results of PERMANOVA analyses for differences among regions in the number of individuals of most abundant taxa on (a) A 2021, (b) A 2013 and (c) S 2019-2022 databases. Monte Carlo permutations were used when permutations were limited.
* p-value < 0.05; ** p-value < 0.01; ^ pooling when p > 0.25.

Factors	df	MS	F	MS	F	MS	F	MS	F
a. A 2021		***Nereis* sp.**		**Corophiidae**		**Gammaridae**		**Melitidae**	
[Chl a]	1	4.619	2.419	0.790	1.500	0.198	0.275	17.420	10.038
Region = Re	1	1.103	0.577	2.159	4.102	0.217	0.300	4.616	2.660
Port (Re)	1	1.909	7.852*	0.075	0.128^	0.723	4.414	1.735	11.416**
Residuals	8	0.243		0.583		0.164		0.152	
		Palaemon serratus		***Pisidia bluteli***		**Ascidiidae**		***Mytilus galloprovincialis***	
[Chl a]	1	2.737	0.951	46.003	80.970**	8.384	0.518	7.984	12.353**
Region = Re	1	0.001	0.001	10.089	17.758**	1.033	0.064	0.418	0.647
Port (Re)	1	2.877	32.787**	0.012	0.019^	16.182	39.341**	0.750	1.183^
Residuals	8	0.878		0.638		0.411		0.633	

b. A 2013		**Mytilidae**		**Columbellidae**		**Pectinidae**		**Palaemonidae**	
[Chl a]	1	0.261	0.175	0.449	0.054	0.539	0.122	0.021	0.026
Port habitat	1	3.024	6.440*	0.071	0.009	1.224	0.402	0.009	0.002
Region = Re	1	5.226	11.129**	0.053	0.006	0.062	0.018	2.311	0.505
Port (Re)	1	0.041	0.086^	15.292	14.981**	5.731	12.903**	7.474	12.511**
Residuals	43	0.480		1.021		0.444		0.597	

c. S 2019-2022		**Polychaeta**		**Terebellidae**		**Alpheidae**		**Grapsidae**	
[Chl a]	1	0.012	0.031	2.047	0.745	2.300	1.640	1.668	1.483
Immersion time	1	7.879	5.861*	2.219	0.826	0.474	0.428	0.080	0.188
Region = Re	1	3.985	2.848	1.288	0.476	0.040	0.147	0.197	0.300
Port (Re)	7	1.071	10.146**	2.209	7.119**	1.160	1.988	0.952	1.695
Residuals	15	0.106		0.310		0.584		0.562	
		Palaemonidae		**Porcellanidae**		**Pectinidae**			
[Chl a]	1	0.753	0.731	0.262	0.093	0.350	0.241		
Immersion time	1	1.018	0.996	0.035	0.034	0.044	0.068		
Region = Re	1	0.043	0.086	0.308	0.105	1.556	0.896		
Port (Re)	7	0.845	5.105**	3.110	8.175**	1.397	4.760**		
Residuals	15	0.165		0.380		0.293			

Table S7. (a) PERMANOVA results for differences between dock and pontoon Biohut in the abundance of dominant species and those contributing to differences among Biohut on the A2021 reduced database (b) Pairwise test for differences among pontoon (P) and dock (D) Biohut for each port (CPC and SPE) when p of interaction term was < 0.05. Monte Carlo permutations were used when permutations were limited.

* p < 0.05; ** p-value < 0.01; ^ pooling at p > 0.25.

Factors	**df**	**MS**	**F**	**MS**	**F**	**MS**	**F**
a.		**Melitidae**		**Corophiidae**		***Nereis* sp.**	
Port	1	5.410	7.739*	3.263	9.851*	3.218	17.977**
Port habitat = PH	1	18.518	26.488**	0.005	0.015	5.519	30.832**
Port x PH	1	17.494	25.023**	2.406	7.264*	0.027	0.134^
Residuals	8	0.699		0.331		0.198	
		Athanas nitescens		**Ascidiidae**		***Mytilus galloprovincialis***	
Port	1	2.906	3.193	7.969	18.807**	10.947	17.719**
Port habitat = PH	1	0.661	0.726	0.522	1.232	0.513	0.831
Port x PH	1	0.388	0.398^	7.214	17.023**	4.593	7.434*
Residuals	8	0.975		0.424		0.618	
		Anthuridae		***Pisidia bluteli***		***Platynereis* sp.**	
Port	1	0.001	0.001	0.434	1.484	0.526	0.589
Port habitat = PH	1	1.811	1.286	4.129	14.121**	6.106	6.840*
Port x PH	1	3.863	2.742	0.622	2.127	1.074	1.234^
Residuals	8	1.409		0.292		0.870	

b.	**Melitidae**	**Corophiidae**	**Ascidiidae**	***Mytilus galloprovincialis***
	t	t	t	t
CPC	9.372** P > D	2.167	5.422** P > D	1.898
SPE	0.086	1.693	1.722	3.188* D > P

Table S8. (a) PERMANOVA results for differences between dock and pontoon Biohut in the abundance of taxa selected for their abundance and contribution to differences in assemblages on the A 2013 reduced database (b) Pairwise test for differences among pontoon (P) and dock (D) Biohut for each port (AGD and BRU) when p of interaction term was < 0.05. Monte Carlo permutations were used when permutations were limited.
* p-value < 0.05; ** p-value < 0.01; ^ pooling at p > 0.25.

Factors	df	MS	F	MS	F	MS	F
a.		**Palaemonidae**		**Columbellidae**		**Cardiidae**	
Port	1	0.499	0.489	0.427	0.704	2.595	5.649
Port habitat = PH	1	0.381	0.373	1.515	2.497	0.106	0.232
Port x PH	1	0.826	0.791^	10.487	17.279**	0.879	1.915
Residuals	8	1.044		0.524		0.459	
		Grapsidae		**Carcinidae**		**Eriphiidae**	
Port	1	0.577	4.720	1.620	4.366	0.026	0.047
Port habitat = PH	1	0.577	4.720	0.111	0.300	0.026	0.047
Port x PH	1	3.665	29.968**	1.196	3.223	0.015	0.025^
Residuals	8	0.122		0.371		0.624	

b.	Columbellidae	Grapsidae
	t	t
AGD	1.302	2.000
BRU	20.018** D > P	6.773** P > D

Figure S1. Mean number of individuals per Biohut (± SE) between the two regions in (a) A 2021 (n = 6), (b) A 2013 (n = 24) and (c) S 2019-2022 (West: n = 14; East: n = 12) database. n.s. = not significant.

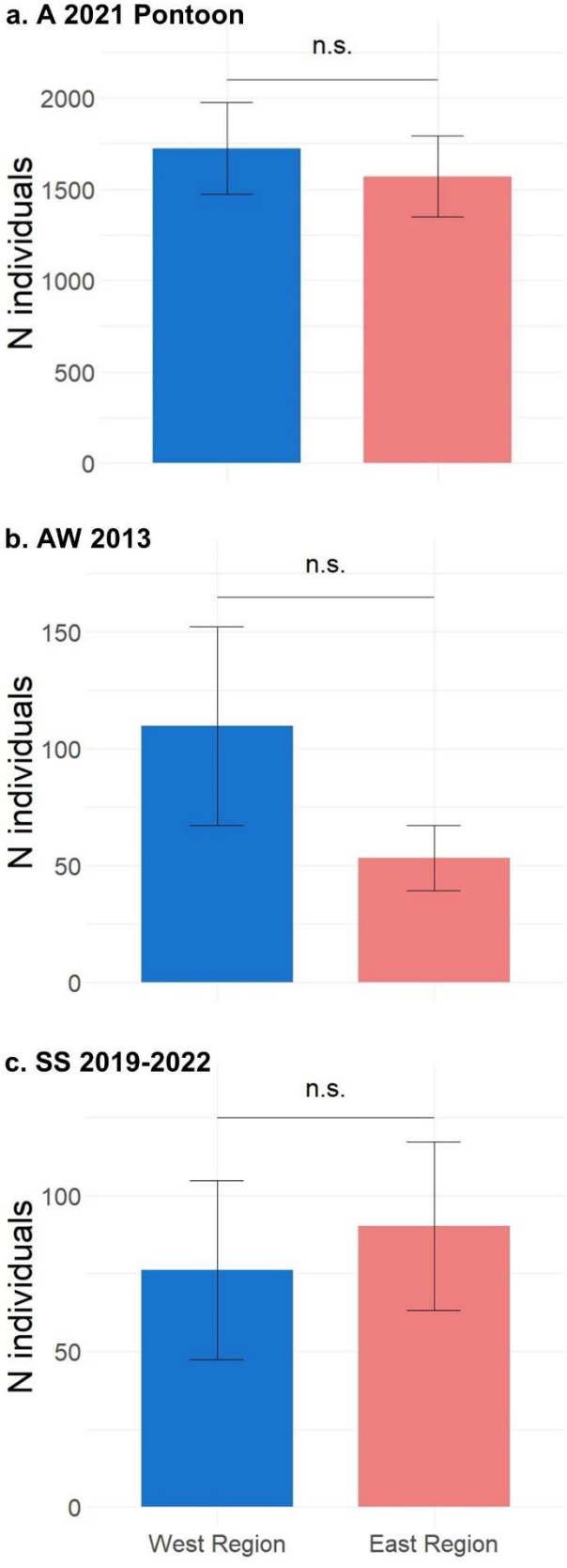
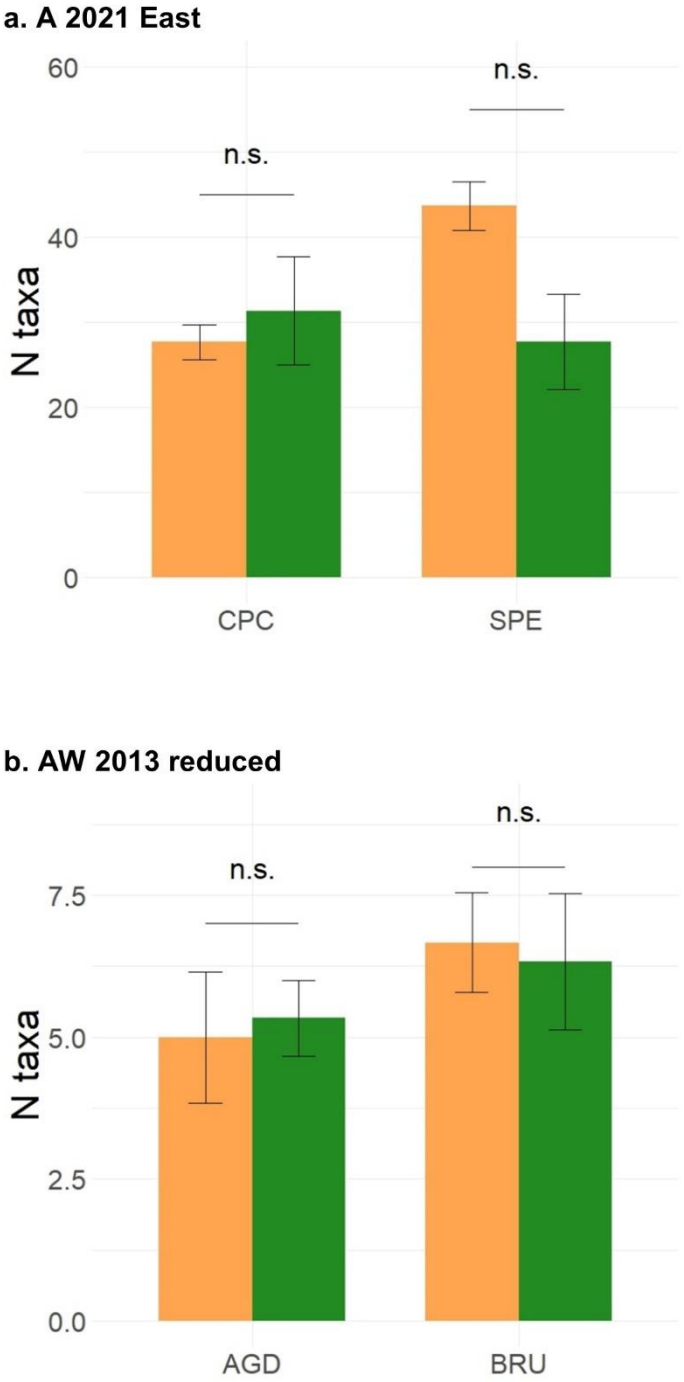


Figure S2. Mean number of taxa (± SE, n = 3) for Dock and Pontoon Biohut (a) from the ports of A 2021 reduced (CPC: Cannes Port-Canto; SPE: Saint-Pierre des Embiez) and (b) from the ports of the AW 2013 reduced dataset (AGD: Agde; BRU: Le Brusc). PERMANOVA results are also reported. n.s. = not significant.



APPENDIX C: CHAPTER 3 SUPPLEMENTARY MATERIAL

Table S1. Depth and *Posidonia* meadows morphological traits (mean ± SE) in each distance (D1: c. a. 300 m away from the marina; D2: c. a. 1 000 m away from the marina) in the 4 study sites (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). n indicate number of sampled.

Artificial fish habitats	Site	Distance	Depth (m)	*Posidonia oceanica* fresh leaves (n = 5)					*Posidonia oceanica* dead leaves (n = 2)	
				Density (n. of shoots / m²)	n. leaves / shoot	Canopy height (mm)	DW epiphytes / DW leaves	LAI (m²/m²)	Degradation level	DW epiphytes / DW leaves ^^
Equipped	SPE	D1	3.3	138.40 ± 9.68	5.60 ± 0.25	471.00 ± 39.03	0.11 ± 0.01	2.21 ± 0.25	2	0.26 ± 0.01
		D2	4.5	105.60 ± 13.42	6.20 ± 1.02	522.40 ± 51.83	0.12 ± 0.01	2.41 ± 0.58	2	0.24 ± 0.06
	MIR	D1	2.4	171.20 ± 24.57	5.60 ± 0.51	530.00 ± 35.67	0.17 ± 0.03	3.12 ± 0.76	2	0.34 ± 0.02
		D2	4.0	212.00 ± 25.24	5.40 ± 0.25	715.00 ± 91.72	0.17 ± 0.05	4.94 ± 0.97	3	0.31 ± 0.03
Not equipped	SAN	D1	8.0	118.40 ± 10.01	6.20 ± 0.37	867.40 ± 50.89	0.03 ± 0.01	4.53 ± 0.68	1	0.08 ± 0.02
		D2	8.0	144.80 ± 9.07	5.40 ± 0.40	656.80 ± 16.74	0.05 ± 0.01	2.84 ± 0.38	2	0.25 ± 0.03
	CAR	D1	4.0	144.80 ± 12.23	7.00 ± 0.78	553.00 ± 21.48	0.14 ± 0.04	3.58 ± 0.66	1	0.36 ± 0.04
		D2	6.0	196.80 ± 15.87	5.60 ± 0.40	656.40 ± 68.98	0.08 ± 0.02	4.75 ± 0.91	2	0.58 ± 0.13

Table S2. (a) Pairwise test on the *Posidonia oceanica* characteristics (shoot density, epiphytes (mgDW.leaf biomass^{-1}) and leaf area index (LAI)) for differences between sites when $p < 0.05$. (b) Pairwise test on *P. oceanica* canopy height for differences among distances in site when interaction term was $p < 0.05$. Monte Carlo permutations were used when permutations were limited. ^ 4th root transformation; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; 1 = marina equipped with artificial fish habitats; 2 = marina not equipped with artificial fish habitats.

a.	Shoot density		Fresh leaves epiphytes biomass ^		LAI		Dead leaves epiphytes biomass ^	
	t		t		t		t	
SPE^1 vs MIR^1	3.58**	SPE^1 < MIR^1	1.51		2.49*	SPE^1 < MIR^1	1.81	
SPE^1 vs SAN^2	0.90		8.09***	SPE^1 > SAN^2	2.75*	SPE^1 < SAN^2	2.47	
SPE^1 vs CAR^2	3.76**	SPE^1 < CAR^2	0.99		2.89**	SPE^1 < CAR^2	2.97*	SPE^1 < CAR^2
MIR^1 vs SAN^2	3.18**	MIR^1 > SAN^2	5.67***	MIR^1 > SAN^2	0.48		6.08**	MIR^1 > SAN^2
MIR^1 vs CAR^2	1.03		1.85		0.16		2.20*	MIR^1 < CAR^2
SAN^2 vs CAR^2	3.25**	SAN^2 < CAR^2	2.88**	SAN^2 < CAR^2	0.71		4.54**	SAN^2 < CAR^2

b.		t	
Canopy height	**SPE^1**	0.79	
	MIR^1	1.88	
	SAN^2	3.93*	D1 > D2
	CAR^2	1.43	

Table S3. Mean $\delta^{13}C$ and $\delta^{15}N$ ratio (± SE) for all potential sources of organic matter sampled in each distance (D0: inside marina; D1: c. a. 300 m away from the marina; D2: c. a. 1 000 m away from the marina) in the 4 study sites (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). n indicate number of sampled

Artificial fish habitats	Site	Distance	Sedimental organic matter (SOM)		Fresh leaves of *P. oceanica* (POS)		Epiphytes of *P. oceanica* fresh leaves (EPH)		Dead leaves of *P. oceanica* (POS DL)		Epiphytes of *P. oceanica* dead leaves (EPH DL)		Particular organic matter (POM)		Superficial sediments (SED)		Phaeophyceae (BROWN)		Rhodophyta (RED)	
			$\delta^{13}C$ (‰)																	
			n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se
Equipped	SPE	D0											3	-19.88 ± 0.05	2	-17.14 ± 0.04	3	-19.79 ± 2.20	1	-18.59
		D1	5	-16.18 ± 0.49	5	-12.81 ± 0.43	5	-19.20 ± 0.34	2	-11.81 ± 0.10	2	-18.93 ± 0.91	5	-20.50 ± 0.42						
		D2	2	-16.78 ± 0.81	5	-12.97 ± 0.29	5	-19.25 ± 1.63	2	-11.49 ± 0.57	2	-14.09 ± 0.46	5	-20.01 ± 0.04						
	MIR	D0											5	-20.95 ± 0.57	6	-20.77 ± 0.41	4	-24.30 ± 0.30	2	-19.30 ± 2.82
		D1	5	-19.22 ± 0.25	5	-13.50 ± 0.20	5	-20.39 ± 1.12	2	-12.20 ± 0.12	2	-20.50 ± 1.36	5	-20.13 ± 0.23						
		D2	5	-18.20 ± 0.18	5	-12.42 ± 0.57	5	-22.29 ± 0.35	2	-11.80 ± 0.04	2	-18.47 ± 3.37	5	-19.83 ± 0.11						
Not equipped	SAN	D0											5	-16.93 ± 0.10	6	-15.05 ± 0.74	4	-19.79 ± 0.59	1	-20.20
		D1	5	-13.57 ± 0.21	5	-13.29 ± 0.29	5	-23.08 ± 1.51	2	-12.26 ± 0.44	2	-21.45 ± 0.29	4	-16.86 ± 0.05						
		D2	5	-15.36 ± 0.43	5	-13.57 ± 0.41	5	-22.91 ± 0.60	2	-11.94 ± 0.22	2	-19.63 ± 1.04	5	-16.97 ± 0.09						
	CAR	D0											5	-20.45 ± 0.43	5	-20.75 ± 1.57	1	-22.46	3	-18.25 ± 1.30
		D1	4	-16.58 ± 0.55	5	-11.46 ± 0.36	5	-24.30 ± 0.35	2	-10.31 ± 0.06	2	-18.37 ± 1.03	5	-19.83 ± 0.08						
		D2	5	-16.79 ± 0.46	5	-12.03 ± 0.32	5	-18.68 ± 0.14	2	-10.13 ± 0.31	2	-17.90 ± 0.83	5	-20.71 ± 0.54						
Artificial fish habitats	Site	Distance	$\delta^{15}N$ (‰)																	
			n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se	n.	Mean ± se
Equipped	SPE	D0											3	5.16 ± 0.31	2	2.22 ± 0.11	3	4.41 ± 0.68	1	8.15
		D1	5	4.18 ± 0.05	5	4.06 ± 0.16	5	5.05 ± 0.13	2	4.85 ± 0.18	2	5.58 ± 0.14	5	5.16 ± 0.04						
		D2	2	5.64 ± 0.05	5	3.54 ± 0.11	5	4.04 ± 0.11	2	4.55 ± 0.47	2	4.94 ± 0.29	5	5.16 ± 0.03						
	MIR	D0											5	5.28 ± 0.06	6	4.02 ± 0.16	4	5.30 ± 0.50	2	5.88 ± 0.38
		D1	5	5.05 ± 0.16	5	5.03 ± 0.13	5	4.59 ± 0.18	2	6.40 ± 0.11	2	4.51 ± 0.39	5	5.33 ± 0.08						
		D2	5	3.84 ± 0.33	5	5.38 ± 0.18	5	5.82 ± 0.28	2	6.40 ± 0.02	2	6.65 ± 0.07	5	5.34 ± 0.05						
Not equipped	SAN	D0											5	5.52 ± 0.10	6	4.12 ± 0.40	4	6.74 ± 0.59	1	8.11
		D1	5	5.75 ± 0.34	5	6.00 ± 0.19	5	4.96 ± 0.12	2	6.19 ± 0.61	2	5.53 ± 0.09	4	5.14 ± 0.09						
		D2	5	3.97 ± 0.35	5	5.70 ± 0.10	5	4.98 ± 0.12	2	5.48 ± 0.37	2	4.81 ± 0.03	5	5.03 ± 0.04						
	CAR	D0											5	5.73 ± 0.07	5	6.63 ± 0.36	1	5.72	3	9.75 ± 0.24
		D1	4	7.37 ± 0.27	5	5.58 ± 0.12	5	7.41 ± 0.11	2	7.04 ± 0.31	2	7.22 ± 0.03	5	5.60 ± 0.04						
		D2	5	6.70 ± 0.14	5	7.30 ± 0.09	5	7.6 ± 0.17	2	7.17 ± 0.14	2	7.70 ± 0.18	5	5.54 ± 0.08						

Table S4. (a) Pairwise test on δ15N values of fresh leaves of *P. oceanica* (POS), dead leaves of *P. oceanica* (POS DL), particulate organic matter (POM) and superficial sediments (SED) for differences between sites when $p < 0.05$. Pairwise test of POS, epiphytes of *P. oceanica* fresh leaves (EPH), sedimentary organic matter (SOM), epiphytes of *P. oceanica* dead leaves (EPH DL) and POM for (b) differences among distances in sites and (c) differences among sites in distances when interaction term was $p < 0.05$. Monte Carlo permutations were used when permutations were limited. SPE = Saint-Pierre des Embiez; MIR = Port-Miramar; SAN = Port of Sanary-sur-mer; CAR = Port of Carqueiranne); * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; 1 = marina equipped with artificial fish habitats; 2 = marina not equipped with artificial fish habitats.

a.	δ13C								δ15N			
	POS		POS DL		POM		SED		POS DL		SED	
	t		t		t		t		t		t	
SPE[1] vs MIR[1]	0.17		1.20		0.63		4.84**	SPE[1] > MIR[1]	6.62**	SPE[1] < MIR[1]	5.94**	SPE[1] < MIR[1]
SPE[1] vs SAN[2]	1.50		1.20		18.64***	SPE[1] < SAN[2]	1.54		2.61		2.63*	SPE[1] < SAN[2]
SPE[1] vs CAR[2]	3.26**	SPE[1] < CAR[2]	4.31**	SPE[1] < CAR[2]	0.66		1.37		7.92**	SPE[1] < CAR[2]	7.29***	SPE[1] < CAR[2]
MIR[1] vs SAN[2]	1.20		0.40		15.24***	MIR[1] < SAN[2]	6.73***	SAN[2] > MIR[1]	1.56		0.25	
MIR[1] vs CAR[2]	3.14*	MIR[1] < CAR[2]	10.54***	MIR[1] < CAR[2]	0.08		0.02		3.89*	MIR[1] < CAR[2]	7.03***	MIR[1] < CAR[2]
SAN[2] vs CAR[2]	4.86**	SAN[2] < CAR[2]	6.47**	SAN[2] < CAR[2]	13.79***	SAN[2] > CAR[2]	3.47**	SAN[2] > CAR[2]	3.21*	SAN[2] < CAR[2]	4.60**	SAN[2] < CAR[2]

b.			Marinas equipped with artificial fish habitats				Unequipped marinas			
			SPE[1]		MIR[1]		SAN[2]		CAR[2]	
			t		t		t		t	
δ13C	**D1 vs D2**	**EPH**	0.03		1.62		0.11		14.99***	D1 < D2
		SOM	0.65		3.32*	D1 < D2	3.76**	D1 > D2	0.31	
δ15N	**D1 vs D2**	**POS**	2.68*	D1 > D2	1.53		1.41		11.16***	D1 < D2
		EPH	5.97***	D1 > D2	3.78**	D1 < D2	0.12		0.93	
		SOM	16.48***	D1 < D2	3.29*	D1 > D2	3.67**	D1 > D2	2.35*	D1 > D2
		EPH DL	2.01		5.38*	D1 < D2	8.11*	D1 > D2	2.56	
	D0 vs D1	**POM**	0.02		0.44		2.67*	D0 > D1	1.60	
	D0 vs D2		0.02		0.68		4.28**	D0 > D2	1.83	
	D1 vs D2		0.01		0.08		1.07		0.66	

Table S4. Continued

c.			SPE[1] vs MIR[1]	SPE[1] vs SAN[2]	SPE[1] vs CAR[2]	MIR[1] vs SAN[2]	MIR[1] vs CAR[2]	SAN[2] vs CAR[2]
			t	t	t	t	t	t
$\delta^{13}C$	EPH	D1	1.02	2.51^{*} $SPE^1 > SAN^2$	10.50^{***} $SPE^1 > CAR^2$	1.44	3.34^{*} $MIR^1 > CAR^2$	0.78
		D2	1.82	2.11	0.35	0.89	9.52^{***} $MIR^1 < CAR^2$	6.85^{***} $SAN^2 < CAR^2$
	SOM	D1	5.55^{**} $SPE^1 > MIR^1$	4.93^{**} $SPE^1 < SAN^2$	0.54	17.56^{***} $MIR^1 < SAN^2$	4.74^{**} $MIR^1 < CAR^2$	5.63^{**} $SAN^2 > CAR^2$
		D2	2.70^{*} $SPE^1 > MIR^1$	1.71	0.02	6.13^{***} $MIR^1 < SAN^2$	2.86^{*} $MIR^1 < CAR^2$	2.30^{*} $SAN^2 > CAR^2$
$\delta^{15}N$	POS	D1	4.70^{**} $SPE^1 < MIR^1$	7.73^{***} $SPE^1 < SAN^2$	7.47^{***} $SPE^1 < CAR^2$	4.20^{**} $MIR^1 < SAN^2$	3.09^{*} $MIR^1 < CAR^2$	1.86
		D2	8.64^{***} $SPE^1 < MIR^1$	14.86^{***} $SPE^1 < SAN^2$	26.16^{***} $SPE^1 < CAR^2$	1.55	9.30^{***} $MIR^1 < CAR^2$	11.80^{***} $SAN^2 < CAR^2$
	EPH	D1	2.06	0.52	13.54^{***} $SPE^1 < CAR^2$	1.7	12.27^{***} $MIR^1 < CAR^2$	14.81^{***} $SAN^2 < CAR^2$
		D2	6.32^{***} $SPE^1 < MIR^1$	5.75^{***} $SPE^1 < SAN^2$	18.12^{***} $SPE^1 < CAR^2$	2.85^{*} $MIR^1 > SAN^2$	5.34^{***} $MIR^1 < CAR^2$	12.84^{***} $SAN^2 < CAR^2$
	SOM	D1	5.20^{***} $SPE^1 < MIR^1$	4.57^{**} $SPE^1 < SAN^2$	13.16^{***} $SPE^1 < CAR^2$	1.86	7.82^{***} $MIR^1 < CAR^2$	3.61^{*} $SAN^2 < CAR^2$
		D2	3.26^{*} $SPE^1 > MIR^1$	2.88^{*} $SPE^1 > SAN^2$	4.33^{**} $SPE^1 < CAR^2$	0.26	7.92^{***} $MIR^1 < CAR^2$	7.26^{**} $SAN^2 < CAR^2$
	EPH DL	D1	2.56	0.26	11.43^{*} $SPE^1 < CAR^2$	2.56	6.90^{*} $MIR^1 < CAR^2$	18.60^{**} $SAN^2 < CAR^2$
		D2	5.83^{*} $SPE^1 < MIR^1$	0.47	8.13^{*} $SPE^1 < CAR^2$	24.70^{**} $MIR^1 > SAN^2$	5.34^{*} $MIR^1 < CAR^2$	15.52^{**} $SAN^2 < CAR^2$
	POM	D0	0.52	1.36	2.35	1.98	4.98^{***} $MIR^1 < CAR^2$	1.71
		D1	1.8	0.28	6.99^{***} $SPE^1 < CAR^2$	1.57	3.00^{*} $MIR^1 < CAR^2$	4.85^{**} $SAN^2 < CAR^2$
		D2	3.04^{*} $SPE^1 < MIR^1$	2.34	4.66^{**} $SPE^1 < CAR^2$	4.49^{***} $MIR^1 > SAN^2$	2.32^{*} $MIR^1 < CAR^2$	5.71^{**} $SAN^2 < CAR^2$

Table S5. Mean standard length, weight, $\delta^{13}C$ and $\delta^{15}N$ ratio (± SE) for *Diplodus* spp. samples for each distance (inside and outside the marina) in the 4 study sites (SPE: Saint-Pierre des Embiez; MIR: Port-Miramar; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). n indicate number of sampled.

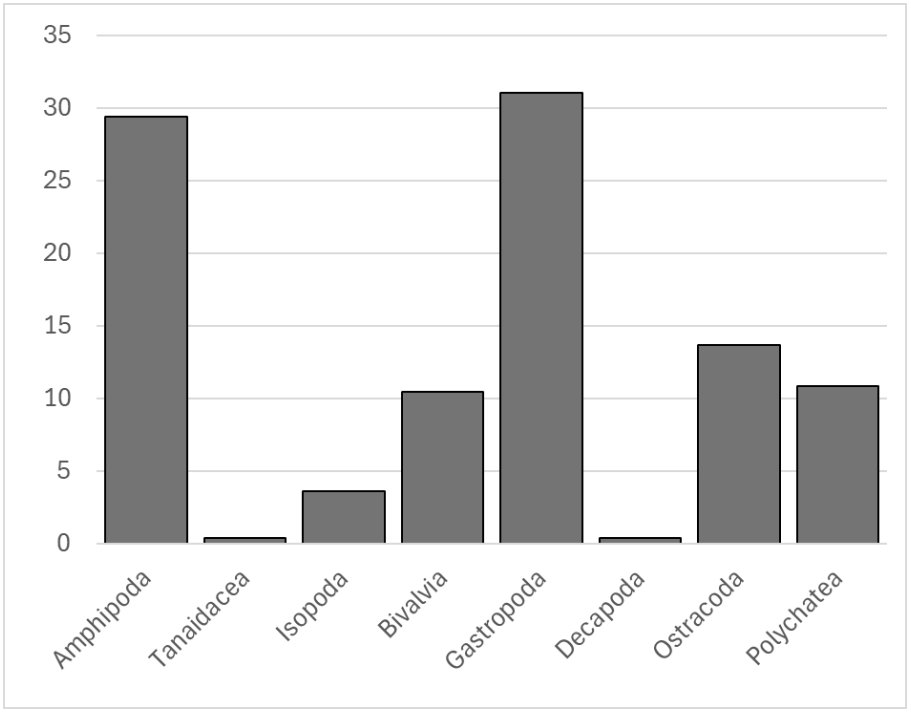
Artificial fish habitats	Site	Distance	n.	Standard length (mm)	Weight (g)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)
Equipped	SPE	Inside marina	7	121.71 ± 3.88	61.14 ± 6.13	-16.35 ± 0.64	9.36 ± 0.21
		Outside marina	6	132.17 ± 17.74	88.83 ± 31.06	-15.80 ± 0.40	10.45 ± 0.56
	MIR	Inside marina	7	120.14 ± 9.42	66.14 ± 15.38	-17.93 ± 0.26	9.76 ± 0.44
Not equipped	SAN	Inside marina	7	108.00 ± 6.21	44.00 ± 7.07	-16.33 ± 0.25	10.17 ± 0.09
		Outside marina	7	117.29 ± 7.96	56.14 ± 9.94	-16.63 ± 0.26	10.84 ± 0.20
	CAR	Inside marina	5	109.60 ± 11.71	50.60 ± 13.25	-17.06 ± 0.83	11.53 ± 0.15
		Outside marina	10	121.70 ± 3.35	54.80 ± 4.76	-17.27 ± 0.43	10.63 ± 0.40

Table S6. Mean number of individuals per stomach content (± SE) for each taxon in *Diplodus* spp. samples for each distance (inside and outside the marina) in the 3 study sites considered (SPE: Saint-Pierre des Embiez; SAN: Port of Sanary-sur-mer; CAR: Port of Carqueiranne). n indicate number of stomachs.

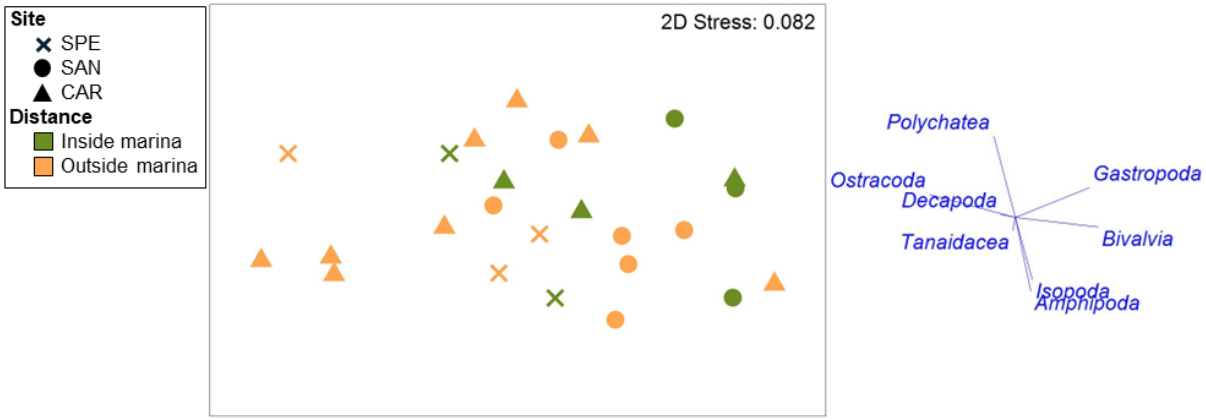
Artificial fish habitats	Site	Distance	n =	Amphipoda	Tanaidacea	Isopoda	Bivalvia	Gastropoda	Decapoda	Ostracoda	Polychaeta
Equipped	SPE	Inside marina	2	1.50 ± 1.50	-	-	-	-	-	-	0.50 ± 0.50
		Outside marina	3	3.67 ± 2.73	0.33 ± 0.33	-	-	-	-	8.33 ± 8.33	1.67 ± 1.2
Not equipped	SAN	Inside marina	3	-	-	-	5.33 ± 3.93	9.67 ± 9.17	-	-	-
		Outside marina	7	7.71 ± 6.89	-	1.29 ± 1.29	0.86 ± 0.34	0.71 ± 0.18	0.14 ± 0.14	-	0.57 ± 0.43
	CAR	Inside marina	3	1.33 ± 0.88	-	-	1.00 ± 1.00	12.33 ± 11.35	-	-	1.00 ± 0.58
		Outside marina	8	0.13 ± 0.13	-	-	0.13 ± 0.13	0.75 ± 0.75	-	1.13 ± 0.52	1.75 ± 0.90
Total			26	73	1	9	26	77	1	34	27

Figure S1. (a) Relative abundance (%) of each taxon identified in the stomach content containing food. (b) Non-metric multidimensional scaling ordination (nMDS) plot for the taxonomic composition of *Diplodus* spp. stomach contents and the relative contribution of taxa to variations.

a.



b.



APPENDIX D: EXTENDED ANALYSIS AND ADDITIONAL OUTCOMES FROM OUR SAMPLING CAMPAIGNS

In addition to the studies detailed in the previous chapters, we further valued the sampling campaigns of this thesis and collected additional data and samples to deepen our understanding of AFH ecological patterns, including species functional diversity and trophic relations assessment, acoustic signature measurements, and biodiversity comparison with marine reserves in the French Mediterranean coast.

A brief description of this work is presented hereafter.

1. *Functional diversity and trophic relationships of species dwelling in artificial fish habitats*

The abundance of organisms and the specific richness are two primary metrics used to describe taxonomic patterns in a given ecosystem. However, as detailed in the general introduction (Box 1, page 4) using functional traits, used to describe the functional diversity by differentiating species by their role and functional contributions, are also essential for understanding ecological patterns (Díaz and Cabido, 2001; Mason *et al.*, 2005; Pimiento *et al.*, 2020).

The effectiveness of ecological engineering solutions can greatly depend on the functional traits of species, such as feeding behaviour, diet and mobility (Pimiento *et al.*, 2020).

We plan to compare the functional diversity of the species colonising the AFH in 2 marinas and to evaluate the trophic relationship and isotopic niches of the most abundant invertebrates taxa and 2 fish species *Diplodus annularis* and *Gobius paganellus* between sites and between habitats (pontoon suspended vs dock mounted AFH).

We preserved (at -20°C) a subset of organisms collected from 3 pontoon-suspended and 3 dock-mounted AFH sampled in 2 sites during the sampling campaign detailed in chapter 2 (Figure 1, page 35).

The invertebrates and fish were each measured, and their size used as a functional trait. Additionally, information on other functional traits, including morphology, diet, feeding behaviour, lifespan, larval dispersion and mobility, were obtained from the scientific

literature (Clare *et al.*, 2022; Goldschmid, 1984; Zander and Hagemann, 1986). Differences between the type of AFH will be tested using permutational analysis of variance (PERMANOVA) for each functional trait separately, using Port (fixed) and Type of AFH (fixed) as factors. In addition, functional diversity will be analysed using 3 indices of functional diversity (functional richness, functional evenness and functional divergence).

The trophic niches and the trophic relationship of the most abundant invertebrate taxa found in a minimum of 3 pontoon-suspended and 3 dock-mounted AFH and well as that of two fish species (*D. annularis* and *G. paganellus*) will be evaluated using stable isotopes analysis. All materials that will be used for stable isotope analysis have been lyophilized (freeze-dryer: Cosmos-80 - Cryotec; MARBEC, Sète, France), powdered using a mortar and pestle. The stable isotope ratio of the samples will be analysed using an isotope ratio mass spectrometer (Delta V Plus Continuous Flow - ThermoFisher Scientific) at the AETE-ISO analytical platform (OREME – Montpellier, France).

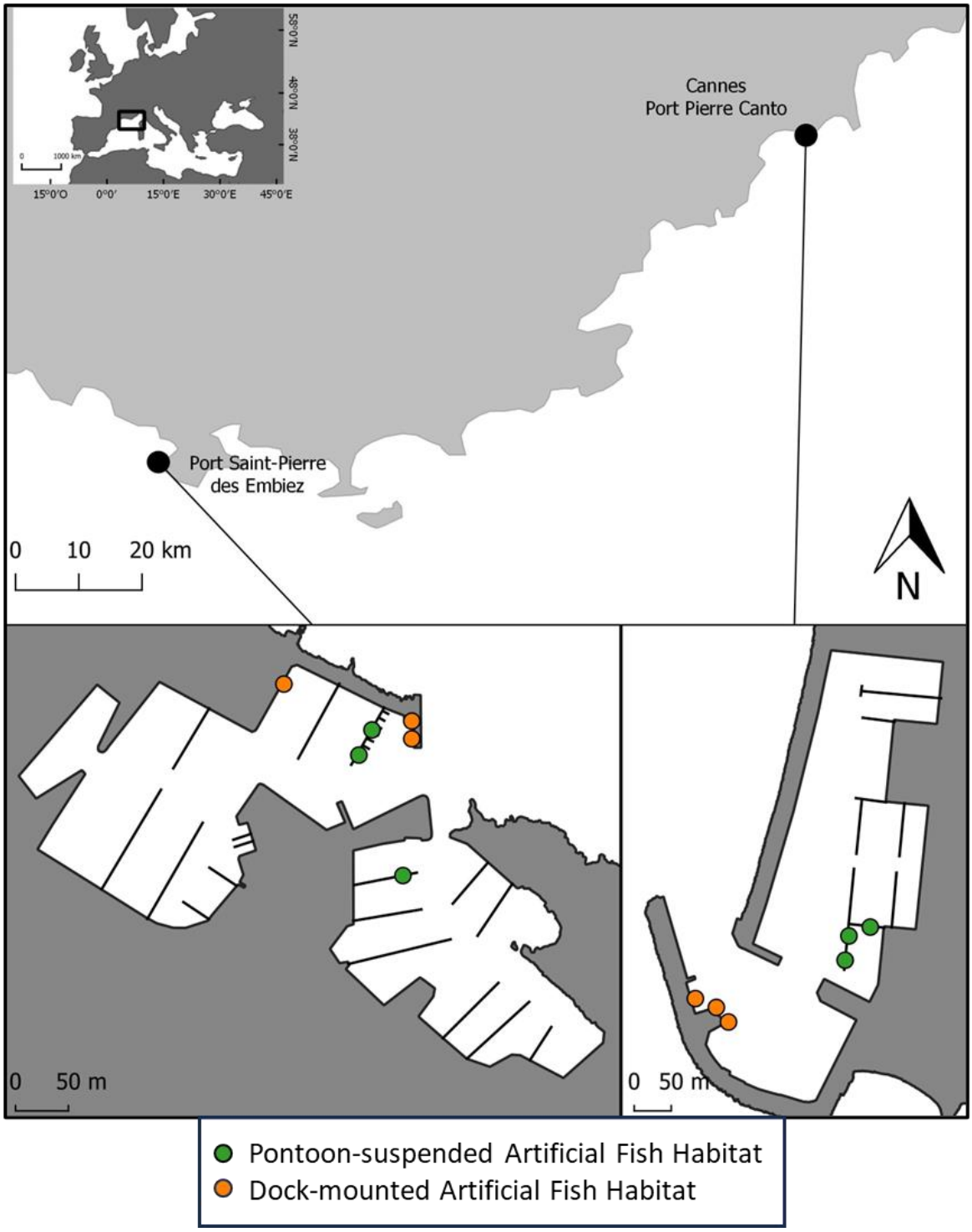


Figure 1. Map of the 2 marinas equipped with artificial fish habitats (AFH) sampled along the French Mediterranean coastline (Northwestern Mediterranean Sea). Colours are used to show the 3 pontoon-suspended (green) and the 3 dock-mounted (orange) AFH sampled.

2. *Bioacoustic monitoring comparing biological sounds produced by Artificial fish habitats and Posidonia oceanica meadows*

The sounds intentionally generated or induced by the movements or the behaviour of living organisms, play a key role in the ecological functioning of coastal areas. Indeed, many marine organisms, including fish (Luczkovich *et al.*, 2008; Tricas and Boyle, 2014) and invertebrates (Popper *et al.*, 2001), rely on sound for communications or other social interactions such as reproduction or territorial protections (Hughes *et al.*, 2014). Biological sounds are determinant in predator-prey interactions. For instance, some species can use sounds generated by their potential preys to locate them whereas some species can detect their predators by the sounds they produce. Additionally, the acoustics cues produced by coastal organisms can influence the behaviour of the early stages of many marine species to locate suitable habitats for settlement (Lillis *et al.*, 2013; Simpson *et al.*, 2005; Stanley *et al.*, 2012). Thus, the sounds produced by the organisms colonising Artificial Fish Habitats (AFH) could be helpful for attracting some organisms, making these habitats more suitable for settlement than other man-made structures, thereby enhancing their effectiveness.

In this context, it was interesting to assess the acoustic signatures of artificial fish habitats deployed inside marinas and to compare them with the biological sounds produced by other non-equipped habitats inside the marina and to natural habitats adjacent to the marina.

From 12th to 23rd September 2022, we recorded the acoustics signals at 7 different areas in and outside the marina of Saint Pierre des Embiez (Six-Fours-les-Plages, France; **Error! Reference source not found.**a). In the natural habitat, we used structures of 1m² on which 4 hydrophones were attached and connected to an autonomous recorder (**Error! Reference source not found.**b) immersed horizontally inside a *Posidonia oceanica* meadow, a sandy and a rocky bottom habitat. Inside the marina, we recorded the biological signature of 1 pontoon-suspended AFH, 1 dock-mounted AFH, a linear of 10 m of docks equipped with AFH (which represents 4 dock-mounted side by side AFH) and 1 dock not equipped, using a vertical structure of 1m² with also 4 hydrophones and an autonomous recorder deployed underwater at 2 meters from the recorded habitats and at the same depth (**Error! Reference source not found.**c). The seagrass, rocky and sandy habitats were used as a control for

natural environments, the unequipped dock as a man-made structure without ecological restoration structure, while the three areas with AFH represented man-made structures with different ecological engineering solutions. This sampling design allowed us to compare the density of sounds produced by benthic organisms per m² and the acoustic diversity of benthic sounds in each area. The results are currently being analysed by the Chorus company (Grenoble, France).

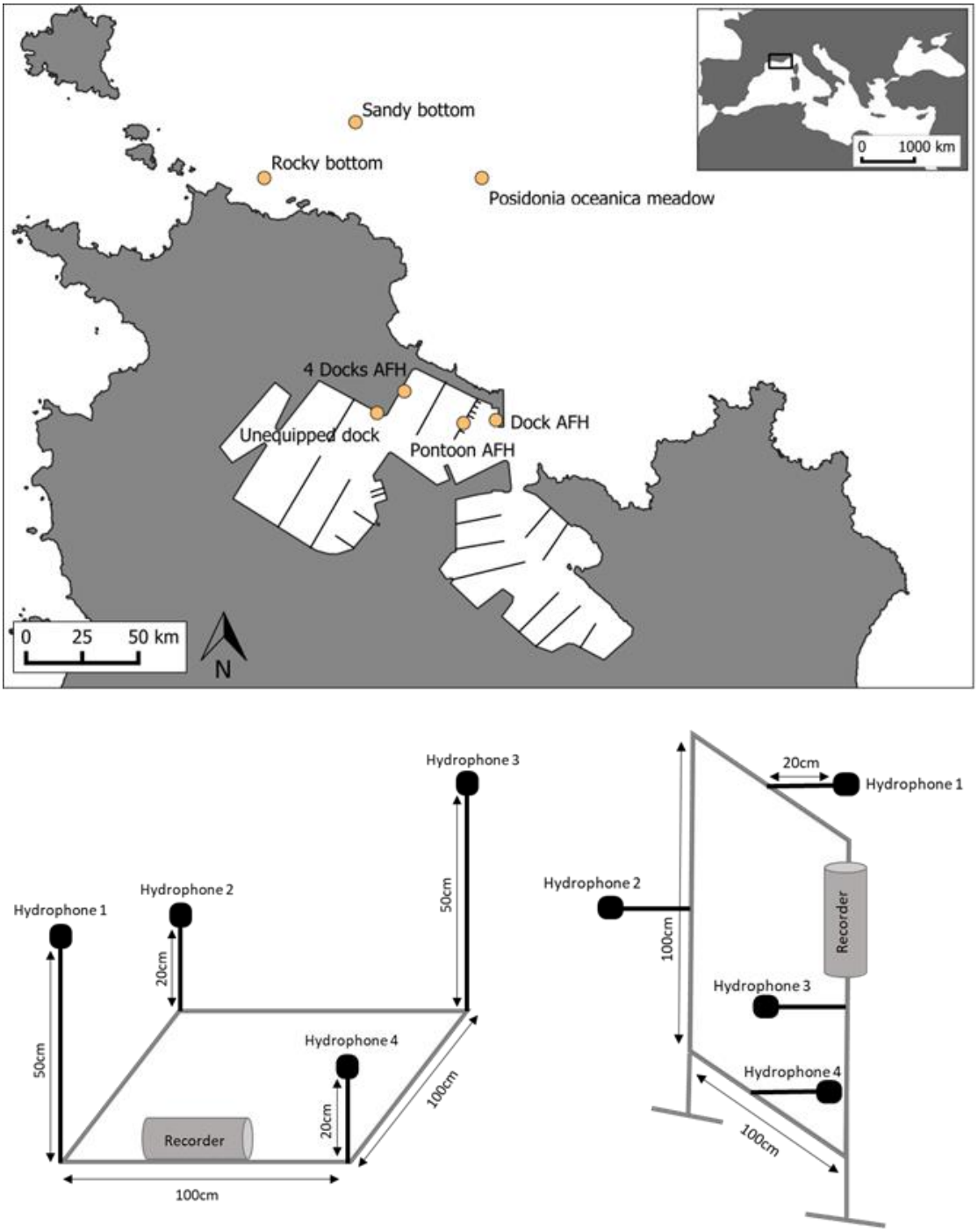


Figure 2. (a) Map of the study site indicating the different habitats that were recorded; (b) recording structure used in the natural habitats; (c) recording structure used inside the marina

3. *Alpha and beta-diversity between seaports and marine reserves using environmental DNA (eDNA) metabarcoding*

Environmental DNA (eDNA) metabarcoding is a technique increasingly used in marine environments to monitor biodiversity (Cheang *et al.*, 2020; Sigsgaard *et al.*, 2016). This non-invasive sampling method consists of analysing DNA fragments in water and is used as a complement to traditional sampling methods such as visual surveys or sample collection, by, for instance, giving indications on the presence of some species that cannot be observed due to their size or their behaviour (Aglieri *et al.*, 2023; Collins *et al.*, 2018; Miya, 2022; Taberlet *et al.*, 2012).

Several invertebrate individuals collected in the AFH during the sampling campaign detailed in Chapter 2 were identified in the field and brought to the laboratory to perform DNA sequencing. These data were added to the reference genetic databases developed by SPYGEN laboratory. In addition, eDNA metabarcoding samplings were performed by scientists from the CEFE laboratory in 3 of the study sites.

The data collected contributed to a broader understanding of marine biodiversity in coastal areas by comparing *alpha* and *beta*-diversity in 6 seaports and 4 strictly no-take marine reserves nearby along the French Mediterranean coast using eDNA metabarcoding. This study was detailed in the scientific paper "The Tree of Life eDNA metabarcoding reveals a similar taxonomic richness but dissimilar evolutionary lineages between seaports and marine reserves" by Bastien Macé, David Mouillot, Alicia Dalongeville, Morgane Bruno, Julie Deter, Alix Varenne, Anaïs Gudefin, Pierre Boissery and Stéphanie Manel, was published in the Molecular Ecology journal in 2024 (Macé *et al.*, 2024).