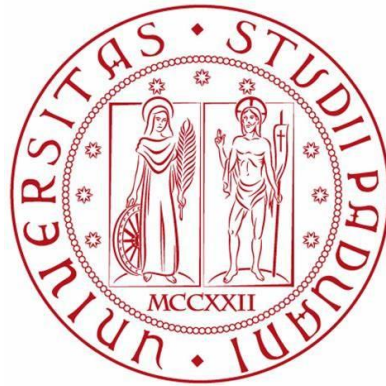


UNIVERSITÀ DEGLI STUDI DI PADOVA
DIPARTIMENTO DI BIOLOGIA
Corso di Laurea magistrale in Marine Biology



TESI DI LAUREA

The Contribution of Artificial Structures to Ecosystem Functioning at Landscape Level

Relatore: Prof.ssa Laura Airoidi

Dipartimento di Biologia

Correlatore: Dott. Davide De Battisti

Dipartimento di Biologia

Laureando: Bayan Kassar

ANNO ACADEMICO 2022/2023

Table of Contents

| | |
|---|----|
| 1. Introduction..... | 3 |
| 1.1. The sprawl of artificial structures | 3 |
| 1.2. Seawalls are a common category of coastal protection | 5 |
| 1.3. Artificial structures as “novel” habitats | 7 |
| 1.4. The Venice Lagoon | 9 |
| 1.5. Study aims..... | 11 |
| 2. Materials and Methods | 12 |
| 2.1. Study Area..... | 12 |
| 2.2. Filtration rates | 16 |
| 2.3. Data Analysis | 20 |
| 3. Results | 21 |
| 3.1. Overall characteristics of the assemblages | 21 |
| 3.2. Assemblage level difference among substrates and urbanization levels | 27 |
| | 29 |
| 3.3. Abundance differences among structures and levels of urbanization..... | 30 |
| 3.4. Filtration rates | 31 |
| 3.5. Carbon content of shells | 33 |
| 4. Discussion | 35 |
| 4.1. General Species Distribution | 35 |
| 4.2. Abundances of the most prevalent species | 37 |
| 4.3. Importance of Oysters and Mussels in the Ecosystem | 39 |
| 5. Conclusion..... | 43 |
| 6. Bibliography..... | 45 |

Abstract

Artificial structures are becoming ubiquitous along urbanized coastlines, as in Venice Lagoon, yet their contribution to the structure and functioning of the ecosystem at landscape level is still little known. To address this gap in knowledge, through field sampling, we investigated how species abundance and composition varies on seawalls and pilings, the two most abundant types of artificial structures within the Venice lagoon, in relation to structures' proximity to urban centers. We then coupled these results with literature data, to evaluate the influence that organisms growing on artificial structures, primarily oysters and mussels, have on water filtration and inorganic carbon content in shells, which underpins two crucial ecosystem services, water clarity, and control of atmospheric-oceanic CO₂ flux. Our findings revealed significant variations in the composition and abundance of species between the two different types of structures, as well as between the urbanized and less urbanized sites. In total, we found that 24 species were present on seawalls, while 23 species were present on pilings. Three species i.e. oysters (*Ostreidae* spp.), mussels (*Mytilus galloprovincialis*), and barnacles (*Cirripedia* spp.), were dominant, with oysters being more abundant on seawalls while the others being more abundant on pilings. At the lagoon level, we estimated that oysters can filter slightly more than 91 thousand m³ of water per day, while mussels only approximately 24 thousand m³/day. Regarding the content of carbon, oyster shells contained an estimation of 42 Tons of carbon, in comparison to 14 Tons for mussels. Importantly, filtration rates and shell carbon content were consistently higher in low urbanized areas in comparison to high urbanized ones across all species and artificial structures. These findings highlight that organisms growing on artificial structures can provide valuable ecosystem functions, but also that their efficacy varies with the level of urbanization. Understanding how species composition vary with structure types and how this variation reflects on ecosystem functioning is crucial within this unique and rapidly changing ecosystem where the need for coastal protection is increasing in the light of predicted climate change.

1. Introduction

1.1. The sprawl of artificial structures

Coastal areas support the development of human civilization around the world since millennia, concentrating a high density of population and human activities (Lotze et al., 2006). In fact, more than 60% of world's population lives in coastal zones even though it occupies less than 15% of the earth's land surface (Martínez et al., 2007)

This coastal urbanisation introduced a variety of man-made infrastructures in marine landscapes including shore-parallel (e.g., seawalls, bulkheads, revetments) and shore-perpendicular structures (e.g., groynes, jetties, and breakwaters) (Bulleri & Chapman, 2004). Construction in marine environments has impacted a minimum of 32,000 km² of seafloor (Bugnot et al., 2020), with a total modified area around ports, wind farms, breakwaters, tunnels, and bridges estimated to be in the range of 1.0–3.4×10⁶ km². The creation of artificial habitats, primarily for aquaculture purposes, constitutes 71% of this area, with commercial ports accounting for 14%, and artificial reefs making up 11% (Bugnot et al., 2020). In Spain, France, and Italy, up to 50% of the shorelines are developed for harbors and ports (Airoldi et al., 2008). Marine infrastructures will further proliferate in response to a growing coastal population that is expected to increase by 40–50% in 2030, particularly in low-elevation coastal areas (Neumann et al., 2015), expansions of coastal cities, and threats from climate-related increase in storminess and sea level rise (Airoldi & Bulleri, 2011). Thus, construction will continue to sprawl into the ocean, with a global physical footprint projected to increase by at least 23% (Bugnot et al., 2020).

Coastal defenses can be very large (e.g., La Spezia Breakwater, Italy, and Plymouth Breakwater, England, Figure 1.1.) and often create a network that can span extensive stretches of the coastline (e.g., along the north Adriatic sea, Airoldi et al. 2005a). Similarly to terrestrial systems where urbanization leads to a degradation of habitats, alter species composition, and increases homogenisation in communities (McKinney & Lockwood, 1999), coastal urbanization reduces biodiversity, alters community structure and species interactions from local to large scale (Mayer-Pinto et al., 2018). Also,

artificial structures can act as ‘steppingstones’ between regions, often facilitating the spread of non-indigenous species (Airoidi & Bulleri, 2011).

At the local scale, artificial structures provide a substrate for a variety of rocky intertidal organisms. Multiple studies have investigated the capacity of these structures to sustain a benthic community similar to that of natural rocky shores and there is now mounting evidence that they do not (Bulleri & Chapman, 2004; Carvalho et al., 2013). For example, Chapman (2003) found that 50% of the mobile taxa on rocky shores were absent from nearby seawalls. Also, urbanisation alters the total number of individuals per mobile species as well as changes species identity (Airoidi & Bulleri, 2011). This lack of correspondence with natural habitats, partially arise because hard structures are often built from materials (Grasselli et al., 2024) that lack the topographic complexity that characterizes natural rocky shores, which it has an important role in the distribution of intertidal species(Underwood et al., 2004). Indeed, experimentally increasing the topographic complexity of artificial structures, such as pools and pits, can lead to a local increase in biodiversity (Chapman & Blockley, 2009).

At present, studies on the impacts of artificial structures on marine ecosystems, tend to focus on the assessment of species diversity and community structure, the predominant types of species interactions, and the risks of spread and settlement of non-indigenous species (Mayer-Pinto et al., 2018). Considering the future increase in coastal development in response to both human population growth and climate change(COOPER et al., 2012), there is a growing interest in using coastal artificial structures to sustain and provide ecosystem functioning and services (Dafforn et al., 2015). Indeed, many studies are manipulating the material, texture, and shape of these structures to support the local biodiversity with the underlying assumption that ecosystem functions would also be improved (Chapman & Underwood, 2011). Surprisingly, however, few studies have empirically investigated the capacity of the novel communities growing on artificial structures to provide and sustain target ecosystem functioning and services. Therefore, it is crucial not only to examine the structure of species communities associated to different types of artificial structures, but

also to understand how these structural changes translate to changes in relevant ecosystem functions (Mayer-Pinto et al., 2017).



Figure 1.1. La Spezia breakwater, Italy (Image: blosslynspage.wordpress.com)



Figure 1.2. Plymouth breakwater, England. (cryllacottages.co.uk)

1.2. Seawalls are a common category of coastal protection

Coastal protection is important for safeguarding the hinterland from flooding and preventing the erosion of shorelines. Flooding poses a widespread and long-term threat, requiring full protection along the entire coastline to withstand storm events. Shoreline erosion poses more localized and variable risks, affecting specific sections of the coast on smaller spatial and temporal scales or, in some cases, affecting entire coastlines over larger scales (Lauzon et al., 2019). To address these challenges, coastal engineers have at their disposal several traditional protection measures, including groins, revetments, seawalls, and dams. Each of these measures is designed to tackle a specific problem at a specific scale. For example, groins and revetments are commonly employed to mitigate erosion threats on smaller spatial and temporal scales. In contrast, seawalls, and dams, are primarily applied to offer protection on more extensive spatial and temporal scales, particularly against the risk of flooding (Borsje et al., 2011).

Coastal armoring can be traced back to millennia, to ancient civilizations. For instance, the Minoans built the oldest known seaport around 1800 BC in Alexandria, and coastal defenses were established in China and northern Europe as early as 175 BC. (’Loke et al., 2019; ’Charlier et al., 2005). Sea walls are one of the most common structures for coastal protection and are often found in the case of narrow or steep beaches, where a typical breakwater is either too large or not economical. These structures are largely vertical with a compact footprint, and so take up minimal space at the sea floor and tend to have a particularly homogenous physical structure (Grasselli & Aioldi, 2021). In addition to that, sea walls are extremely strong and durable, and will last for centuries if they are maintained properly.

Climate change have increased the needs of seawalls and other armored structures for coastal protection. Over the last 150 years, on average the sea level rose about 2.5 mm per year globally (Zanchettin et al., 2021) and IPCC predictions reports further strong increments of sea level in the next decades (OECD). For instance, in the Venice Lagoon (Italy), by 2100 sea level is predicted to rise to between 32 and 62 cm according to the RCP 2.6 scenario and between 58 and 110 cm for the RCP 8.5 scenario (Zanchettin et al., 2021). Although sea-level rise risks are complex and difficult to understand, it is almost certain that we will experience a relative sea level rise between 17 and 53 cm by 2100 (Carbognin et al., 2010). In turn, this rise coupled with the increments of increase in waves and tides, will likely require the creation of sea walls to shield various shorelines. Furthermore, climate change and urban development have led to extensive losses of coastal vegetation (Globally, 25-50% of salt marshes, 35% of mangroves, 30% of coral reefs and 29% of seagrasses; McKinley et al., 2020; Barbier et al., 2011), heightened the vulnerability of coastal areas to flooding and thus, possibly pushing for increasing the need to build more seawalls. Altogether, it is becoming urgent to understand what the changes in ecosystem functioning due to these increased artificial structures will be.

1.3. Artificial structures as “novel” habitats

Seawalls, pilings, marinas, pontoons, and similar artificial structures serve as “novel” (Hobbs et al., 2009) hard substrates that function as habitats for marine organisms typically found in rocky bottoms (Airoidi et al, 2009; González-Duarte et al., 2016). While artificial and natural habitats may consist of similar hard materials, they may not support comparable intertidal communities (Chapman & Bulleri, 2003). Artificial structures are known to favor the settlement of non-indigenous species, potentially leading to a homogenization of biological communities, and enabling the formation of unique species compositions not typically found in natural habitats (Airoidi, 2014; McKinney & Lockwood, 1999), thus, implicating the structure and functioning of the surrounding environment.

The composition and structure of intertidal assemblages are influenced by many elements: for instance, the surface of sea walls is typically vertical while natural rocky shores show a broad spectrum of inclines (Chapman & Bulleri, 2003). In general, inclination is consistently steeper in artificial than in natural habitats (Grasselli & Airoidi, 2021). Artificial infrastructures are usually built of diverse materials and often show reduced levels of spatial variation and microhabitat diversity (Bulleri & Airoidi, 2005). In addition, artificial structures create sheltered habitats, which modify water circulation and renovation (Erixon Aalto & Ernstson, 2017). Furthermore, artificial structures are linked with intense human activities that, among other consequences, entails a greater occurrence of physical disruptions such as vessel-induced scours and swashes, maintenance related activities, and elevated pollution levels(Airoidi et al., 2009b). Lastly, marine infrastructures have a significant impact on the environment, affecting adjacent habitats by altering light availability, water and sediments flow, wave energy, and resource transport (Dugan et al., 2011). Taking all these factors together, there is robust evidence that artificial structures can restrict the biological fitness of various species by altering competition, predation, and recruitment patterns(Airoidi et al., 2008), ultimately affecting the provisioning of essential functions and services in urbanized coastal system (Dugan et al., 2011).

What caused the observed differences in community assemblages between artificial structures and natural reefs is not well understood, but knowledge is rapidly accumulating. Several factors such as construction material of the artificial structure, or the types of habitats being compared can contribute to these variations (Grasselli & Airoidi, 2021). For instance, wave exposure and water transport are significant factors influencing the difference in assemblages between natural and artificial structures (Davis, 2002). A study conducted in the north-west of Italy showed that seawalls harbored a smaller density of the limpet, *Patella aspera*, and the barnacle, *Chthalamus stellatus*, with respect to both breakwaters and natural rocky shores which was related to the greater cover of the brown encrusting alga, *Ralfsia verrucosa* (Bulleri & Chapman, 2004). Other studies showed that rocky shores had 40% and 70% more grazers than nearby seawalls or pilings, respectively. Opposite to that, scavengers were eight times more abundant on seawalls compared to pilings or natural rocky shores, and algae exhibited greater diversity on natural rocky shores and seawalls than on pilings (Mayer-Pinto et al., 2017b). According to this study, oysters were more abundant on pilings than on seawalls or rocky shores, but they were also smaller in size. Seawalls were identified as the most invaded habitats by non-indigenous species, while pilings supported greater secondary productivity (the growth and accumulation of living biomass within a community of living organisms, it is the heterotrophic equivalent of net primary production by autotrophs (Benke & Huryn, 2006)) than other habitats. Therefore, it is crucial to evaluate how does community composition and structure differ among distinct types of artificial habitats, and their possible influence on ecosystem functioning.

1.4. The Venice Lagoon

The Venice lagoon (Italy) is a great case study for investigating the effect of artificial infrastructure on the biodiversity and functionality of the ecosystem at landscape level since human activities have significantly altered the morphology and size of the Venice Lagoon throughout history. The northern islands of the lagoon have been inhabited since the Roman times, and by the late 13th century Venice was one of Europe's largest cities with 100,000 residents. Today, the city attracts over 25 million visitors each year. The Venice Lagoon represents a paradigmatic case of ecosystem alteration in the Anthropocene since human activities continuously modified the environment through the centuries. These alterations include diverting major rivers away from the lagoon to prevent sedimentation in its marginal areas (15th to 17th century), the construction of rigid defenses to protect the barrier islands from storm waves (1740–1782), creating multiple sets of jetties at the inlets (1808–1927), land reclamation for urban and industrial development (1927–1960), subsidence resulting from groundwater and natural gas extraction (about 9cm from 1930 to 1970), the construction of artificial salt marshes (since the 1990s), and more recently, the installation of mobile barriers (MOSE Project) at the inlets to protect Venice from flooding (since 2003). All such human imprints are visible or can be deduced by comparing modern and historical maps (Madricardo et al., 2019).

The Venice Lagoon is in the north-west Adriatic Sea. It is the largest lagoon system in Italy, and one of the largest in the Mediterranean Sea, with a total area of 500 km² and a length of 50 km (Molinaroli et al., 2009). Water exchange between the lagoon and the northern Adriatic Sea takes place through three inlets located on the eastern side of the lagoon. These inlets are named, from north to south, Lido, Malamocco, and Chioggia. The first inlet is around 1000 m wide, and the others about 500 m. The maximum depth is around 8 m for Chioggia and 14 m for Malamocco and Lido (Solidoro et al., 2010). Most of the lagoon is very shallow, with average depths of 1 m, but there are also a few deep channels (maximum depth around 15 m) leading inwards from each inlet and branching inside the basin (Solidoro et al., 2010). The lagoon is characterized by a “mosaic” pattern for physical, chemical, and biological variables due to the complex

morphology of the lagoon bottom and the consequent irregular hydrology (Ravera, 2000). It is also characterized by complex dynamics, including estuarine and marine environments, salt marshes and human settlements like the city of Venice and the Porto Marghera industrial zone (Ravera, 2000).

The Venice lagoon has a semidiurnal tidal regime with a range of about ± 0.7 m. Tidal exchanges with the sea may reach $8000 \text{ m}^3\text{s}^{-1}$ and typically amounts to about one-third of the total lagoon volume per tidal cycle (Gačić & Solidoro, 2004). During the spring tide cycle, about 15% of the region is subjected to partial flooding or drying (Umgiesser et al., 2004a). Adriatic waters entering the lagoon are typically oligotrophic, or at most mesotrophic (Bernardi Aubry et al., 2004). The low level of the lagoon with respect to the sea has increased the frequency of flooding events (Carbognin et al., 2004).

To protect the coastal stability against erosion, a variety of defensive structures have been employed in Venice lagoon. These defenses range from the ancient "murazzi" of Venice to modern solutions such as groins, seawalls, breakwaters, and more current inventions like "longard" tubes and other specific protection structures (Carbognin & Marabini, 1987). Engineering techniques for coastal defense management are generally categorized into two main categories which are, hard engineering methods and soft engineering methods, where the latter are particularly suitable for safeguarding delicate ecosystems and landscapes (Angeli et al., 2015).

Hard engineering methods include seawalls made of concrete or rock, breakwaters made of concrete blocks and natural boulders, groins that are barriers or walls of concrete, rock, gravel, gabions, wood, submerged groins that are barriers or walls of concrete, rock, gravel, gabions, rock armor, revetments that are wooden or rock armor revetments, and floodgates. On the other hand, soft engineering methods include beach nourishment, sand dune stabilization (planting vegetation), permeable defense, submerged barriers (sand-filled bags), and longard tubes (sand-filled tubes) (Angeli et al., 2015).



Figure 1.4.1. Venice Lagoon (Google earth).

The lagoon is an open system exposed to natural and anthropogenic stressors and characterized by extremely heterogeneous morphological structure and variable physicochemical (Cucco et al., 2009), biogeochemical (Umgiesser et al., 2004b), and biological (Magni et al., 2009) conditions. These conditions contribute to the complex and ever-changing nature of the lagoon, which constitutes a complex system of major historical, artistic, and environmental interest. At present, the managers of the lagoon are passing through a delicate phase in the quest for an equilibrium between the needs of humans and the restoration and conservation of the environmental system (Lionello, 2012).

1.5. Study aims

The objective of this thesis is to gain a deeper understanding of the distribution of species inhabiting two dominant and ubiquitous types of artificial structures in the Venice lagoon, and the potential contribution to relevant ecosystem functioning. Specifically, we examined the composition and abundance of species growing on seawalls and pilings, aiming to explain how their distribution varies in relation to the typology of structure and the urbanization level within the lagoon.

Further, we examined the influence that the communities associated with these artificial structures have on two relevant functions, filtration rates and carbon content in shells, which underpin two crucial ecosystem services for the lagoon. Regarding filtration rate

and shell carbon content, we focused on two key filtering species in the lagoon: oysters and mussels.

We formulated the hypothesis that species composition and population density of benthic communities would be influenced by the type of structure, expecting variations between samples collected from seawalls and pilings due to their different shapes and material compositions (concrete for seawalls and wood for pilings). We also predicted differences in the samples collected from seawalls and pilings among various sites, depending on the urbanization level. It was expected that sites closer to urban centers and/or ports would exhibit poorer compositions and abundance of benthic communities in comparison to sites with lower urbanization levels. These reduced abundances would lead to lower potential filtration rates by dominant filter feeders and potential lower shell growth.

2. Materials and Methods

2.1. Study Area

The study took place in Venice Lagoon, between the southern and central part of the lagoon. In this area extensive seawalls, also known as coastal barriers or flood barriers, surround most of the islands in the lagoon. Moreover, all waterways in the lagoon are delimited by wooden pilings. The average salinity of the lagoon system is between 33-34 psu, and the average temperature is between 9.8°C and 25.2°C winter and summer respectively (seatemperature.info).

The study mainly focused on the assemblages in the intertidal zone growing on both seawalls and pilings. We did not sample the subtidal portions of these structures due to high turbidity and low visibility. The sampling included seawalls and pilings from different regions to represent different levels of human pressures in the lagoon. For seawalls, Lusenio, Lido di Venezia, and Pellestrina represented high, medium, and low urbanization levels respectively, (Figure 2.1.1.). The seawalls of all locations were built of concrete, except for three sites where seawalls were built of limestones (Pellestrina sites 14, 15, 16; Figure 2.1.1.). For pilings, Chioggia, the lower central lagoon and

upper central lagoon regions represented high, medium, and low urbanization levels, respectively (Figure 2.1.2.).

The various locations were chosen to represent distinct levels of urbanization and human pressures on marine systems. Lusenizio is a highly urbanized site deeply enclosed within the town of Chioggia where only small boats with small mobility have access (Figure 2.1.3). Pellestrina and Lido di Venezia are more open systems with lower density of urban settlement compared to Lusenizio but with bigger boats which usually travel for longer distances than the former (Figure 2.1.4.). Lido di Venezia is considered more urbanized than Pellestrina with a population density of 4,672 /Km², compared to a population density of 3,391/Km² for Pellestrina (<https://www.citypopulation.de/>).

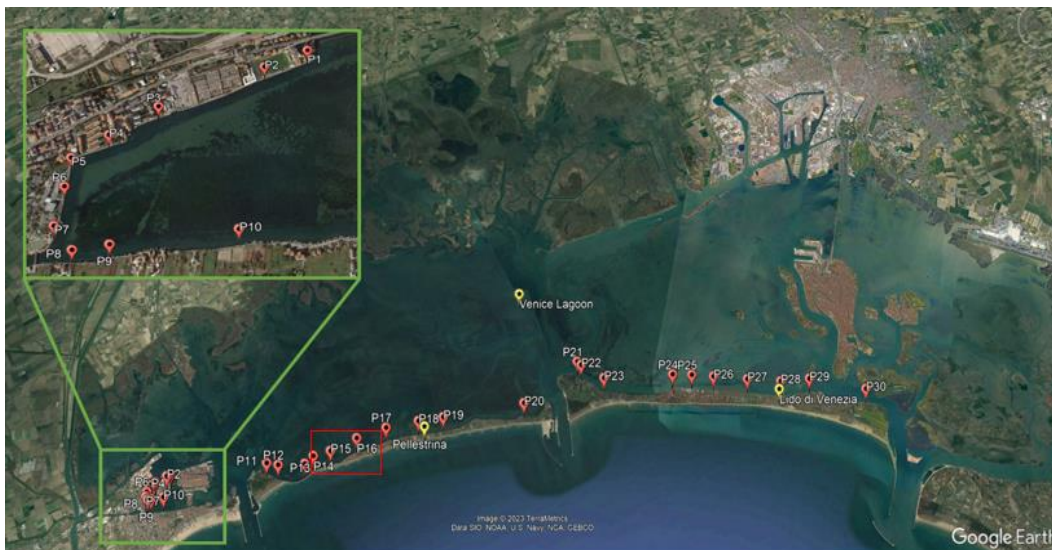


Figure 2.1.1. The locations of the 30 seawall's samples taken from Lusenizio, Pellestrina and Lido (High, low, medium urbanization levels respectively). (Highlighted in red the 3 seawall locations made of limestone).

Boats with low mobility can become ‘hyper-fouled’ with epibiota as many are not subject to the same antifouling procedures as ships (Godwin et al., 2003). Smaller recreational boats, which are the main boats used in Lusenizio for example, undergo less maintenance and can accumulate more fouling than bigger boats, mainly dominant in Pellestrina and Lido, that are typically well maintained and treated with antifouling coating (Mineur, 2012). Additionally, small recreational boats usually spend more time in harbors (sometimes months) while the other type is often out in the open sea.



Figure 2.1.2. The locations of the 42 pilings samples taken from Chioggia, in blue, Lower central lagoon, in red, and Upper central lagoon, in yellow, representing high, medium, and low urbanization levels.

As for the distinct locations of pilings, the upper central lagoon area was the least urbanized area located near saltmarshes in the lagoon, while Chioggia is highly urbanized being in proximity to human settlements and harbors. Parts of the sampled pilings in Chioggia were in Lusenizio (6 pilings in total), which is the enclosed region within the town of Chioggia. The lower central lagoon is considered to have a medium urbanization level. Pilings in the lower central lagoon area were mainly in front of Pellestrina which is an urbanized region but relatively less urbanized than Chioggia (Figure 2.1.2.)



Figure 2.1.3 Lusenizio lagoon, Chioggia 2019 (source: Flickr).



Figure 2.1.4 A modern cruise ship moving towards the mouth of Lido to go out to sea (Photo: Paolo Peretti).

The intertidal assemblages were sampled for each type of structure. For sea walls, 10 samples were collected at 10 different sites for each urbanization level, which resulted in a total of 30 samples. For the piling, 42 samples were collected randomly to cover the whole study area (14 samples for the high urbanization level, 12 for the low urbanization level, and 16 in the medium urbanization level). Thus, a total of 72 samples were collected for the study.

Seawalls were sampled between the 18th and 28th of April 2023. Each sample consisted in a 10 x 10 cm quadrat, which was placed randomly on the intertidal region of the seawall, and all living organisms inside the quadrat were scraped and preserved in the fridge to be analyzed later. Sorting was done within one to two days from collection, and species were identified to the lowest taxonomic level possible. Mobile species (e.g., polychaetas) were preserved in ethanol to be counted later. Sessile species (e.g. oysters) were dried in the oven at 80°C for at least 24 hours then weighed to estimate species abundance (Figure 2.1.1.).

Pilings were sampled between the 6th and 14th of June 2023, using the same procedure illustrated for the seawalls (Figure 2.1.2.; 2.1.5).



Figure 2.1.5. Field sampling of pilings.

2.2. Filtration rates

One of the objectives of this study was to estimate how the variation of distribution of species is affecting relevant ecosystem functions, such as filtration of seawater by filter feeders. For this purpose, the filtration rate of both oysters and mussels at landscape level was calculated by integrating abundance data from our samples with values of filtration rates obtained from literature. The feeding and filtration physiology of oysters have, in fact, been extensively studied in relation to a variety of factors potentially affecting filtration rates, including environmental elements like temperature, flow rate, salinity, seston concentration, particle size, and the size of the oysters themselves (Riisgård et al., 2015), which has allowed to obtain realistic filtration equations. A literature review was conducted to gather information on filtration rates specific to oysters and mussels. The filtration rates are expressed in Lgh^{-1} , where L represents the liters of water filtered, grams of the dry weight of the organism, and hours.

2.2.1. Estimating the filtration rate at the lagoon level

To have a conservative estimate of the filtration rate for oysters and mussels in the lagoon, we only considered the period when all the organisms are fully covered by the tide. Thus, considering that in the study area, oysters and mussels grow within a 40cm band above mean sea level, we calculated the total amount of time (in hours) during the year that tides were above this 40 cm threshold, averaged for the years 2020, 2021, 2022. Based on this data, we obtained an estimate of submersion equal to a total of 1036 hour for 2020, 1161 hours for 2021, and 856 hours for 2022, with the average for the 3 years being 1018 hours.

For seawalls, we estimated the total amount (in grams) of oyster and mussels present in our study areas. First, we estimated the surface area available in our study area for the growth of these organisms. To do so, using Google Earth (Google Earth 2021), we measured (in meters) the length of the seawalls in the three studied locations (Lusenzio, Pellestrina, and Lido). Second, we multiplied this length (for each location) by 40 cm, which is the band within which oyster and mussels mainly grow. Third, we calculated the average amount of oysters and mussels present in our sampling quadrats (10 x 10

cm) for each location. Based on this value, we calculated the average weight of both species for a meter square. Lastly, we multiplied this average weight per meter square by the total surface area of seawalls at the lagoon level.

For pilings, their number was estimated for each of the three sites. First, we measured the length of the water channels in the three sites using Google Earth, where the pilings are located (figure 2.5.1.). Then, we divided this length by 50m, which is the estimated distance between each two consecutive pilings to estimate their total number. Chioggia (high urbanization level) had an estimation of 570 pilings, LCL (medium urbanization level) 1002 pilings, and for the UCL (Low urbanization level) 1,359 piling. Then, the surface area of one piling was calculated by multiplying the perimeter of one piling (119cm on average) by the 40cm band. The obtained value was multiplied by the total number of pilings in each site to estimate the surface area. Subsequently, the average weight of oysters and mussels was calculated in our sampling quadrat. Based on this value, we calculated the average weight of both species for a meter square. Using this value together with the total area available for species growth on pilings we estimated the dry weight of both species at the level of the whole pilings' surface area available at the lagoon level.



Figure 2.5.1. Spread of pilings among the lagoon (Blue = High urbanization level, red = medium urbanization level, green = low urbanization level).

For *Crassostrea gigas*, Bayne (2009) showed that the average filtration rate is 4.6 L/hr/g of dry tissue weight. By using the measured total dry weight, we estimated the tissue dry weight of oysters using a conversion factor obtained from (Bayne, 2009) which is 0.024. Thus, the filtration rate of oysters for seawalls and pilings was calculated separately using equation 1.:

$$4.6 (\text{Dry weight of oysters in our samples} \times 0.024)$$

These values were converted into m³ / hour by multiplying them with 0.001 m³. Afterwards, the amount of meter cubes filtrated in total in one day was calculated separately for both substrates by multiplying these values by the average hours of submersion during a year divided by the days of the year, using equation 2.:

$$\begin{aligned} & \text{Estimated oyster filtration rate in our samples} \\ & \times \left(\frac{\text{hours of submersion per year}}{365} \right) \end{aligned}$$

For *Mytilus galloprovincialis*, the same procedure was repeated but using the conversion factor from total mussel's dry weight to soft tissue dry weight of 0.053 obtained from Palmerini & Bianchi, 1994. The filtration rate used was 2.6 liter per hour per 1 gram obtained from Galimany et al., 2011, with equation 3. taking the following form:

$$2.6 \times (\text{Dry weight of mussels in our samples} \times 0.053)$$

Then the total mussel filtration rate per day was calculated using equation 4:

$$\begin{aligned} & \text{Estimated mussel filtration rate in our samples} \\ & \times \left(\frac{\text{hours of submersion per year}}{365} \right) \end{aligned}$$

To better understand how urbanization is affecting ecosystem functions, we estimated the filtration rates for both species among the sites with different levels of urbanization of each structure type using the previously mentioned procedures. The filtration rate of oysters for seawalls and pilings was calculated by substituting the dry weight of oysters at each of the six locations separately in equation 5:

$$4.6 \times (\text{Dry weight of oysters at specific site} \times 0.024)$$

Filtration rates of mussels for seawalls and pilings was calculated by substituting the dry weight of mussels at each of the six locations separately in equation 6:

$$2.6 \times (\text{Dry weight of mussels at specific site} \times 0.053)$$

Then, each value of the obtained filtrations rates for oysters and mussels for each site was substituted in equations 2 and 4 respectively to estimate the filtration rates for each specific site when the intertidal region is submersed with water.

2.2.2. Carbon contents of shells

The carbon content of shells was estimated at the lagoon level for both species. According to Hickey (2004), 100 grams of the oysters shells contains 12 grams of inorganic Carbon. By estimating the total weight of oysters at the lagoon level we were able to estimate the amount of carbon content in the lagoon using equation 7:

Carbon content

$$= \frac{\text{Total dry weight of oysters}}{100} \times \text{carbon in 100 grams of oyster}$$

For mussels, the same procedure was applied knowing that the amount of carbon in 100 grams of mussel shells is 23.3g according to Tamburini et al. (2022) , using equation 8:

Carbon content

$$= \frac{\text{Total dry weight of mussels}}{100} \times \text{carbon in 100 grams of mussels}$$

For estimating the carbon shell content for each species at each urbanization level, equations 9 and 10 were used for oysters and mussels respectively.

Carbon content of oysters at a specific site

$$= \frac{\text{Total dry weight of oysters at this site}}{100} \times C \text{ in } 100g \text{ of oyster}$$

Carbon content of mussels at a specific site

$$= \frac{\text{Total dry weight of mussels at this site}}{100} \times C \text{ in } 100g \text{ of mussel}$$

2.3. Data Analysis

The abundances of species represented by the dry weight of sessile species and the number of individuals for mobile species were plotted for each of the two structure types, seawalls, and pilings, and then for the three different levels of urbanization of each structure type.

PERMANOVA was employed to assess the impact of two factors, specifically structure type (two levels: seawalls and pilings) and level of urbanization (three levels: high, medium, low), on sessile and mobile species abundances. Then, for each structure type, a PERMANOVA test was employed to assess the effect of urbanization level, both on sessile and mobile species. Dispersion around the centroid test was employed to check for the assumptions of homogeneity of variance for the PERMANOVA results for both structures (two levels, piling or seawall) and level of urbanization (three levels: high, medium, low, for each structure type). Pairwise tests using the pairwise.adonis function were applied when PERMANOVA results were significant, with a chosen significance level of 0.05 for all test, to pinpoint which group of data were significantly different from the other. Non-metric Multidimensional Scaling (NMDS) using the Bray-Cutris dissimilarity matrix, were used to plot the abundance of species among different structure types and levels or urbanization. NMDS plots were done separately for the dry weight of sessile species, and number of individuals for mobile species.

Two samples t- tests were employed to assess and compare the means of different samples categorized by structure types, namely Seawalls and Pilings. Within each structure category, ANOVA tests was employed for a further comparison among three

distinct urbanization levels: high, medium, low, for both seawalls and pilings separately. Thus, the tests were performed for both structures and for the three levels of urbanization within each structure type. In case of significant results, Tukey's Honestly Significant Difference (HSD) test was applied with a chosen significance level of 0, to pinpoint which group of data were significantly different from the other. Unlike for the seawalls samples, pilings samples for the 3 urbanization levels were unequal in number, thus Welch - ANOVA was used in this case instead of one-way ANOVA which considers the uneven number of samples to correctly compute the variances, providing more robust results.

All statistical analyses and graphs were done using R (R core team, 2022).

3. Results

3.1. Overall characteristics of the assemblages

Species identified on both structures at the different locations were reported in Tables 3.1.1 and 3.1.2 respectively, and the mean dry weight of sessile species as well as the number of individuals per mobile species were plotted (Figure 3.1.1, 3.1.2, 3.1.3).

Oysters (*Ostreidae* unidentified), mussels (*Mytilus galloprovincialis*), and barnacles (*Cirripedia* unidentified) were the most prevalent species by dry weight, with oysters having a higher mean weight on seawalls compared to pilings, while mussels and barnacles having a higher mean weight on pilings compared to seawalls (Figure 3.1.1. A). For the different algal species, the mean dry weight was low for seawalls samples (*Ulva intestinalis*, Ceramiales, unidentified green filamentous algae, *Bryopsis simplex*, *Ulva linza*) while it was zero for most piling samples except for *Ulva intestinalis* and *Ulva linza*. (Figure 3.1.1.B). The rest of the species present on both seawalls and pilings had an exceptionally low to almost negligible dry weight and that included: *Codium fragile*, *Chetomorpha sp.*, unidentified green turf algae, *Cladorpha sp.*, Ascidiacea unidentified, and Veneridae unidentified.

As for the number of mobile species organisms, *Spheroma* sp., *Amphipoda* sp., Nemertea, Actinaria, *Lepidochitona cinerea*, Nereidae, and *Eupolyornia nebolosa* had the highest number. The first four species were on average more abundant on pilings than on seawalls, while the mean abundance of the last three species was higher on seawalls (Figure 3.1.1.B). The mean abundance of the remaining species was exceptionally low and almost negligible (between 0 and 0.30); species found were Platyhelminthes, Picnogonida, *Syllis* sp., *Acanthochitona* sp., *Hydroschendyla submarina*, *Enchytraeus adriaticus* and *Carcinus aestuarii* (Table 3.1.3).

Table 3.1.1. List of identified taxa found on seawalls and pilings during the study. Symbols - or + indicate presence or absence respectively.

| Phylum | Class | Family or higher taxonomic unit | Species | Seawalls | Pilings |
|------------------------|-------------------------|---------------------------------|---|--------------|---------|
| Chlorophyta | Ulvoephyceae (class) | Ulvoaceae | <i>Ulva intestinalis</i> | + | + |
| | | | <i>Ulva linza</i> | + | - |
| | | Codiaceae | <i>Codium fragile</i> | + | - |
| | | Cladophoraceae | <i>Chetomorpha</i> sp. | - | + |
| | | Cladophoraceae | <i>Cladophora</i> sp. | - | + |
| | | Bryopsidaceae | <i>Bryopsis simplex</i> var. <i>plumata</i> | + | - |
| | | Unidentified green filamentous | Unidentified | + | - |
| | Unidentified green turf | Unidentified | + | - | |
| Rhodophyta | Florideophyceae | Ceramiales (order) | Unidentified | + | + |
| Mollusca | Bivalvia | Ostreidae | Unidentified | + | + |
| | | Mytilidae | <i>Mytilus galloprovincialis</i> | + | + |
| | | | <i>Xenostrobus</i> sp. | + | + |
| | | Veneridae | Unidentified | - | + |
| | Gastropoda | Patellidae | <i>Patella</i> sp. | + | - |
| | Polyplacophora | Tonicellidae | <i>Lepidochitona cinerea</i> | + | - |
| Acanthochitonidae | | <i>Acanthochitona</i> sp. | + | - | |
| Porifera | | | Unidentified | + | + |
| Cnidaria | Anthozoa | Actinaria (order) | Unidentified | - | + |
| Bryozoa | | | Unidentified | + | + |
| Anellida | Polycheta | Syllidae | <i>Syllis</i> sp. | + | + |
| | | Terebellidae | <i>Eupolymnia nebulosa</i> | + | + |
| | | Nereidae | Unidentified | + | + |
| | Clitellata | Enchytraeidae | <i>Enchytraeus adriaticus</i> | + | + |
| Nemertea | | | Unidentified | - | + |
| Platyhelminthes | | | Unidentified | + | + |
| Arthropoda | Chilopoda | Schendylidae | <i>Hydroschendyla submarina</i> | + | + |
| | Malacostraca | Spheromatidae | <i>Spheroma</i> sp. | + | + |
| | | Amphipoda (order) | Unidentified | + | + |
| | | Carcinidae | <i>Creinus aestuarii</i> | - | + |
| | Thecostraca | Cirripedia (subclass) | Unidentified | + | + |
| | Picnogonida | | | Unidentified | + |
| Chordata | Ascidiacea | | Unidentified | - | + |

Table 3.1.2. List of identified taxa found on the different locations of seawalls and pilings during the study. Symbols - or + indicate presence or absence respectively.

| Phylum | Class | Family or higher taxonomic unit | Species | Lusenzio | Pellestrina | Lido | Chioggia | UCL | LCL |
|------------------------|----------------------|---------------------------------|---|----------|-------------|------|----------|-----|-----|
| Clorophyta | Ulvoephyceae (class) | Ulveaceae | <i>Ulva intestinalis</i> | + | + | - | + | + | + |
| | | | <i>Ulva linza</i> | - | - | + | - | - | - |
| | | Codiaceae | <i>Codium fragile</i> | - | - | + | - | - | - |
| | | Cladophoraceae | <i>Chetomorpha</i> sp. | - | - | - | - | + | + |
| | | Cladophoraceae | <i>Cladophora</i> sp. | - | - | - | - | + | + |
| | | Bryopsidaceae | <i>Bryopsis simplex</i> var. <i>plumata</i> | - | + | + | - | - | - |
| | | Unidentified green filamentous | Unidentified | - | - | + | - | - | - |
| | | Unidentified green turf | Unidentified | - | - | + | - | - | - |
| Rhodophyta | Florideophyceae | Ceramiales (order) | Unidentified | - | + | + | - | + | + |
| Mollusca | Bivalvia | Ostreidae | Unidentified | + | + | + | + | + | + |
| | | Mytilidae | <i>Mytilus galloprovincialis</i> | + | + | + | + | + | + |
| | | | <i>Xenostrobus</i> sp. | - | + | + | + | + | - |
| | | Veneridae | Unidentified | - | - | - | - | - | + |
| | Gastropoda | Patellidae | <i>Patella</i> sp. | + | - | - | - | - | - |
| Polyplocophora | Tonicellidae | <i>Lepidochitona cinerea</i> | - | + | + | - | - | - | |
| | Acanthochitonidae | <i>Acanthochitona</i> sp. | - | - | + | - | - | - | |
| Porifera | | | Unidentified | + | - | + | + | + | + |
| Cnidaria | Anthozoa | Actinaria (order) | Unidentified | - | - | - | + | + | + |
| Bryozoa | | | Unidentified | - | - | + | - | + | - |
| Anellida | Polycheta | Syllidae | <i>Syllis</i> sp. | - | - | + | - | - | + |
| | | Terebellidae | <i>Eupolyornia nebulosa</i> | - | - | + | + | + | + |
| | | Nereidae | Unidentified | - | + | + | + | + | + |
| | Clitellata | Enchytraeidae | <i>Enchytraeus adriaticus</i> | - | - | + | - | + | - |
| Nemertea | | | Unidentified | - | - | - | + | + | + |
| Platyhelminthes | | | Unidentified | - | - | + | - | + | + |
| Arthropoda | Chilopoda | Schendylidae | <i>Hydroschendyla submarina</i> | - | - | + | - | + | - |
| | Malacostraca | Spheromatidae | <i>Spheroma</i> sp. | - | - | + | + | + | + |
| | | Amphipoda (order) | Unidentified | - | - | + | + | + | + |
| | | Carcinidae | <i>Carcinus aestuarii</i> | - | - | - | - | - | + |
| | Thecostraca | Cirripedia (subclass) | Unidentified | + | - | - | + | + | + |
| Picnogonida | | | Unidentified | - | - | + | + | - | - |
| Chordata | Ascidacea | | Unidentified | - | - | - | - | + | - |

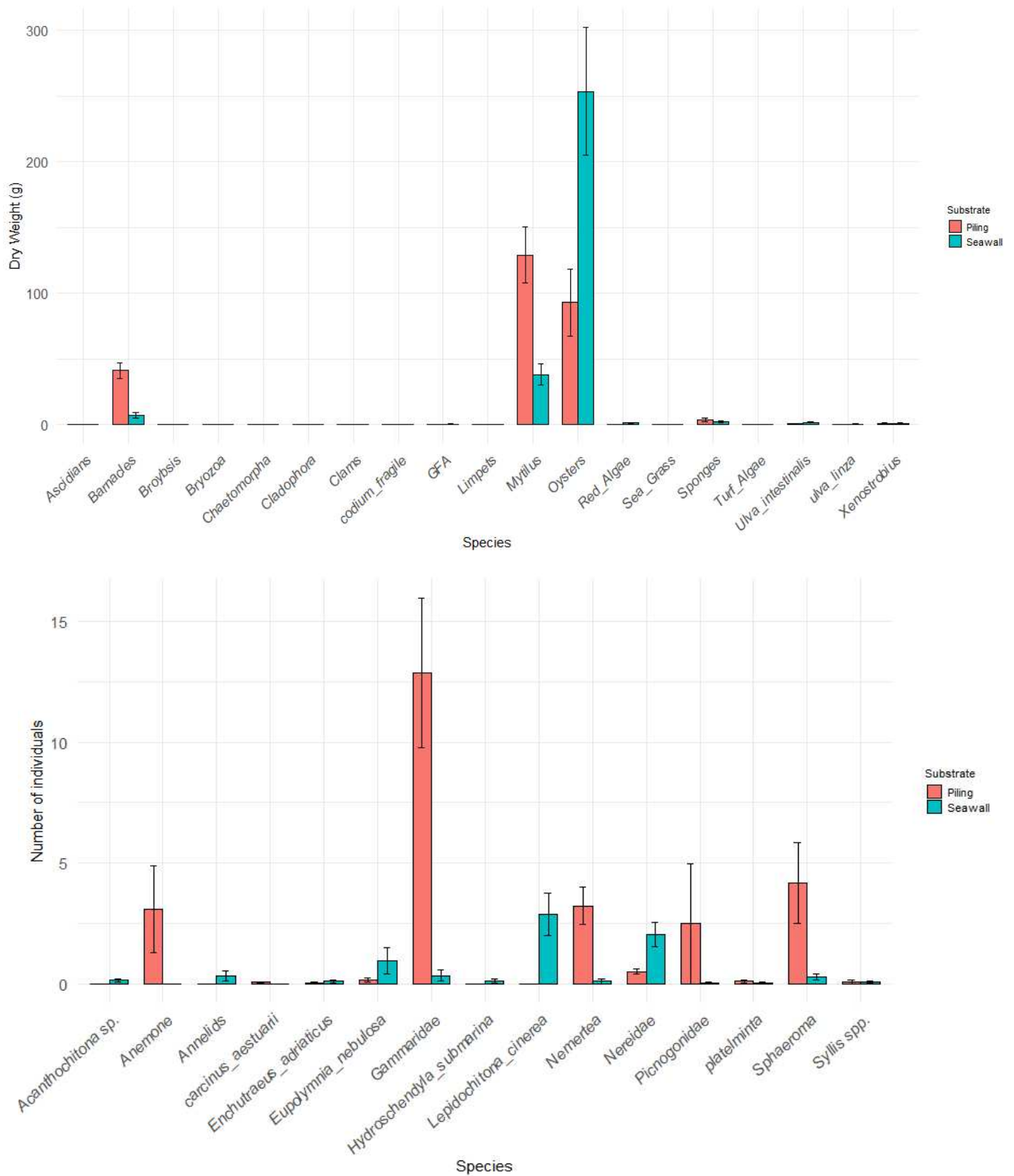


Figure 3.1.1. Abundance of species represented by the mean dry weight of sessile species (Panel 1) and number of individuals per mobile species (Panel 2) for both seawalls and pilings.

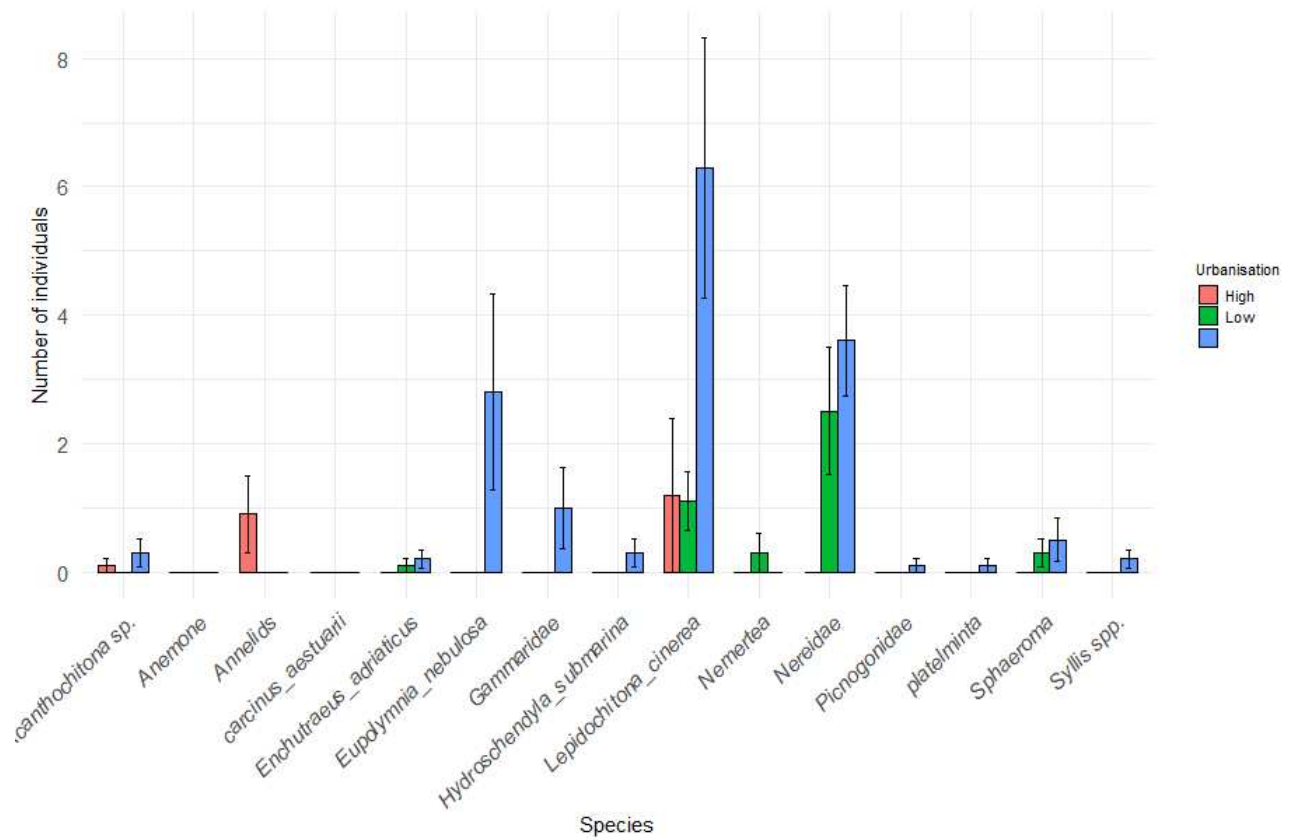
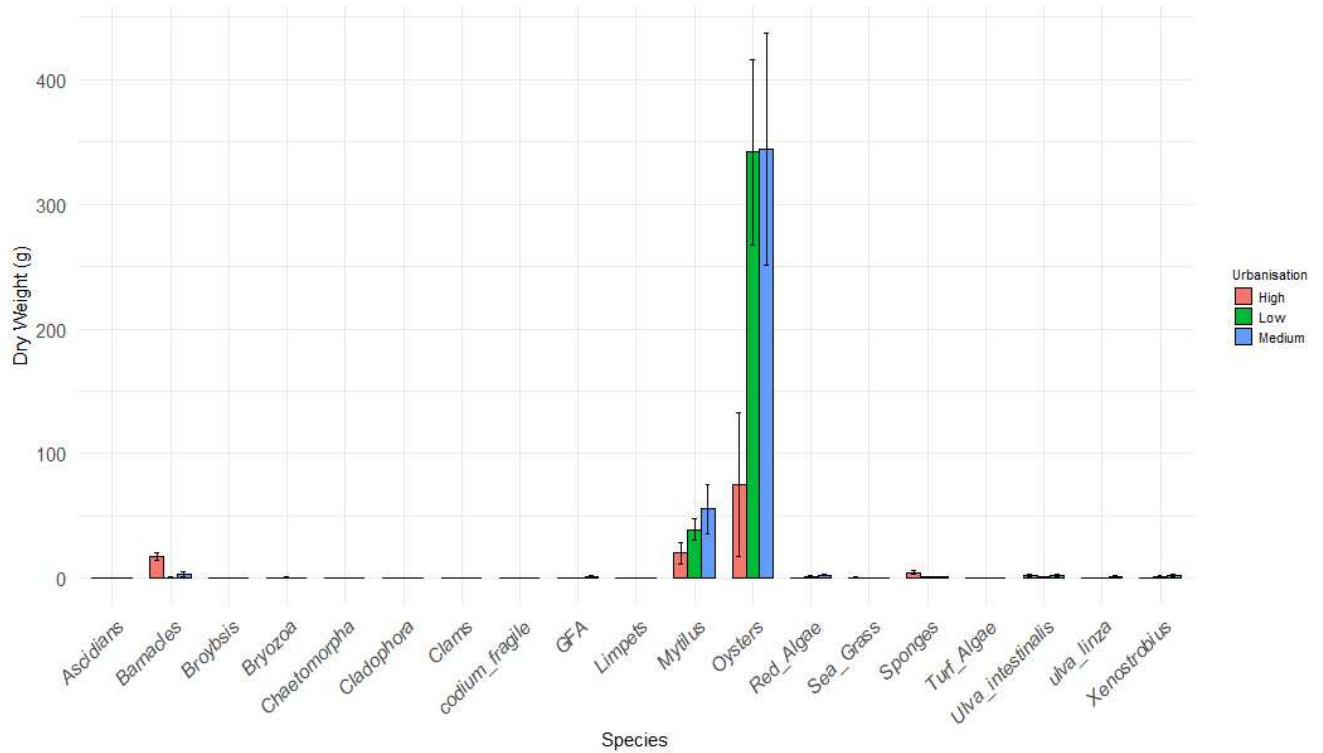


Figure 3.1.2. Abundances of species represented by the mean dry weight of sessile species (Panel 1) and number of individuals per mobile species (Panel 2) on the seawalls in the 3 different levels of urbanization.

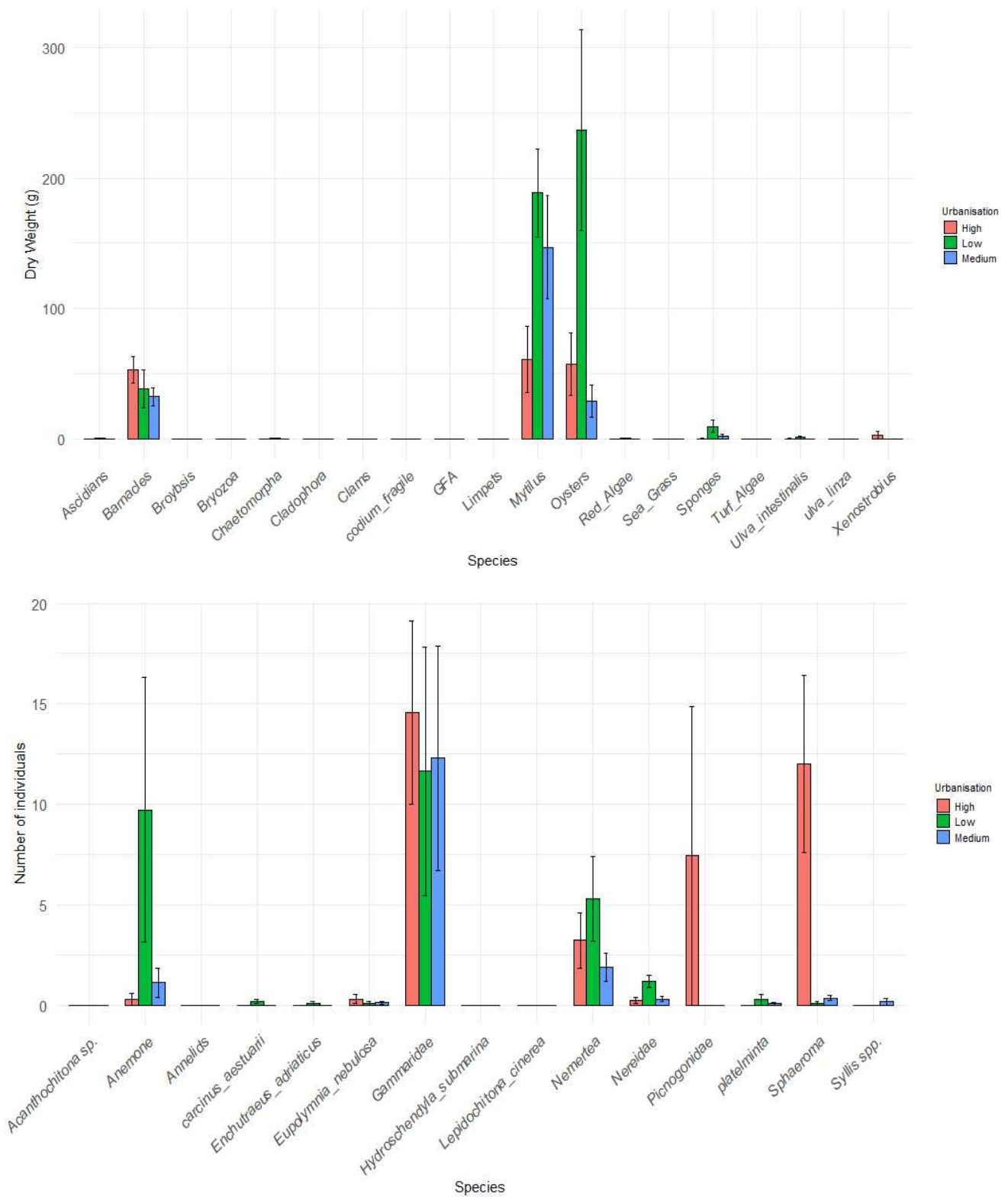


Figure 3.1.3. Mean dry weight of sessile species (Panel 1) and number of individuals per mobile species (Panel 2) on pilings for the 3 different locations (Chioggia, upper central lagoon (UCL), and lower central lagoon (LCL); colors blue, orange and grey respectively).

3.2. Assemblage level difference among substrates and urbanization levels

PERMANOVA results showed that structure type had a significant effect on the abundances of both sessile and mobile species (table 3.2.1., figure 3.2.1.).

Table 3.2.1. PERMANOVA results showing the impact of structure type on mobile and sessile species

| Sessile Species | | | | | | Mobile Species | | | | |
|------------------|----|----------------|------|----------|--------------|----------------|----------------|------|----------|--------------|
| Source | df | Sum of squares | R2 | Pseudo-F | p-value | df | Sum of squares | R2 | Pseudo-F | p-value |
| Structure | 1 | 0.04 | 0.13 | 9.99 | 0.001 | 1 | 0.051 | 0.05 | 11.87 | 0.001 |
| Residual | 69 | 0.28 | 0.87 | | | 69 | 0.029 | 0.29 | | |
| Total | 70 | 0.32 | 1 | | | 70 | 0.35 | 1 | | |

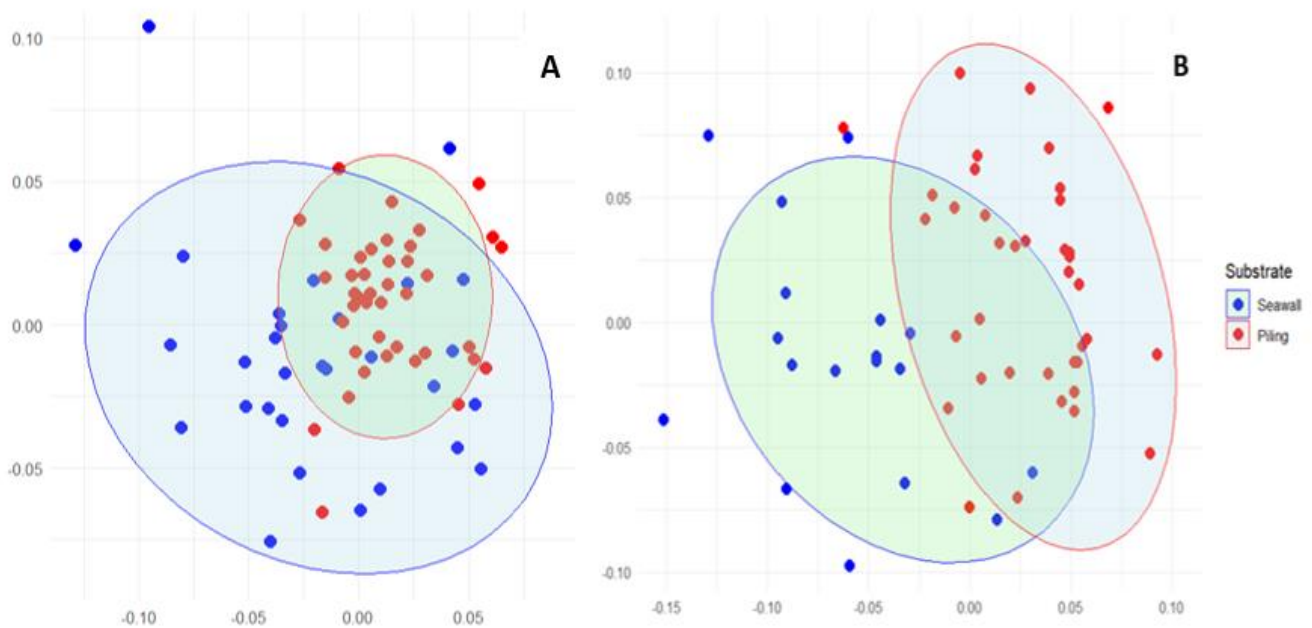


Figure 3.2.1. The NMDS plots of dry weight of sessile species (panel A) and number of organisms per mobile species (panel B) on the two structures seawalls and pilings (Red and green respectively).

| | Sessile Species | | | | | Mobile Species | | | | |
|---------------------|-----------------|----------------|-------|-------|--------------|----------------|----------------|-------|--------|--------------|
| Pilings | | | | | | | | | | |
| Source | df | Sum of squares | R2 | F | p-value | df | Sum of squares | R2 | F | p-value |
| Urbanization | 2 | 0.026 | 0.13 | 2.90 | 0.005 | 2 | 0.023 | 0.107 | 2.2725 | 0.009 |
| Residual | 38 | 0.169 | 0.87 | | | 38 | 0.190 | 0.893 | | |
| Total | 40 | 0.195 | 1 | | | 40 | 0.213 | 1 | | |
| Seawalls | | | | | | | | | | |
| Source | df | Sum of squares | R2 | F | p-value | df | Sum of squares | R2 | F | p-value |
| Urbanization | 2 | 0.063 | 0.202 | 3.422 | 0.001 | 2 | 0.038 | 0.115 | 1.749 | 0.059 |
| Residual | 27 | 0.249 | 0.798 | | | 27 | 0.292 | 0.885 | | |
| Total | 29 | 0.312 | 1 | | | 29 | 0.329 | 1 | | |

Table 3.2.2. PERMANOVA results for the abundances of mobile and sessile species among the different levels or urbanization for both structure types.

On pilings, PERMANOVA results showed that there are significant differences among the communities of sessile species for the three levels of urbanization, which was shown in the NMDS plot (table 3.2.2., figure 3.2.2.A.). Pairwise test showed that the abundances of sessile species of the high urbanization level site were significantly different from abundances for the low urbanization level, but there were no significant differences between high and medium or low and medium urbanization levels (table 3.2.3.). Regarding the abundances of mobile species, PERMANOVA results showed a significant difference in communities among the different urbanization levels (Figure 3.2.2.C, table 3.2.2.). Pairwise test showed that there are no significance differences among the different urbanization levels (table 3.2.3.).

On seawalls, the PERMANOVA showed that there is a significant difference in sessile species assemblages among the urbanization levels (table 3.2.2., figure 3.2.2. B). Pairwise test showed that the assemblages of sessile species varied significantly between high and low as well as between high and medium urbanization levels, in contrast, there was no significant differences in the sessile species communities between low and medium urbanization levels (table 3.2.3.). Communities of mobile species on seawalls showed no significance differences among levels of urbanization (table 3.2.2, figure 3.2.2.D).

Table 3.2.3. Pairwise test results for the abundances of sessile species for the different urbanization levels of seawalls and pilings, and the abundances of mobile species for the different urbanization levels of pilings.

| Variable | | Pairs | F Model | R2 | P value | P adjusted |
|----------|-----------------|----------------|---------|-------|---------|------------|
| Pilings | Sessile species | High vs Low | 3.474 | 0.131 | 0.011 | 0.033 |
| | | High vs Medium | 1.010 | 0.035 | 0.451 | 1 |
| | | Low vs Medium | 2.476 | 0.090 | 0.036 | 0.108 |
| | Mobile species | High vs Low | 2.258 | 0.089 | 0.036 | 0.108 |
| | | High vs Medium | 2.607 | 0.085 | 0.042 | 0.126 |
| | | Low vs Medium | 0.668 | 0.026 | 0.648 | 1 |
| Seawalls | Sessile species | High vs Low | 7.163 | 0.285 | 0.001 | 0.003 |
| | | High vs Medium | 4.118 | 0.186 | 0.001 | 0.006 |
| | | Low vs Medium | 0.658 | 0.035 | 0.767 | 1 |

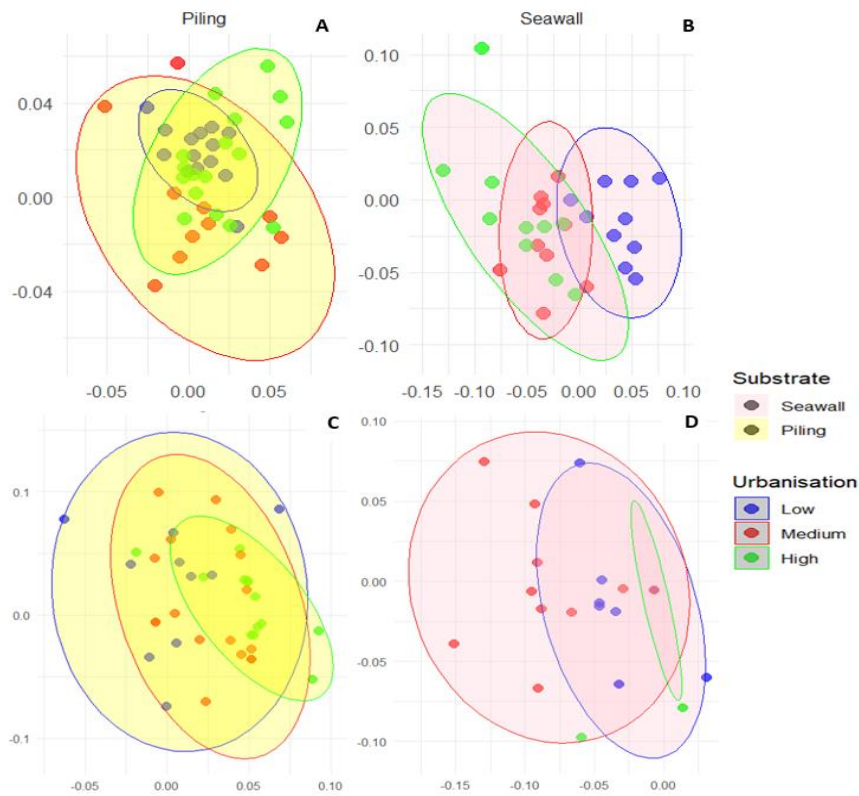


Figure 3.2.2. The NMDS plot of A. Abundance of sessile species on pilings, B. Abundances of sessile species on seawalls, C. Abundances of mobile species on pilings, and D. Abundances of mobile species for seawalls based on the levels of urbanization.

3.3. Abundance differences among structures and levels of urbanization

The two-sample t-test showed that there were no difference in the abundances of sessile species between pilings and seawalls, while there was a significant difference in the abundances of mobile species between the two types of structures (table 3.3.1.).

ANOVA tests did not show significant differences in the abundances of either sessile or mobile species among levels of urbanization for seawalls (table 3.3.1.). On pilings there were no significant differences abundances of mobile species among the various levels of urbanization, yet there were differences in the abundances of sessile species (table 3.3.1.). Tukey’s test results showed that sites with the highest urbanization levels exhibited the lowest weight (g) in total (mean 9.788 ± 3.757) in comparison to both medium urbanization level (mean 11.281 ± 4.387) and low urbanization level (mean 27.208 ± 4.387) sites. Notably, the sites with the lowest urbanization levels exhibited the highest mean dry weight (table 3.3.2.)

Table 3.3.1. Two samples t-test to compare the abundances of sessile and mobile species between seawalls and pilings. One-way and Welch ANOVA results for comparing the abundances of sessile and mobile species for the different levels or urbanization of seawalls and pilings. Significance level = 0.05, significant p-value is highlighted in bold.

| Variable | Test | df | SS | MS | T-statistic | p. value | |
|-----------------|-------------------------------------|--------------------|----------|---------|-------------|---------------|---------------|
| Sessile species | Among seawalls and pilings | Two samples t-test | 1,084.30 | | 0.487 | 0.627 | |
| | Levels of urbanization for seawalls | ANOVA | 2 | 7707 | 3853 | 0.527 | 0.59 |
| | Levels of urbanization for pilings | Welch | 2 | 40823.5 | 20411.7 | 5.357 | 0.0048 |
| Mobile species | Among seawalls and pilings | Two samples t-test | 711.4 | | -3.7049 | 0.0002 | |
| | Levels of urbanization for seawalls | ANOVA | 2 | 11.9 | 5.972 | 1.994 | 0.137 |
| | Levels of urbanization for pilings | Welch | 1 | 192 | 192.2 | 2.657 | 0.103 |

Table 3.3.2. Tukey's test for the abundances of sessile species among the three different urbanization levels of pilings (High, low, and medium), significance level = 0.01, significant p-values were highlighted in bold.

| Group | emmean | SE | df | p. value |
|----------------------------------|---------------|-----------|-----------|-----------------|
| High urbanization level | 9.788 | 3.757 | 753.000 | 0.028 |
| Low urbanization level | 27.208 | 4.387 | 753.000 | 0.0001 |
| Medium urbanization level | 11.281 | 3.637 | 753.000 | 0.006 |

3.4. Filtration rates

To calculate the filtration rate of oysters on seawalls at the lagoon level, we proportionally deduced that total estimated weight of oysters on seawalls throughout the whole lagoon to be around 422,909,698 g (422,9 Tons). Using this value, we were able to estimate the filtration rate of oysters on seawalls across the whole lagoon by using equation 2, which yielded a total filtration rate of 85,819 m³/day (figure 3.4.1). The estimated total weight of mussels on seawalls across the Lagoon was 58,225,452 g (58,2 Tons). Using equation 4, we estimated the filtration rate of mussels on seawalls to be about 15,972 m³/day.

Table 3.4.1. Estimated dry weight in Tons for oysters and mussels for the entire structures for different sites of seawalls (Lusenzio, Pellestrina, and Lido) and pilings (Chioggia, upper central lagoon, and lower central lagoon).

| Site | Estimated dry weight of oysters (Tons) | Estimated dry weight of mussels (Tons) |
|-----------------------------|---|---|
| Lusenzio | 39.40 | 10.63 |
| Pellestrina | 161.50 | 18.46 |
| Lido | 73.45 | 11.81 |
| Chioggia | 1.26 | 1.34 |
| Upper central lagoon | 15.07 | 12.02 |
| Lower central lagoon | 1.44 | 7.32 |

For oysters on pilings, we estimated that the total weight of oysters within the portion of the studied lagoon, was around 17,910,684 g (17.9 Tons). This weight was substituted in equation 2. to estimate the total filtration rate of oysters on pilings, which gave a value of 5,564 m³/day. The same process was applied to mussels growing on pilings. The total weight of mussels present in the entire lagoon was estimated to be 22,600,914 g (22.6 Tons). This weight was substituted in the equation 4 to get an estimated filtration rate of 8,068 m³/day. Estimated filtration rates for mussels and barnacles on both structures were plotted in Figure 3.4.1.

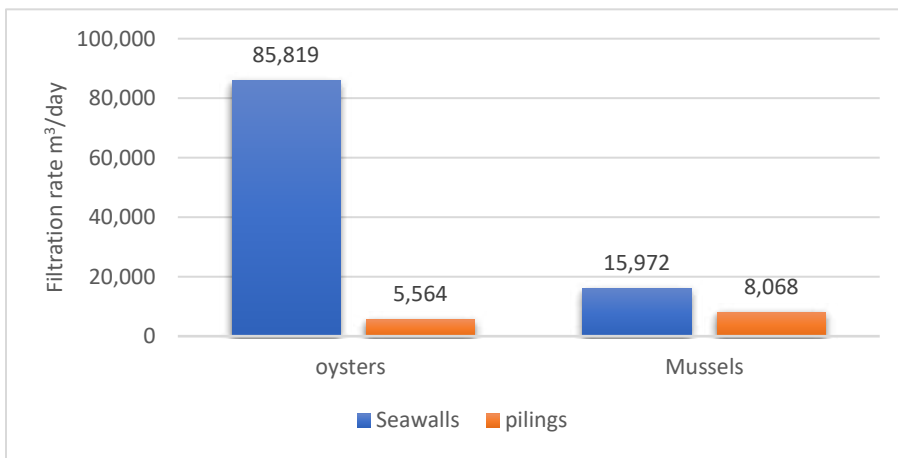


Figure 3.4.1. Estimated filtration rate of oysters and mussels per day at the lagoon level.

Finally, to estimate the total filtration rate of the two species at the lagoon level, the filtration rates of each species on both structures were summed up, obtaining an estimate of filtration rate for oysters equal to 91, 383 m³/day, while for mussels equal to 24,040 m³/day.

To estimate the filtration rates of oysters and mussels at each urbanization level, we substituted the weight estimations of both species at each site reported in table 3.4.1. in equations 5 and 6, for oysters and mussels respectively. The obtained filtrations rates were reported in table 3.4.2. Filtration rates were significantly higher at the low urbanization levels for both species and structures in comparison to medium and high urbanization levels.

Table 3.4.2. Filtration rate estimation of oysters and mussels at each urbanization level of seawalls and pilings.

| Substrate | Urbanization Level | Filtration Rates | |
|-----------|--------------------|------------------|---------|
| | | Oysters | Mytilus |
| Seawalls | High | 12,339 | 4,152 |
| | Medium | 22,971 | 4,611 |
| | Low | 50,509 | 7,209 |
| Pilings | High | 396 | 523 |
| | Medium | 453 | 2,857 |
| | Low | 4,715 | 4,688 |

3.5. Carbon content of shells

The amount of carbon immobilized in the shells of oysters and mussels was estimated at the lagoon level by substituting the total weight of oysters and mussels for seawalls and pilings in equations 7 and 8 respectively. For oysters on seawalls, an estimated total weight of 422,9 Tons, is estimated to contain 32.9 Tons of carbon. While on pilings, an estimate of 17.9 Tons of oysters is estimated to contain 2.12 Tons of carbon. For mussels, an estimate of 58,2 Tons on seawalls contains an estimate of 9.45 Tons of carbon (Figure 3.5.1.). While an estimate of 22.6 Tons of mussel growing on pilings can contain up to 4.8 Tons of carbon (figure 3.5.1.).

To estimate the carbon shell content for oysters and mussels on seawalls and pilings at each level of urbanization, the estimated dry weight of oysters and mussels for all urbanization levels were substituted in equations 9 and 10 respectively. The obtained estimations were reported in table 3.5.1. Carbon shell content was significantly higher at the low urbanization levels for both species and structures in comparison to medium and high urbanization levels.

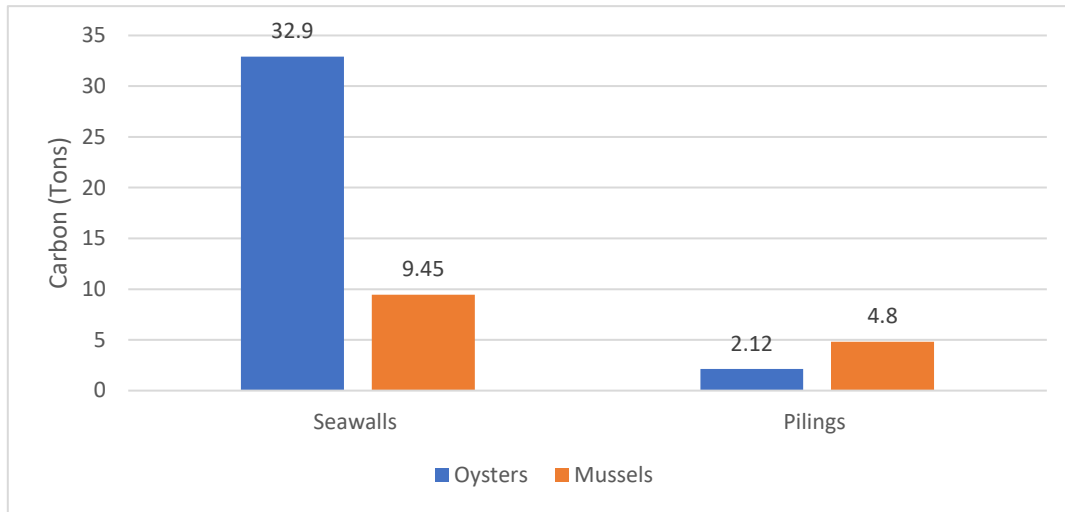


Figure 3.5.1. Carbon shell content estimation in Tons for oysters and mussels on seawalls and pilings at the lagoon level.

Table 3.5.1. Carbon content estimations of oysters and mussels at each urbanization level of seawalls and pilings.

| Substrate | Urbanization Level | Carbon Shell Content (Tons) | |
|-----------|--------------------|-----------------------------|---------|
| | | Oysters | Mytilus |
| Seawalls | High | 4.73 | 2.40 |
| | Medium | 8.80 | 2.75 |
| | Low | 19.38 | 4.30 |
| Pilings | High | 0.15 | 0.30 |
| | Medium | 0.17 | 1.70 |
| | Low | 1.80 | 2.80 |

4. Discussion

The results of this thesis provided a general picture of the distribution and composition of species among the two most abundant types of artificial structures in distinct locations of Venice lagoon, and how this can translate into an effect on relevant ecosystem functions such as filtration rates and carbon content in shells.

4.1. General Species Distribution

This thesis adds to the common knowledge that different structures support different compositions of species (Clynick, 2008). Seawalls supported different sets of sessile and mobile species than pilings, and the abundance of species varied with urbanization level as well. Sessile species were more prevalent on seawalls than on pilings except for mussels and barnacles that were more prevalent on pilings. For mobile species, pilings supported fewer species than seawalls but with higher abundance. Although the composition of species was different among structures, there was no significant difference in the total mean dry weight of sessile species between pilings and seawalls, suggesting an overall similar secondary production between the two types of structures. Conversely, there was a significant difference in the mean number of individuals per mobile species among the two structures, with pilings supporting significantly higher numbers.

During the sampling process, it was noted that except for the newly installed pilings which were not included in the sampling process, the sampled pilings were partially eroded. Thus, this erosion might be a key factor for shaping the composition of species on this type of structure. Anchored species that grow directly on the structure might get detached easily when the structure gets eroded, especially heavier ones like oysters. Indeed, oysters had lower mean dry weight on pilings in comparison to seawalls (on average 101.82 g opposite to 340.66 g for all samples). On the other hand, mussels and barnacles were more prevalent on pilings (141.84g and 18.89g respectively) than seawalls (38.20g and 13.59g respectively, which seems to contradict the previous

hypothesis. However, once pilings break, they create a rough surface, characterized by pits and crevices. Many studies highlighted that these features could alter environmental conditions (Thorson, 1964), increasing the niches available for colonization and shelter for organisms ((Loke et al., 2015; Hanlon et al., 2018). Thus, the cavities created by piling erosion may have created safe spots for barnacles and mussels to grow, which were less exposed to wave and thus to lower changes of detachment. Moreover, although pilings supported few species in number than seawalls, the rough surfaces after piling breakage may have provided a refugia from predators for some mobile species (Espan et al., 1998), leading an overall higher abundance of this group of organisms.

Urbanization in coastal areas can have varying effects on species distribution and community composition (Momota & Hosokawa, 2021). Stress related to urbanization (e.g. pollution) can filter out species, or specific functional groups, that are not adapted to urban conditions, and consequently decreasing the diversity and abundance at small, local spatial scales (Piano et al., 2020; Saari et al., 2017). For example, Piano et al, (2020) demonstrated that urbanization drove declines in the abundance and species richness in several investigated groups. In contrast, hostile urban areas can select for a few synanthropic species with heightened competitive advantages, and thus raising the overall abundance of organisms (Shochat et al., 2010). Therefore, there is currently limited consensus regarding the expected response of overall organism abundance to urbanization. Our results reflect this differential effect of urbanization on species diversity and organisms' abundance. For sessile species, on seawalls, the most urbanized site had distinct community composition and an overall lower abundance in weight with respect to both medium and low urbanization. For pilings, the difference in community composition and abundance in weight was only found between sites with high and low urbanization levels, but not between high and medium or low and medium urbanization level.

For mobile species on seawalls, there were no differences among the different levels of urbanization, neither in community composition nor in abundance (measured as numbers of individuals). On pilings, results showed a significance difference in species

composition, but further analyses were not able to pinpoint which sites varied specifically from others because of the high small-scale variability among sampled quadrats. These outcomes might be explained by the fact that all sites included in the study were very wide, covering large stretches of coastline, potentially including large within-location spatial variability. Thus, the lack of statistical significance could possibly be due to the large spatial variability.

Differently from what was observed on sea walls, the abundances of sessile and mobile species associated to pilings varied significantly among the distinct levels of urbanization, with the least urbanized area, exhibiting the highest average abundances. In contrast, species abundances were notably lower and quite similar between the sites with high and medium urbanization levels, with values nearly three times lower than that of the low urbanization level. This might be because this site was far from urbanized centers and samples were mostly taken close to the saltmarshes with no urbanization.

4.2. Abundances of the most prevalent species

On seawalls, oysters had the lowest abundances in the most urbanized site, compared to medium and low urbanization levels. Similarly on pilings, oysters had almost four times lower abundances in sites with high and medium urbanization levels compared to the site with low urbanization level. These findings are consistent with the fact that urbanization and coastal development act as stressors that are increasingly affecting oyster growth (Thomsen et al., 2006). Eutrophication, urban development, and changed land-use practices are likely to have large-scale negative effects on oyster reefs and associated biota. Pollution resulting from urbanization can lead to impaired reproduction, mortality, or developmental defects at early life stages of oysters (Mai et al., 2012). Further work potentially exploring the role of some of these stressors would be needed to explain lower abundances of oysters in the highly urbanized sites in comparison to the other less urbanized ones.

Mussels showed a great variation in abundances among the structure types, with pilings supporting significantly higher abundances than seawalls (129.93g opposite to 55.12g).

The abundance of mussels did not differ among seawall sites with different urbanization levels. Conversely, mussels on pilings showed significant differences among sites with the site having low urbanization level exhibiting the highest mean dry weight while the site having high urbanization level exhibiting the lowest mean dry weight. Cajaraville et al. (1992) found that the exposure of mussels to specific pollutants led to a significant reduction in both their flesh and shell growth. This decrease was evident through various sizes, conditions, and allometric parameters when compared to the control group. As previously hypothesized, the differences in the levels of urbanization among seawall locations have been less strong than those among piling locations, which could explain the different patterns observed between pilings and seawalls.

The abundance of barnacles on pilings was five times higher than the abundance on seawalls (41.84g opposite to 7.14g). Unexpectedly, the site with highest urbanization level had the highest mean dry weight of barnacles among the different seawall sites, while the mean dry weight was comparable among the distinct sites of pilings. Sessile invertebrates in marine environments frequently face limitations when it comes to available settlement space, and many communities have evolved under the influence of intense spatial competition (Rossi & Snyder, 2001). Osman et al. (1989) found that the presence of other sessile invertebrates, such as barnacles, ascidians, and bryozoans, was linked to increased mortality and limited growth in newly settled oyster spat. Zajac et al. (1989) also observed that, even if competitors did not cause mortality in oysters, they did reduce the growth rate of oyster species. Due to site having high urbanization level exhibiting generally lower dry weight for oysters in comparison to the rest of the sites for seawalls, this might have created less competition for space for barnacles to grow and prevail particularly in this location, while the rest of the locations had generally higher dry weight of oysters, leading to less space available for barnacles. The same explanation might be applied to the difference observed between the two different structures, since pilings that have lower mean dry weight for oysters in comparison to seawalls supported a higher mean dry weight of barnacles.

4.3. Importance of Oysters and Mussels in the Ecosystem

The estimated filtration rates suggested that mussels are the main filter feeders for pilings while oysters are the main filter feeders on seawalls.

The estimated filtration rate of oysters on both structures was 91,383 m³/day, while the filtration rate of mussels was 24,040 m³/day across the entire lagoon. On seawalls, the total filtration rate provided by both oysters and mussels was 101,791 m³/day which is about 10 times higher than the filtration rate for both species on pilings which was 13,632 m³/day. For both species, the estimation of filtration rate was higher on seawalls than on pilings since the total area available for species growth on seawalls is 9 times higher than that on pilings, and thus seawalls supported higher abundance of species in general.

4.3.1.1. Filtration Rates

Oysters and mussels are the main ecosystem engineers associated with seawalls and pilings in Venice Lagoon. Ecosystem engineers create, maintain, and modify habitats by substantially changing the chemical and physical composition of structures (Šobotník & Dahlsjö, 2017). Ecosystem engineers affect resident organisms, the resources they rely on, and the abiotic stressors they experience (Guy-Haim et al., 2018). Thus, changes in the distribution and abundance of these taxa may also have widescale consequences to estuarine and coastal ecology (Connell, 2000). Bivalves may filter the entire volume of water three or more times for every single exchange affected by tidal flushing and runoff (Connell, 2000). This influences at least two key functions, the flux of particles between the water and the sediments and the recycling of nutrients (Soetaert & Middelburg, 2009). Hence, change in the distribution and abundances of bivalves may result in substantial changes in the biomass of phytoplankton and larvae that are important components of coastal ecosystems (Connell, 2000).

The literature shows that the filtration capacities (pumping, retention, and filtration rates) differ between species. At equal dry weight (1 g) and at 15 °C, filtration rate of *Mytilus galloprovincialis* is estimated to be 4.08 L of water in one hour, vs. an

equivalent volume of 3.7 L per hour for *Magallana gigas* and the *Ostrea edulis* (Richard et al., 2022a). Filtration rate also increases with the weight of the organism following an allometric law (Cescon & Jiang, 2020; Richard et al., 2022b). Thus, when these rates are related to weight, smaller organisms have higher filtration activity than larger ones (Cescon & Jiang, 2020). These relationships are also positively influenced by temperature (Gosling, 2015). The volume of water and associated particles that oysters and mussels can remove via filter-feeding is of interest to managers in ecosystems where nutrient pollution may lead to phytoplankton blooms and deteriorated water quality (Ehrich & Harris, 2015). For example, bivalves have been used as bottom-up mitigation of eutrophication in the USA, where the American oyster, *Crassostrea virginica*, regulates regeneration of nitrogen and phosphorus (Kellogg et al., 2014). Our estimations showed that oysters across the lagoon can filter up to 91,383 m³/day, while mussels across the lagoon can filter up to 24,040 m³/day. Thus, these two species undergo a huge service in filtrating the water of the lagoon.

Oysters act as benthic-pelagic couplers, filtering particles from the water column and producing feces and pseudofeces (bio-deposits) rich in organic carbon (C) and nitrogen (N), that accumulate in nearby sediments (Filippini et al., 2023). Additionally, the filter-feeding behaviour of oysters fosters an ideal environment for nitrification and denitrification processes (Filippini et al., 2023).

As reported earlier, we hypothesized that different levels of urbanization might have an influence on species compositions and/or abundances, which will in turn influence ecosystem services undergone by these species. To better understand this relation, we measured how filtration rates would vary based on the level of urbanization of each site for both seawalls and pilings.

For filtration rates, oysters on seawalls had the lowest filtration rates in the site with high urbanization level, while the filtration rates were the highest in the site with low urbanization levels (12,399 and 50,509 m³/day respectively). This was also observed for pilings, where oysters in sites with high urbanization level had a filtration rate of 396 m³/day, in comparison to 4,715 m³/day for low urbanization levels.

Similarly for mussels, on seawalls, sites with highest urbanization levels were associated with the lowest filtration rates, while sites with lowest urbanization levels were associated with highest filtration rates (4,152 and 7,209 m³/day respectively). Likewise, mussels on pilings showed lowest filtration rates in relation to high urbanization levels, while showing high filtration rates in relation to low urbanization levels (523 and 4,688 m³/day respectively).

4.3.1.2. Carbon content in shells

Recognizing the significance of oysters in the carbon cycle has underscored the presence of substantial gaps in our understanding of accretion and erosion rates, carbon budgets, and the extent of carbon storage, alongside the importance of buried carbonate material (Burrows et al., 2014). Oysters have complex effects on CO₂ emission dynamics, serving as both sources and sinks of atmospheric CO₂ (Fodrie et al., 2017). Carbon dioxide is released during the process of calcification, but carbon is stored as a part of the shell growth of the organism (Fodrie et al., 2017). However, the sink or source status of oyster reefs will likely vary due to a number of variables such as sediment type, source of sediment input, age and density of the reef (Fodrie et al., 2017). At cold temperatures, the production of feces and pseudofeces is reduced, leading to lower rates of carbon deposition during the winter and early spring seasons (Levinton et al., 2023). The rates of deposition can vary significantly due to other numerous factors, including the weight of the organisms involved (Tsuchiya et al., 1980), food concentration (Cranford et al., 2011), turbidity (Fréchette & Grant, 1991), and the overall carbon content of suspended particles (Blomberg et al., 2017). Despite all these variations, (Hickey, 2004) reported that shells of oysters contain approximately 12g of carbon for every 100g of dry weight. In the context of the Venice lagoon, where the estimated dry weight of oysters on both structures is around 440.8 tons, it can be inferred that oysters in this ecosystem contains approximately 42.35 tons of carbon.

Also, mussels remove particles (e.g., phytoplankton, silt, zooplankton, bacteria, metals) from water bodies by filtering water to meet their nutritional demands (Kreeger et al., 2018). This leads to a change in nutrient cycling and toxicants concentrations (Collas et

al., 2020). Mussels have been shown to result in an immediate improvement in water clarity, especially in nutrient-enriched aquatic systems (H. H. & A. Bij de, 1990). In a study by Kent *et al.* (2017), it was observed that the presence of live horse mussels (*Modiolus modiolus*) led to a doubling in sedimentation rates, increasing from 2.14 g m⁻² day⁻¹ to 4.29 g m⁻² day⁻¹. Similarly, Giles *et al.* (2006) found a 40% enhancement in sedimentation rates at a mussel farm (410 g m⁻² day⁻¹) when compared to a reference site (290 g m⁻² day⁻¹). Consequently, the natural filtering capacity of mussels can significantly enhance the overall ecosystem quality (Newton *et al.*, 2011). The recorded accumulation of approximately 80.8 tons of mussels within the Venice lagoon is undeniably a significant factor contributing to the increase in sedimentation rates, thus leading to an enhancement in water clarity. This enhancement in water quality favors the presence of seagrasses which was evident in the study area. Further in-depth investigations are required to fully understand the influence that mussels have on a broader scale.

Amongst their role in biofiltration, mussels have an immense potential to serve as a carbon sink. This is attributed to the fact that over 90% of bivalve shells consist of calcium carbonate (CaCO₃), which is synthesized during the biocalcification process and effectively incorporates a molecule of CO₂ (Tamburini *et al.*, 2020). Given their nature as primary consumers, bivalves also release CO₂, but when scaling individual fluxes to the multi-trophic surrounding environment, shells can be considered net sinks of CO₂, consequently providing an additional ecosystem service besides the food provided by their flesh (Filgueira *et al.*, 2019). (Tamburini *et al.*, 2022) reported that mussels can contain an average of 23.3g of carbon for every 100 g of mussels. In the Venice lagoon, where the estimated mussel biomass on both structures is approximately 80.8 tons, it is estimated that the mussels in this habitat can contain around 14.25 tons of carbon.

Among the different urbanization levels, a trend that is similar to filtration rates was observed for carbon shell content. Oysters on seawalls were estimated to contain a lower amount of shell carbon in sites with high urbanization level in comparison to low urbanization levels (4.73 and 19.38 Tons respectively). Similarly on pilings, oyster

shells were estimated to contain up to 0.15 Tons of carbon in sites with high urbanization levels in comparison to 1.8 tons for sites with low urbanization levels.

On the other hand, mussels on seawalls were estimated to contain almost double the amount of carbon in sites with low urbanization levels in comparison to sites with high urbanization levels (4.30 and 2.40 Tons respectively). Lastly, mussels on pilings had also higher estimations of carbon content in sites with low urbanization levels in comparison to sites with high urbanization levels (2.80 and 0.30 Tons respectively).

These estimations unequivocally highlight that urbanization is in fact impacting ecosystems and ecosystems services tangibly.

5. Conclusion

The primary objectives of this thesis were to gain a deep understanding on the distribution patterns of species inhabiting the two most abundant types of artificial structures in the Venice Lagoon (seawalls and pilings) and to understand whether this distribution might vary in relation to distinct levels of urbanization. Additionally, we aimed to explore how this variability in species distribution impacts two relevant ecosystem functions which are filtration rates and shell carbon content by filter-feeding organisms. The key findings of this study indicate that the two different structures, seawalls, and pilings, supported distinct species compositions and exhibited variations in species abundances, with seawalls supporting higher species abundances compared to pilings. Among the different urbanization levels of seawalls, there was an evident difference in species composition mainly between high and low as well as high and medium urbanization levels with no detected variation in species abundances. On the other hand, variations in both species composition and abundances were evident among pilings locations, with the site having the lowest urbanization level, with a dominance of natural or restored saltmarsh habitat, displaying a distinct species composition and a higher abundance compared to the other urbanized locations. At the lagoon level, it was observed that the estimated total area available for species colonization was approximately nine times larger on seawalls in comparison to pilings. Focusing on filter

feeders, the estimated dry weight of oysters and mussels was higher on seawalls than on pilings. These factors significantly contributed to variations in filtration rates between the two structures, with both oysters and mussels on seawalls exhibiting filtration rates approximately ten times higher than those on pilings. For shell carbon content, oysters and mussels on seawalls were estimated to contain approximately 9 times higher carbon content than what is estimated on pilings. Additionally, it was evident that both filtration rates and shell carbon content of both species and structures, were affected by the level of urbanization, with these services being much more profound in association with lower urbanization levels.

However, it's essential to acknowledge the limitations of this thesis. The relatively small sample size for distinct locations, relative to the data variability, posed challenges for the ANOVA test's ability to detect statistical differences between groups in some cases. Thus, future studies should consider a higher sampling effort to better capture location-based differences. Furthermore, sampling took place during one period of the year, which is from late April to mid-late June, and thus the seasonal variations were not taken into consideration. Therefore, future studies should consider sampling through different periods throughout the year to better capture the variation in community composition.

The observed variations in species composition between different structures, and among urbanized and urbanized locations within the structures, in addition to the resulting effects on ecosystem functioning underscore the need for more extensive investigations on larger scales. Such studies will not only advance our understanding of urban structure ecology but also provide deeper insights into the consequences of ongoing urban structure expansion on coastal habitat ecology.

6. Bibliography

- Airoidi, L., Balata, D., & Beck, M. W. (2008). The Gray Zone: Relationships between habitat loss and marine diversity and their applications in conservation. *Journal of Experimental Marine Biology and Ecology*, 366(1–2), 8–15.
<https://doi.org/10.1016/j.jembe.2008.07.034>
- Airoidi, L., & Bulleri, F. (2011). Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *PLoS ONE*, 6(8). <https://doi.org/10.1371/journal.pone.0022985>
- Airoidi, L., Connell, S. D., & Beck, M. W. (2009a). *The Loss of Natural Habitats and the Addition of Artificial Substrata* (pp. 269–280).
https://doi.org/10.1007/b76710_19
- Airoidi, L., Connell, S. D., & Beck, M. W. (2009b). *The Loss of Natural Habitats and the Addition of Artificial Substrata* (pp. 269–280).
https://doi.org/10.1007/b76710_19
- Angeli, M. G., Fabrizio, P., Gasparetto, P., Mertzanis, A., Marabini, F., Angeli, M. G., Mertzanis, K., Pontoni, F., & Gasparetto, P. (n.d.). Coastal zone management and special coastal protection works in vulnerable lagoon ecosystems: The case of " Venice lagoon " (Italy) and " North Amvrakikos gulf lagoons complex " (G... Coastal zone management and special coastal protection works in vulnerable lagoon ecosystems: The case of "Venice lagoon" (Italy) and "North Amvrakikos gulf lagoons complex" (Greece). In *Mykonos island*.
<https://www.researchgate.net/publication/280742431>
- Bayne, B. L. (2009). Carbon and nitrogen relationships in the feeding and growth of the Pacific oyster, *Crassostrea gigas* (Thunberg). *Journal of Experimental Marine Biology and Ecology*, 374(1), 19–30. <https://doi.org/10.1016/j.jembe.2009.04.003>
- Benke, A. C., & Huryn, A. D. (2006). *F:\Pagination\Elsevier US\MSE\Latex-P332907\0mse01.dvi*.
- Bernardi Aubry, F., Berton, A., Bastianini, M., Socal, G., & Acri, F. (2004). Phytoplankton succession in a coastal area of the NW Adriatic, over a 10-year sampling period (1990-1999). *Continental Shelf Research*, 24(1), 97–115.
<https://doi.org/10.1016/j.csr.2003.09.007>
- Blomberg, A., Kallio, T., & Pohjanpää, H. (2017). Antecedents of organizational creativity: Drivers, barriers or both? In *Journal of Innovation Management* (Vol. 5, Issue 1, pp. 78–104). Universidade do Porto - Faculdade de Engenharia.
https://doi.org/10.24840/2183-0606_005.001_0007

- Borsje, B. W., van Wesenbeeck, B. K., Dekker, F., Paalvast, P., Bouma, T. J., van Katwijk, M. M., & de Vries, M. B. (2011). How ecological engineering can serve in coastal protection. In *Ecological Engineering* (Vol. 37, Issue 2, pp. 113–122). <https://doi.org/10.1016/j.ecoleng.2010.11.027>
- Bugnot, A. B., Mayer-Pinto, M., Airolidi, L., Heery, E. C., Johnston, E. L., Critchley, L. P., Strain, E. M. A., Morris, R. L., Loke, L. H. L., Bishop, M. J., Sheehan, E. V., Coleman, R. A., & Dafforn, K. A. (2020). Current and projected global extent of marine built structures. *Nature Sustainability*, 4(1), 33–41. <https://doi.org/10.1038/s41893-020-00595-1>
- BULLERI, F., & AIROLDI, L. (2005). Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, 42(6), 1063–1072. <https://doi.org/10.1111/j.1365-2664.2005.01096.x>
- Bulleri, F., & Chapman, M. G. (2004). Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. *Marine Biology*, 145(2), 381–391. <https://doi.org/10.1007/s00227-004-1316-8>
- Burrows, M. T., Schoeman, D. S., Richardson, A. J., Molinos, J. G., Hoffmann, A., Buckley, L. B., Moore, P. J., Brown, C. J., Bruno, J. F., Duarte, C. M., Halpern, B. S., Hoegh-Guldberg, O., Kappel, C. V., Kiessling, W., O'Connor, M. I., Pandolfi, J. M., Parmesan, C., Sydeman, W. J., Ferrier, S., ... Poloczanska, E. S. (2014). Geographical limits to species-range shifts are suggested by climate velocity. *Nature*, 507(7493), 492–495. <https://doi.org/10.1038/nature12976>
- 'CARBOGNIN, L., & 'MARABINI, F. (1987). *International conference on coastal and port engineering in developing countries*. .
- Carbognin, L., Teatini, P., Tomasin, A., & Tosi, L. (2010). Global change and relative sea level rise at Venice: What impact in term of flooding. *Climate Dynamics*, 35(6), 1055–1063. <https://doi.org/10.1007/s00382-009-0617-5>
- Carbognin, L., Teatini, P., & Tosi, L. (2004). Eustacy and land subsidence in the Venice Lagoon at the beginning of the new millennium. *Journal of Marine Systems*, 51(1-4 SPEC. ISS.), 345–353. <https://doi.org/10.1016/j.jmarsys.2004.05.021>
- Carvalho, J. C., Cardoso, P., Borges, P. A. V., Schmera, D., & Podani, J. (2013). Measuring fractions of beta diversity and their relationships to nestedness: A theoretical and empirical comparison of novel approaches. *Oikos*, 122(6), 825–834. <https://doi.org/10.1111/j.1600-0706.2012.20980.x>
- Cescon, A., & Jiang, J. Q. (2020). Filtration process and alternative filter media material in water treatment. *Water (Switzerland)*, 12(12). <https://doi.org/10.3390/w12123377>

- Chapman, M. G., & Blockley, D. J. (2009). Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. *Oecologia*, *161*(3), 625–635. <https://doi.org/10.1007/s00442-009-1393-y>
- Chapman, M. G., & Bulleri, F. (2003). Intertidal seawalls-new features of landscape in intertidal environments. In *Landscape and Urban Planning* (Vol. 62).
- Chapman, M. G., & Underwood, A. J. (2011). Evaluation of ecological engineering of “armoured” shorelines to improve their value as habitat. In *Journal of Experimental Marine Biology and Ecology* (Vol. 400, Issues 1–2, pp. 302–313). <https://doi.org/10.1016/j.jembe.2011.02.025>
- Clynick, B. J. (2008). Harbour swimming nets: A novel habitat for seahorses. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *18*(5), 483–492. <https://doi.org/10.1002/aqc.856>
- Collas, F. P. L., Koopman, K. R., van der Velde, G., & Leuven, R. S. E. W. (2020). Quantifying the loss of filtration services following mass mortality of invasive dreissenid mussels. *Ecological Engineering*, *149*, 105781. <https://doi.org/10.1016/j.ecoleng.2020.105781>
- Connell, S. D. (n.d.). *Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rocky reefs*. www.elsevier.com/locate/marenvrev
- 'COOPER, J. ', 'PILKEY, O. H. ', & 'ANDREW, G. '. (2012). *Pitfalls of Shoreline Stabilization*.
- Cranford, P. J., Ward, J. E., & Shumway, S. E. (2011). Bivalve Filter Feeding: Variability and Limits of the Aquaculture Biofilter. In *Shellfish Aquaculture and the Environment* (pp. 81–124). Wiley-Blackwell. <https://doi.org/10.1002/9780470960967.ch4>
- Cucco, A., Umgiesser, G., Ferrarin, C., Perilli, A., Canu, D. M., & Solidoro, C. (2009). Eulerian and lagrangian transport time scales of a tidal active coastal basin. *Ecological Modelling*, *220*(7), 913–922. <https://doi.org/10.1016/j.ecolmodel.2009.01.008>
- Dafforn, K. A., Glasby, T. M., Airoidi, L., Rivero, N. K., Mayer-Pinto, M., & Johnston, E. L. (2015). Marine urbanization: An ecological framework for designing multifunctional artificial structures. In *Frontiers in Ecology and the Environment* (Vol. 13, Issue 2, pp. 82–90). Ecological Society of America. <https://doi.org/10.1890/140050>
- Davis, M. W. (2002). Key principles for understanding fish bycatch discard mortality. In *Canadian Journal of Fisheries and Aquatic Sciences* (Vol. 59, Issue 11, pp. 1834–1843). <https://doi.org/10.1139/f02-139>

- De Alberti, D., Russo, R., Terruzzi, F., Nobile, V., & Ouwehand, A. C. (2015). Lactobacilli vaginal colonisation after oral consumption of Respecta® complex: a randomised controlled pilot study. *Archives of Gynecology and Obstetrics*, 292(4), 861–867. <https://doi.org/10.1007/s00404-015-3711-4>
- Dugan, J. E., Airoidi, L., Chapman, M. G., Walker, S. J., & Schlacher, T. (2011). Estuarine and Coastal Structures. In *Treatise on Estuarine and Coastal Science* (pp. 17–41). Elsevier. <https://doi.org/10.1016/B978-0-12-374711-2.00802-0>
- Ehrich, M. K., & Harris, L. A. (2015). A review of existing eastern oyster filtration rate models. In *Ecological Modelling* (Vol. 297, pp. 201–212). Elsevier. <https://doi.org/10.1016/j.ecolmodel.2014.11.023>
- Erixon Aalto, H., & Ernstson, H. (2017). Of plants, high lines and horses: Civic groups and designers in the relational articulation of values of urban natures. *Landscape and Urban Planning*, 157, 309–321. <https://doi.org/10.1016/j.landurbplan.2016.05.018>
- Filgueira, R., Stropole, L. C., Strohmeier, T., Rastrick, S., & Strand, Ø. (2019). Mussels or tunicates: That is the question. Evaluating efficient and sustainable resource use by low-trophic species in aquaculture settings. *Journal of Cleaner Production*, 231, 132–143. <https://doi.org/10.1016/j.jclepro.2019.05.173>
- Filippini, G., Bugnot, A. B., Ferguson, A., Gribben, P. E., Palmer, J., Erickson, K., & Dafforn, K. A. (2023). The influence of oyster reefs and surrounding sediments on nitrogen removal – An in-situ study along the East coast of Australia. *Environmental Research*, 237. <https://doi.org/10.1016/j.envres.2023.116947>
- Fodrie, F. J., Rodriguez, A. B., Gittman, R. K., Grabowski, J. H., Lindquist, N. L., Peterson, C. H., Piehler, M. F., & Ridge, J. T. (2017). Oyster reefs as carbon sources and sinks. *Proceedings of the Royal Society B: Biological Sciences*, 284(1859). <https://doi.org/10.1098/rspb.2017.0891>
- Fréchette, M., & Grant, J. (1991). An in situ estimation of the effect of wind-driven resuspension on the growth of the mussel *Mytilus edulis* L. *Journal of Experimental Marine Biology and Ecology*, 148(2), 201–213. [https://doi.org/10.1016/0022-0981\(91\)90082-8](https://doi.org/10.1016/0022-0981(91)90082-8)
- Gačić, M., & Solidoro, C. (2004). Lagoon of Venice: Circulation, water exchange and ecosystem functioning. In *Journal of Marine Systems* (Vol. 51, Issues 1-4 SPEC. ISS., pp. 1–3). <https://doi.org/10.1016/j.jmarsys.2004.06.001>
- Galimany, E., Ramón, M., & Ibarrola, I. (2011). Feeding behavior of the mussel *Mytilus galloprovincialis* (L.) in a Mediterranean estuary: A field study. *Aquaculture*, 314(1–4), 236–243. <https://doi.org/10.1016/j.aquaculture.2011.01.035>
- Godwin, M., Ruhland, L., Casson, I., Macdonald, S., Delva, D., Birtwhistle, R., Lam, M., & Seguin, R. (2003). *Pragmatic controlled clinical trials in primary care: the*

struggle between external and internal validity.
<http://www.biomedcentral.com/1471-2288/3/28>

González-Duarte, M. M., Megina, C., De Vito, D., Di Camillo, C. G., Puce, S., & Piraino, S. (2016). A unified assessment of marine Mediterranean assemblages: A lesson from benthic hydroids. *Marine Ecology*, 37(1), 155–163.
<https://doi.org/10.1111/maec.12271>

Gosling, E. (2015). How bivalves feed. In *Marine Bivalve Molluscs* (pp. 99–156). Wiley. <https://doi.org/10.1002/9781119045212.ch4>

Grasselli, F., & Airoidi, L. (2021a). How and to What Degree Does Physical Structure Differ Between Natural and Artificial Habitats? A Multi-Scale Assessment in Marine Intertidal Systems. *Frontiers in Marine Science*, 8.
<https://doi.org/10.3389/fmars.2021.766903>

Grasselli, F., & Airoidi, L. (2021b). How and to What Degree Does Physical Structure Differ Between Natural and Artificial Habitats? A Multi-Scale Assessment in Marine Intertidal Systems. *Frontiers in Marine Science*, 8.
<https://doi.org/10.3389/fmars.2021.766903>

Grasselli, F., & Airoidi, L. (2021c). How and to What Degree Does Physical Structure Differ Between Natural and Artificial Habitats? A Multi-Scale Assessment in Marine Intertidal Systems. *Frontiers in Marine Science*, 8.
<https://doi.org/10.3389/fmars.2021.766903>

Grasselli, F., Strain, E. M. A., & Airoidi, L. (2024). Material type and origin influences the abundances of key taxa on artificial structures. *Coastal Engineering*, 187, 104419. <https://doi.org/10.1016/j.coastaleng.2023.104419>

Guy-Haim, T., Lyons, D. A., Kotta, J., Ojaveer, H., Queirós, A. M., Chatzinikolaou, E., Arvanitidis, C., Como, S., Magni, P., Blight, A. J., Orav-Kotta, H., Somerfield, P. J., Crowe, T. P., & Rilov, G. (2018). Diverse effects of invasive ecosystem engineers on marine biodiversity and ecosystem functions: A global review and meta-analysis. In *Global Change Biology* (Vol. 24, Issue 3, pp. 906–924). Blackwell Publishing Ltd. <https://doi.org/10.1111/gcb.14007>

H. H., R., & A. Bij de, V. (1990). *Zebra mussels (Dreissena polymorpha): a new perspective for water quality management*. 200, 437–450.

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution*, 24(11), 599–605.
<https://doi.org/10.1016/j.tree.2009.05.012>

“J. P. Hickey.” (2004). *Carbon Sequestration Potential of Shellfish*.

Kellogg, M. L., Smyth, A. R., Luckenbach, M. W., Carmichael, R. H., Brown, B. L., Cornwell, J. C., Piehler, M. F., Owens, M. S., Dalrymple, D. J., & Higgins, C. B.

- (2014). Use of oysters to mitigate eutrophication in coastal waters. *Estuarine, Coastal and Shelf Science*, 151, 156–168.
<https://doi.org/10.1016/j.ecss.2014.09.025>
- Kreeger, D. A., Gatenby, C. M., & Bergstrom, P. W. (2018). Restoration Potential of Several Native Species of Bivalve Molluscs for Water Quality Improvement in Mid-Atlantic Watersheds. *Journal of Shellfish Research*, 37(5), 1121.
<https://doi.org/10.2983/035.037.0524>
- Lauzon, R., Murray, A. B., Cheng, S., Liu, J., Ells, K. D., & Lazarus, E. D. (2019). Correlation Between Shoreline Change and Planform Curvature on Wave-Dominated, Sandy Coasts. *Journal of Geophysical Research: Earth Surface*, 124(12), 3090–3106. <https://doi.org/10.1029/2019JF005043>
- Levinton, J., Arena, B., Pena, R., & Darnell, M. Z. (2023). Superior performance of a trailing edge low-latitude population of an intertidal marine invertebrate. *Journal of Experimental Marine Biology and Ecology*, 563.
<https://doi.org/10.1016/j.jembe.2023.151896>
- Liang, H., He, Y. D., Theodorou, P., & Yang, C. F. (2023a). The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecology Letters*, 26(9), 1629–1642.
<https://doi.org/10.1111/ele.14277>
- Liang, H., He, Y., Theodorou, P., & Yang, C. (2023b). The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecology Letters*, 26(9), 1629–1642.
<https://doi.org/10.1111/ele.14277>
- Lionello, P. (2012). The climate of the Venetian and North Adriatic region: Variability, trends and future change. *Physics and Chemistry of the Earth*, 40–41, 1–8.
<https://doi.org/10.1016/j.pce.2012.02.002>
- Lotze, H. K., Lenihan, H. S., Bourque, B. J., Bradbury, R. H., Cooke, R. G., Kay, M. C., Kidwell, S. M., Kirby, M. X., Peterson, C. H., & Jackson, J. B. C. (2006). Depletion degradation, and recovery potential of estuaries and coastal seas. *Science*, 312(5781), 1806–1809.
<https://doi.org/10.1126/science.1128035>
- Madricardo, F., Foglini, F., Campiani, E., Grande, V., Catenacci, E., Petrizzo, A., Kruss, A., Toso, C., & Trincardi, F. (2019). Assessing the human footprint on the sea-floor of coastal systems: the case of the Venice Lagoon, Italy. *Scientific Reports*, 9(1).
<https://doi.org/10.1038/s41598-019-43027-7>
- Magni, P., Tagliapietra, D., Lardicci, C., Balthis, L., Castelli, A., Como, S., Frangipane, G., Giordani, G., Hyland, J., Maltagliati, F., Pessa, G., Rismondo, A., Tataranni, M., Tomassetti, P., & Viaroli, P. (2009). Animal-sediment relationships: Evaluating the “Pearson-Rosenberg paradigm” in Mediterranean coastal lagoons. *Marine Pollution Bulletin*, 58(4), 478–486.
<https://doi.org/10.1016/j.marpolbul.2008.12.009>

- Mai, H., Cachot, J., Brune, J., Geffard, O., Belles, A., Budzinski, H., & Morin, B. (2012). Embryotoxic and genotoxic effects of heavy metals and pesticides on early life stages of Pacific oyster (*Crassostrea gigas*). *Marine Pollution Bulletin*, *64*(12), 2663–2670. <https://doi.org/10.1016/j.marpolbul.2012.10.009>
- Martínez, M. L., Intralawan, A., Vázquez, G., Pérez-Maqueo, O., Sutton, P., & Landgrave, R. (2007). The coasts of our world: Ecological, economic and social importance. *Ecological Economics*, *63*(2–3), 254–272. <https://doi.org/10.1016/j.ecolecon.2006.10.022>
- Mayer-Pinto, M., Cole, V. J., Johnston, E. L., Bugnot, A., Hurst, H., Airoidi, L., Glasby, T. M., & Dafforn, K. A. (2018). Functional and structural responses to marine urbanisation. *Environmental Research Letters*, *13*(1). <https://doi.org/10.1088/1748-9326/aa98a5>
- Mayer-Pinto, M., Johnston, E. L., Bugnot, A. B., Glasby, T. M., Airoidi, L., Mitchell, A., & Dafforn, K. A. (2017a). Building 'blue': An eco-engineering framework for foreshore developments. *Journal of Environmental Management*, *189*, 109–114. <https://doi.org/10.1016/j.jenvman.2016.12.039>
- Mayer-Pinto, M., Johnston, E. L., Bugnot, A. B., Glasby, T. M., Airoidi, L., Mitchell, A., & Dafforn, K. A. (2017b). Building 'blue': An eco-engineering framework for foreshore developments. *Journal of Environmental Management*, *189*, 109–114. <https://doi.org/10.1016/j.jenvman.2016.12.039>
- McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. In *Trends in Ecology and Evolution* (Vol. 14, Issue 11, pp. 450–453). Elsevier Ltd. [https://doi.org/10.1016/S0169-5347\(99\)01679-1](https://doi.org/10.1016/S0169-5347(99)01679-1)
- 'Mineur, F. (2012). *Changing Coasts: Marine Aliens and Artificial Structures*. 50.
- Molinaroli, E., Guerzoni, S., Sarretta, A., Masiol, M., & Pistolato, M. (2009). Thirty-year changes (1970 to 2000) in bathymetry and sediment texture recorded in the Lagoon of Venice sub-basins, Italy. *Marine Geology*, *258*(1–4), 115–125. <https://doi.org/10.1016/j.margeo.2008.12.001>
- Momota, K., & Hosokawa, S. (2021). Potential impacts of marine urbanization on benthic macrofaunal diversity. *Scientific Reports*, *11*(1). <https://doi.org/10.1038/s41598-021-83597-z>
- Neumann, B., Vafeidis, A. T., Zimmermann, J., & Nicholls, R. J. (2015). Future Coastal Population Growth and Exposure to Sea-Level Rise and Coastal Flooding - A Global Assessment. *PLOS ONE*, *10*(3), e0118571. <https://doi.org/10.1371/journal.pone.0118571>
- Newton, R. J., Jones, S. E., Eiler, A., McMahon, K. D., & Bertilsson, S. (2011). A Guide to the Natural History of Freshwater Lake Bacteria. *Microbiology and Molecular Biology Reviews*, *75*(1), 14–49. <https://doi.org/10.1128/mnbr.00028-10>
- Palmerini, P., & Bianchi, C. N. (1994). Biomass measurements and weight-to-weight conversion factors: a comparison of methods applied to the mussel *Mytilus galloprovincialis*. *Marine Biology*, *120*(2), 273–277. <https://doi.org/10.1007/BF00349688>

- Piano, E., Souffreau, C., Merckx, T., Baardsen, L. F., Backeljau, T., Bonte, D., Brans, K. I., Cours, M., Dahirel, M., & Debortoli, N. (n.d.). Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Global Change Biology*, 2020(3). <https://doi.org/10.1111/gcb.14934>
- Ravera, O. (2000). The Lagoon of Venice : the result of both natural factors and human influence. In *J. Limnol* (Vol. 59, Issue 1).
- Richard, M., Bec, B., Bergeon, L., Hébert, M., Mablouké, C., & Lagarde, F. (2022a). Are mussels and oysters capable of reducing the abundances of *Picochlorum* sp., responsible for a massive green algae bloom in Thau lagoon, France? *Journal of Experimental Marine Biology and Ecology*, 556. <https://doi.org/10.1016/j.jembe.2022.151797>
- Richard, M., Bec, B., Bergeon, L., Hébert, M., Mablouké, C., & Lagarde, F. (2022b). Are mussels and oysters capable of reducing the abundances of *Picochlorum* sp., responsible for a massive green algae bloom in Thau lagoon, France? *Journal of Experimental Marine Biology and Ecology*, 556. <https://doi.org/10.1016/j.jembe.2022.151797>
- Riisgård, H. U., Funch, P., & Larsen, P. S. (2015). The mussel filter-pump - present understanding, with a re-examination of gill preparations. *Acta Zoologica*, 96(3), 273–282. <https://doi.org/10.1111/azo.12110>
- Rossi, S., & Snyder, M. J. (2001). Competition for Space Among Sessile Marine Invertebrates: Changes in HSP70 Expression in Two Pacific Cnidarians. *The Biological Bulletin*, 201(3), 385–393. <https://doi.org/10.2307/1543616>
- Saari, U., Baumgartner, R., & Mäkinen, S. (2017). Eco-Friendly Brands to Drive Sustainable Development: Replication and Extension of the Brand Experience Scale in a Cross-National Context. *Sustainability*, 9(7), 1286. <https://doi.org/10.3390/su9071286>
- Šobotník, J., & Dahlsjö, C. A. L. (2017). Isoptera ☆. In *Reference Module in Life Sciences*. Elsevier. <https://doi.org/10.1016/b978-0-12-809633-8.02256-1>
- Soetaert, K., & Middelburg, J. J. (2009). Modeling eutrophication and oligotrophication of shallow-water marine systems: the importance of sediments under stratified and well-mixed conditions. In *Eutrophication in Coastal Ecosystems* (pp. 239–254). Springer Netherlands. https://doi.org/10.1007/978-90-481-3385-7_20
- Solidoro, C., Bandelj, V., Bernardi, F., Camatti, E., Ciavatta, S., Cossarini, G., Facca, C., Franzoi, P., Libralato, S., Canu, D., Pastres, R., Pranovi, F., Raicevich, S., Socal, G., Sfriso, A., Sigovini, M., Tagliapietra, D., & Torricelli, P. (2010). *Response of the Venice Lagoon Ecosystem to Natural and Anthropogenic Pressures over the Last 50 Years* (pp. 483–511). <https://doi.org/10.1201/ebk1420088304-c19>
- Tamburini, E., Turolla, E., Lanzoni, M., Moore, D., & Castaldelli, G. (2022). Manila clam and Mediterranean mussel aquaculture is sustainable and a net carbon sink. *Science of The Total Environment*, 848, 157508. <https://doi.org/10.1016/j.scitotenv.2022.157508>

- Tamburini, G., Bommarco, R., Wanger, T. C., Kremen, C., van der Heijden, M. G. A., Liebman, M., & Hallin, S. (2020). Agricultural diversification promotes multiple ecosystem services without compromising yield. *Science Advances*, 6(45).
<https://doi.org/10.1126/SCIADV.ABA1715>
- Thomsen, F., Lüdemann, K., Kafemann, R., & Piper, W. (2006). *Effects of offshore wind farm noise on marine mammals and fish*. www.offshorewind.co.uk
- Tsuchiya, M. (1980). Biodeposit production by the mussel *Mytilus edulis* L. on rocky shores. *Journal of Experimental Marine Biology and Ecology*, 47(3), 203–222.
[https://doi.org/10.1016/0022-0981\(80\)90039-8](https://doi.org/10.1016/0022-0981(80)90039-8)
- Umgiesser, G., Canu, D. M., Cucco, A., & Solidoro, C. (2004a). A finite element model for the Venice Lagoon. Development, set up, calibration and validation. *Journal of Marine Systems*, 51(1-4 SPEC. ISS.), 123–145. <https://doi.org/10.1016/j.jmarsys.2004.05.009>
- Umgiesser, G., Canu, D. M., Cucco, A., & Solidoro, C. (2004b). A finite element model for the Venice Lagoon. Development, set up, calibration and validation. *Journal of Marine Systems*, 51(1-4 SPEC. ISS.), 123–145. <https://doi.org/10.1016/j.jmarsys.2004.05.009>
- Underwood, A. J., Chapman, M. G., & Crowe, T. P. (2004). Identifying and understanding ecological preferences for habitat or prey. *Journal of Experimental Marine Biology and Ecology*, 300(1–2), 161–187. <https://doi.org/10.1016/j.jembe.2003.12.006>
- Zanchettin, D., Bruni, S., Raicich, F., Lionello, P., Adloff, F., Androsov, A., Antonioli, F., Artale, V., Carminati, E., Ferrarin, C., Fofonova, V., Nicholls, R. J., Rubinetti, S., Rubino, A., Sannino, G., Spada, G., Thiéblemont, R., Tsimplis, M., Umgiesser, G., ... Zerbini, S. (2021). Sea-level rise in Venice: Historic and future trends (review article). In *Natural Hazards and Earth System Sciences* (Vol. 21, Issue 8, pp. 2643–2678). Copernicus GmbH.
<https://doi.org/10.5194/nhess-21-2643-2021>