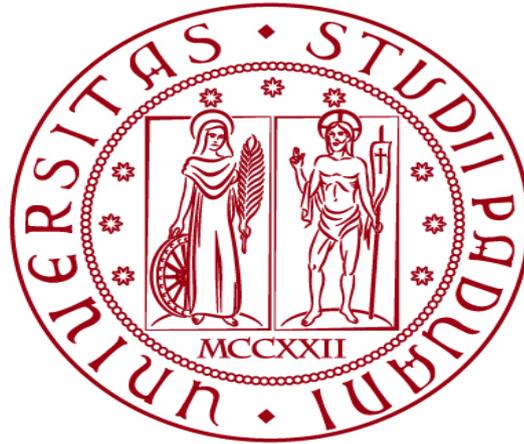**UNIVERSITÀ DEGLI STUDI DI PADOVA**

DIPARTIMENTO DI BIOLOGIA

Corso di Laurea magistrale in Marine Biology

TESI DI LAUREA

Drivers of Species Richness and Community Composition in Marine Artificial

Habitats Isolated from Natural Rocky Shores

Relatore: Prof.ssa Laura Airoldi
Dipartimento di Biologia
Correlatore: Dott. Robin Gauff
Dipartimento di Biologia

Laureando: Hassan Almetwaly

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Abstract

The Theory of Island Biogeography (TIB) explains species diversity on islands as a balance between immigration and extinction rates, influenced by island size and distance from the mainland. Larger and closer islands support higher biodiversity due to increased colonization and lower extinction rates. Artificial hard structures, such as seawalls, piers, and offshore wind farms, are constructed for various human purposes in marine areas that typically consist of soft sediment habitats, altering local ecosystems by providing new habitats for marine organisms, often including Non-Indigenous Species (NIS). Due to their isolated positioning, they also function as artificial islands; however, TIB has never been applied to explain the dynamics of colonization in these systems. This thesis does a TIB extension to marine urban structures (MUS), specifically artificial hard substrates along the Italian coastline. This research treats this kind of infrastructure as island-like and investigates the relationship between species richness, structure size, and isolation from natural rocky shores. The present study integrated sampling across seven biogeographical zones and showed a strong negative correlation of species richness with distance from natural rocky shores, thus indicating that isolation is a primary driver of biodiversity variation on MUS. While higher species diversity was hosted by larger structures, the size effect was modulated by proximity, as structures close to natural rocky shores are subjected to increased connectivity with natural habitats. Isolated structures had unique community compositions when compared to those in proximity to natural rocky shores. This study also determined a higher proportion of NIS on more isolated and larger structures, suggesting that these kinds of environments facilitate the establishment and spread of NIS due to reduced biotic resistance. Therefore, geographical and biological elements must be considered in the design and management of marine urban structures for the future. This thesis puts TIB into current ecological knowledge to increase the understanding of marine urban environments and to propose practical suggestions for increasing the ecological value of such structures. The implications of this study provide critical insights into the biodiversity patterns and ecological functioning of marine urban structures within marine environments.

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1. Introduction

1.1 Urban Expansion into Marine Environments

Urban sprawl is expanding, reaching into the marine environments through the construction of artificial structures along and adjacent to the cost. In Europe, the US, Australia, and Asia, over 50% of shorelines are now modified by hard engineering, including groins and breakwaters, which are man-made coastal defences positioned along the shore or offshore to protect against erosion and wave action in support of human activities (Dafforn et al., 2015). In Spain, France, and Italy, up to 50% of the shorelines are developed for harbours and ports (Airoldi et al., 2008). The expansion of marine infrastructure is expected to continue, and likely escalate, driven by the need for improved defences around ports, harbours, and coastal cities as protection from rising sea levels and increasingly severe coastal storms and flooding (Asif & Muneer, 2007).

Marine construction is one of the most significant human modifications to global seascapes. As of 2018, the physical footprint of built structures covered at least 32,000 km² worldwide, with projections to reach 39,400 km² by 2028. The area of seascape modified around these structures was between 1.0 and 3.4 million km² in 2018, with an expected increase of 50–70% by 2028 for power and aquaculture infrastructure, cables, and tunnels. In 2018, marine construction impacted 1.5% (0.7–2.4%) of global Exclusive Economic Zones, comparable to the global extent of urban land, estimated at 0.02–1.7% (Bugnot et al., 2020).

In many natural coastal areas, the expansion of artificial surfaces is outpacing population growth (European Environment Agency, 2006). For instance, most of the Mediterranean population is concentrated in coastal regions (McGranahan et al., 2007), and coastal areas are projected to experience a major increase in urban extent between 2000 and 2030 (Seto et al., 2011). Italy's coastal landscapes, spanning almost 8300 km, are rich in biodiversity and cultural heritage, yet they are increasingly subjected to land consumption. Artificial surfaces in coastal areas primarily result from industrial defence, and harbour constructions, as well as tourism development. Each year, over 10 km of natural and agricultural land are

hardened (source: **https://sinacloud.isprambiente.it/portal/apps/sites/#/coste**). Coastal municipalities in Italy are 645, covering a total area of about 43,000 km22, equivalent to 14% of the entire national territory with a population of about 17,200,000 inhabitants. The Italian Institute of Statistics (ISTAT) reveals that 30% of the Italian population lives in 646 coastal municipalities. This increasing anthropic pressure has caused a change of 90% of the coastal environment, leaving intact less than 10% of the original habitats (Pasquali & Marucci, 2021).

Sedimentary coastal areas, with their moderate slopes and favourable conditions for infrastructure development, have seen particularly rapid urbanization. These regions, attractive for their pleasant weather, especially during summer, have seen increased anthropic pressure, which has been a key factor in Mediterranean transport and maritime trade (Romano et al., 2016). This development of urban infrastructures to support commercial, residential, and tourist activities along coastal environments have effects on these coasts through exposing their natural habitats, associated species and ecological processes to multiple and profound changes (Firth et al., 2020; Glasby et al., 2017). Any new hard substrata introduced to the marine environment will inevitably be colonised by fouling and epibenthic marine organisms. This gives rise to potential secondary functions of artificial structures as habitat-providers in the marine environment. It has been well-documented that intertidal coastal defences typically support organisms normally found on nearby rocky shores (Airoldi et al., 2009; Chapman, 2003; Chapman & Bulleri, 2003; Connell, 2001; Firth et al., 2015; Moschella et al., 2005; Pinn et al., 2005) but that the colonising assemblages are often not completely analogous (Wang et al., 2023). Understanding the composition of biological assemblages on artificial structures is crucial for assessing their ecological role, potential for habitat enhancement, and risks of facilitating non-indigenous species spread (Bulleri & Airoldi, 2005; Strain et al., 2018). Current knowledge suggests that divergence of benthic assemblages is not simply attributable to incomplete succession but appears to be a persistent state (Miller et al., 2009; Perkol-Finkel et al., 2006). Several factors have been suggested to contribute to maintaining these differences, including effects of construction materials (REF), unique habitat characteristics (Browne & Chapman, 2011; Vaselli et al., 2008), unnaturally high anthropogenic disturbances (Airoldi & Bulleri, 2011), fragmentation and isolation (Airoldi et al.,

2015). Understanding what influences the structure of assemblages associated to artificial structure is fundamental to design artificial structures that support vital native biodiversity and ecosystem functions.

1.2   Theory of Island Biogeography

MacArthur and Wilson, in the mid-1960's, introduced an innovative concept in biogeography, proposing that the species composition of an island reflects a balance between the immigration of new species to the island and extinction of existing ones. This concept, known as the Equilibrium Theory of Island Biogeography, suggests that the biota of an island stabilizes at an equilibrium point where the rates of immigration and extinction come to a balance. The influences of island size and isolation made the central of their theory, where larger islands tend to have lower extinction rates and harbour more species, whereas more isolated islands experience reduced immigration rates, with fewer species at equilibrium (MacArthur & Wilson, 1963; Macarthur & Wilson, 1967).
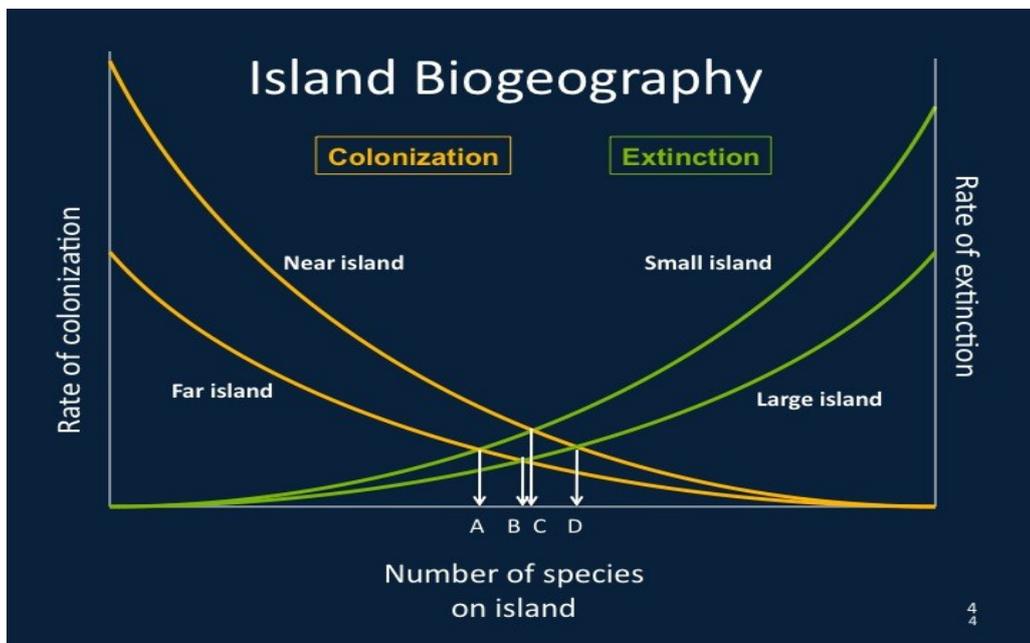

Figure 1 MacArthur and Wilson's equilibrium theory of island biogeography model showing how the number of species on an island is the result of the rates of colonization/immigration and extinction at equilibrium (http://californiachannelislands.blogspot.com/2012/04/macarthur-and-wilson-ii-archipelagos.html) (D. Simberloff & Abele, 1982)

MacArthur and Wilson's model ([Figure 1](#)) demonstrates how the equilibrium of species on an island is governed by the opposing forces of colonization and extinction. While the total number of species remains relatively constant, their composition frequently shifts due to ongoing species turnover. Extinction rates and colonization rates are considered to be comparable, resulting in a dynamic balance. Some of the extinction forces are the result of competition, specifically with newly arrived species from the mainland that are often competitively superior to endemic island species. Consequently, island communities are attributed to the assemblages of species that arrived successively at different times and have not co-evolved to a significant degree (Heaney et al., 2013). Larger islands, by providing a greater diversity of habitats, have a higher carrying capacity and can support more species. Additionally, larger islands are larger targets of natural dispersal and generally can sustain larger populations (Ricklefs & Lovette, 1999), with both contributing to higher species richness. The increase in species richness of an island with its area is attributed to reduced extinction rates, higher niche availability, and a higher chances of colonization (Macarthur & Wilson, 1967). Moreover, niche differentiation and speciation events on larger islands enable a continuous rise in species richness with increasing area, without a theoretical limit (Cornell, 2013).

The impact of the Island Biogeography model on ecology has been substantial, providing context for thousands of studies of islands and island-like habitats. It has also provided the framework for much of the research conducted over several decades on conservation strategy and planning (see Lomolino et al., 2010; Losos et al., 2010 as cited in Heaney et al., 2013).

In the early 2000s, the relevance of the Theory of Island Biogeography to marine systems began to be reconsidered (Lomolino, 2004). While the Equilibrium Theory of Island Biogeography has been influential, it has also faced criticism, with repeated calls for the development of new models and theories (Brown & Lomolino, 2000; Heaney, 2007). Among the critiques is how the theory simplifies complex ecological features and powers, through focusing primarily on species numbers instead of considering the quality of interactions among these species (Simberloff, 1974). Moreover, the theory assumes that the rates of immigration and extinction are constant, which may not be the case in dynamic environments. In response to

these critiques, better comprehensive models have been developed and incorporate additional factors, such as trait of species, quality of habitat, and impacts of humans. One such model is The General Dynamic Model (GDM) of oceanic island biogeography (Triantis & Bhagwat, 2011; Whittaker et al., 2008). The GDM integrates MacArthur and Wilson's equilibrium model within the geological and evolutionary context of oceanic archipelagos, acknowledging the dynamic nature of islands over geological times (Stein et al., 2014).

The GDM put into the front the concept of "island ontogeny," referring to the changes an island undergoes throughout its life cycle and affecting its area, elevation, and habitat diversity. Unlike other static models, the GDM accounts for these temporal changes by incorporating phases of an island formation, growth, and foreseen decline due to natural subsidence and erosion (Whittaker et al., 2008). GDM had been validated by several oceanic archipelagos empirical studies, studying its broad applicability and effectiveness in explaining biodiversity dynamics (Carlton, 2006; Heaney, 2000; Steinbauer et al., 2016).

Among the core aspects of the GDM is the consideration of species diversification and extinction rates in relation to the geological age of the island (Borregaard et al., 2016). It states that islands have different biodiversity phases, an initial colonization phase, a period of peak biodiversity followed by a decline as the island ages and its habitats deteriorate. This dynamic approach contrasts in application with other static models that do not account for changes over time and age of an island. For example, research done on the Hawaiian island has shown that "species richness peaks at intermediate island ages and declines on older islands" (Lim & Marshall, 2017). Similarly, studies on the Canary Islands indicated that "species diversification rates are highest on younger, volcanically active islands and decrease as islands age and erode" (Caujapé-Castells et al., 2010).

The GDM also addresses the impact of human activities, such as habitat destruction and species introductions, which can disrupt natural biodiversity trajectories and accelerate species extinctions (Whittaker & Fernández-Palacios, 2007). These anthropogenic factors can accelerate species extinctions and disrupt ecological balances, leading to novel biodiversity dynamics not accounted for in earlier models. Furthermore, the General Dynamic Model GDM has been expanded to

include "the role of spatial heterogeneity and habitat complexity in promoting species coexistence and diversification" (Cabral et al., 2017). This refinement recognizes that the diversity of habitats within an island can create niches that support a wider range of species, thereby enhancing overall biodiversity.

Spatial heterogeneity and habitat complexity are critical factors that "mediate the processes of species colonization, extinction, and adaptation" (Stein et al., 2014). These factors contribute to the formation of a mosaic of microhabitats, each with unique conditions and resources (Tews et al., 2004), which in turn "facilitate niche differentiation and reduce competitive exclusion among species" (Macarthur & Wilson, 1967). Increased habitat complexity "enhances the availability of refuges and breeding sites" (Sánchez-Bayo & Wyckhuys, 2019), which is essential for the survival and reproduction of various species. This complexity "also promotes higher trophic interactions and food web stability" (Haddad et al., 2015), thereby supporting a more resilient and dynamic ecosystem. The presence of diverse microhabitats "leads to increased functional diversity and ecosystem multifunctionality" (Hector & Bagchi, 2007), which are crucial for maintaining ecosystem processes and services.

In island ecosystems, both the spatial heterogeneity and the habitat complexity drive evolutionary processes by creating opportunities for speciation and adaptation (Losos & Ricklefs, 2009). This leads to the emergence of endemic species that are specifically adapted to the unique island environments (Whittaker et al., 2017). Therefore, understanding and preserving spatial heterogeneity and habitat complexity within islands is crucial for maintaining their biodiversity and ecological integrity.

1.3   Island Biogeography Role in Conservation

Theory of Island Biogeography was one of a series of advances that catalysed the emergence of conservation biology as a distinct scientific discipline. It provides a conceptual framework for the dynamics of species diversity in fragmented habitats, pointing out the interaction between island size, distance from the mainland, and

immigration-extinction dynamics. Applied to fragmented terrestrial landscapes, it predicts that small, isolated habitat patches support fewer species due to increased extinction rates and reduced colonization potential. These principles have been fundamental in the design of reserve networks which maximise species persistence in relation, for example, to factors like reserve size and connectivity (Macarthur & Wilson, 1967; Whittaker & Fernández-Palacios, 2007).

Critics, however, note that naive applications of island biogeography fail to consider complex interactions within habitat fragments such as edge effects, interactions among species, and matrix quality (Lomolino et al., 2010). It is thus essential that these complexities be accounted for in formulating conservation strategies if it is going to be effective. Notwithstanding this critique, the theory of island biogeography remains essential in shaping policies and management practices undertaken to mitigate biodiversity loss in steadily fragmented ecosystems across the world (Whittaker & Fernández-Palacios, 2007). In this light, the "Single Large or Several Small" debate may constitute one important aspect of the nature reserve creation that may be informed. However, in as much as having one large reserve may support more species due to its size, several smaller reserves connected through corridors may also provide effective results in the conservation of biodiversity by enabling the movement of species and thereby exchanges in genes (Diamond, 1975; Simberloff, 1988).

Studies have shown that larger and well-connected MPAs support higher biodiversity and more stable ecosystems. For example, it was demonstrated that MPAs designed with larger areas and connectivity corridors in the Channel Islands significantly increased species diversity and abundance (Carr et al., 2003). Connectivity mitigates the effects of habitat fragmentation and isolation by allowing gene flow and species dispersal between marine habitats (Roberts et al., 2003). These are principles that, once applied, heighten the effectiveness of the restoration projects by marine conservationists to make the marine ecosystems lasting and sustainable in the right manner (Halpern et al., 2010).

Conservation biogeography, defined here as the 'application of biogeographical principles, theories, and analyses to the conservation of biodiversity', becomes thus imperative for tackling such challenges (Whittaker et al., 2005). It consequently

marries ecological and evolutionary principles in informing conservation strategies so that these are suitably couched within the broad comprehension of species richness and habitat dynamism.

1.4 Biogeographical Islands and Island-like Marine Environments

Rosenzweig (1995) posed a question " What exactly constitutes a biogeographical island? " and defined an island as "a self-contained region whose species originate entirely by immigration from outside the region" (Rosenzweig, 1995). An island is indeed an appealing object of study because it is simpler to analyse than a continent or an ocean. It is a distinct, identifiable land with well-defined boundaries, making it easier to note its unique resident species. Moreover, islands, being more numerous than continents or oceans, provide wide range opportunities of studies and research due to their diversity in characteristics; shape, size, degree of isolation, and ecological features (Macarthur & Wilson, 1967).

Islands are unique landscapes where both terrestrial and marine organisms coexist, often separated by just few meters. However, marine species are unlike terrestrial ones, since they have historically received less attention in studies and applications island theory (Dawson, 2016). Biodiversity, defined as the variety of life forms at different levels of biological organization—within species, between species, and across ecosystems—is particularly significant on islands. These island environments are often hosting endemic species and contributing disproportionately to global biodiversity. Due to their isolation, islands act as evolutionary hotspots, characterized by limited gene flow and unique biogeographical connections to continental sources (Whittaker & Fernández-Palacios, 2007). Additionally, due to their isolation, their resident species foster unique ecological dynamics and adaptive strategies. This isolation that is coupled with reduced gene flow from mainland populations, allows for divergent evolutionary paths and rapid diversification (Losos & Ricklefs, 2009).

For habitats to qualify as island-like marine environments, they must meet both a geographical and a biological definition (Dawson, 2016). Geographically,

possessing littoral zones and terrestrial parts. These habitats are classified into two categories: those surrounded by land and those surrounded by sea. Biologically, it is less clear which of these geographic marine islands also function as biogeographic marine islands, where species have special patterns such as endemism, island syndromes, and species–area relationships (McClain et al., 2009).

Remarkably, the pioneering work of MacArthur and Wilson (1963, 1967) laid the foundation for subsequent theoretical developments in island biology. Specifically, this work has inspired conservation biologists to look through the window of similarity between island ecosystems and anthropogenically fragmented habitats (Harris, 1984; Simberloff & Abele, 1982). All insular systems (true islands and island like systems (ILS)) share several characteristics: they are spatially fragmented, the area of each unit is limited, system units are spatially and temporally isolated from each other, and connectivity between units is relatively low. ILS may be of terrestrial, freshwater, marine, or biotic form, while true islands are by definition terrestrial (Itescu, 2019). Substantial physical differences characterize each form and, therefore, each imposes unique constraints on its biota (Dawson, 2016).

The literature has proposed and discussed dozens of island-like systems (ILS), which can be grouped into 12 categories based on common geographic characteristics or biological kingdom (in the case of biotic ILS). These include Animal-generated ILS, Edaphic ILS, Floating ILS, Freshwater ILS, Human-generated ILS, ILS on water body floors, Living animals as ILS, Natural habitat patches as ILS, Saline water ILS, Subterranean ILS, and Topographic ILS (Itescu, 2019). There is also evidence suggesting that hard habitat features in the deep sea, separated from other habitats by sediment, can be considered island-like (Meyer, 2017).

1.5   Study Aim

The objective of this thesis is to evaluate the applicability of the Theory of Island Biogeography to marine artificial hard substrate structures. Precisely, it aims to

establish whether such urban structures could be considered island-like environments and further if the principles of the TIB, traditionally applied to natural terrestrial and marine islands, can be extended to these artificial habitats.

Specifically, it will investigate if species richness on artificial structures follows the species-area relationship, where larger structures harbour greater species diversity, and the species-distance relationship, where there is a negative correlation between species richness and the degree of isolation (distance from natural rocky shores). Additionally, this study will examine the dynamics of non-indigenous species on these structures, exploring how they may influence or be influenced by the characteristics of these artificial environments.

1.6 Hypothesis:

Marine urban structures exhibit patterns of species richness consistent with the Theory of Island Biogeography, such that larger structures support greater species diversity, and species richness decreases with increasing isolation from natural rocky shores.

We predict that species richness will decrease with increasing distance of marine urban structures from natural rocky shores. This is expected due to reduced opportunities for species colonization in isolated environments. Additionally, we anticipate that species composition will become more distinct with isolation, as greater distances between structures limit dispersal and expose communities to more varied local environmental conditions. Furthermore, we predict that smaller marine urban structures will exhibit lower species richness compared to larger structures, consistent with the species-area relationship, due to smaller habitats supporting fewer niches and resources for species. We also hypothesize that the proportion of introduced species will increase with the isolation and size of marine urban structures, as reduced biotic resistance, increased habitat complexity and means of introduction may facilitate the establishment and spread of non-indigenous species.

Understanding whether marine urban structures can be considered island-like environments has significant implications for marine conservation and urban planning. If the TIB principles apply, it suggests that the design and placement of these structures can be optimized to enhance biodiversity. This knowledge could inform the creation of more ecologically valuable urban marine habitats, potentially aiding in biodiversity conservation and the resilience of marine ecosystems in the face of urbanization and climate change. Moreover, applying TIB to these structures will help explain the underlying biodiversity patterns and drivers on marine urban structures, providing insights into the factors that shape species composition and richness in these artificial environments. Furthermore, this study will fill a gap in the literature by extending island biogeography concepts to another human-made environment.

2. Materials and methods

2.1. Sampling Sites and Experimental Design

To test our hypotheses we sampled a variety of marine artificial structures along the Italian coastline, The coastal and marine areas of Italy are comprised of distinct biogeographical zones, each hosting unique ecological communities (Bianchi, 2004). To comprehensively represent these varied communities and avoid biases introduced by biogeographical differences, a systematic sampling strategy was employed, ensuring the inclusion of sites from seven biogeographical zones along the Italian coast (Ligurian Sea, Northern Tyrrhenian, Southern Tyrrhenian, Leonian, Southern Adriatic, Mid Adriatic and Northern Adriatic).

In each BGZ we sampled Natural Rocky Shores (NRS), artificial structures in immediate proximity to those and artificial structures at different distances from NRS. Sixteen sampling sites of artificial hard substrates were distributed across the seven BGZ, along with eight natural rocky shores (NRS Z1, NRS Z2, NRS Z3 (1), NRS Z3 (2), NRS Z4, NRS Z5, NRS Z6, NRS Z7) serving as references for later analysis (Figure 2). Coordinates, latitude and longitude, were captured at each sampling location using GPS-enabled map applications on mobile phones during the fieldwork to establish geospatial data points essential for subsequent spatial analysis and mapping. Each Biogeographical Zone (BGZ) had: 1) one NRS, except for BGZ 3, which had two. These NRS were whenever possible shallow subtidal (2 – 3 m depth) boulder fields, providing complex habitats with varied microhabitats. The boulder fields were selected as natural reference sites due to their structural similarity to the most consistent artificial habitats along the Italian coast, breakwaters, as most structural descriptors were found to be similar between artificial and natural habitats (Grasselli & Airoldi, 2021). This was made to minimize structural differences between natural and artificial habitats for a more accurate comparison. 2) an artificial structure in immediate proximity to the natural rocky shore (< 20 km), often shallow subtidal breakwaters situated on sandy substrates. 3) if available one to three artificial structures as described above with higher isolation (mid-range 20 - 60 km or far > 60 km). These structures were often

offshore breakwaters or rock harbour jetties. We aimed to have the exposition to waves and aspect in relation to the cardinal points similar within the same BGZ.
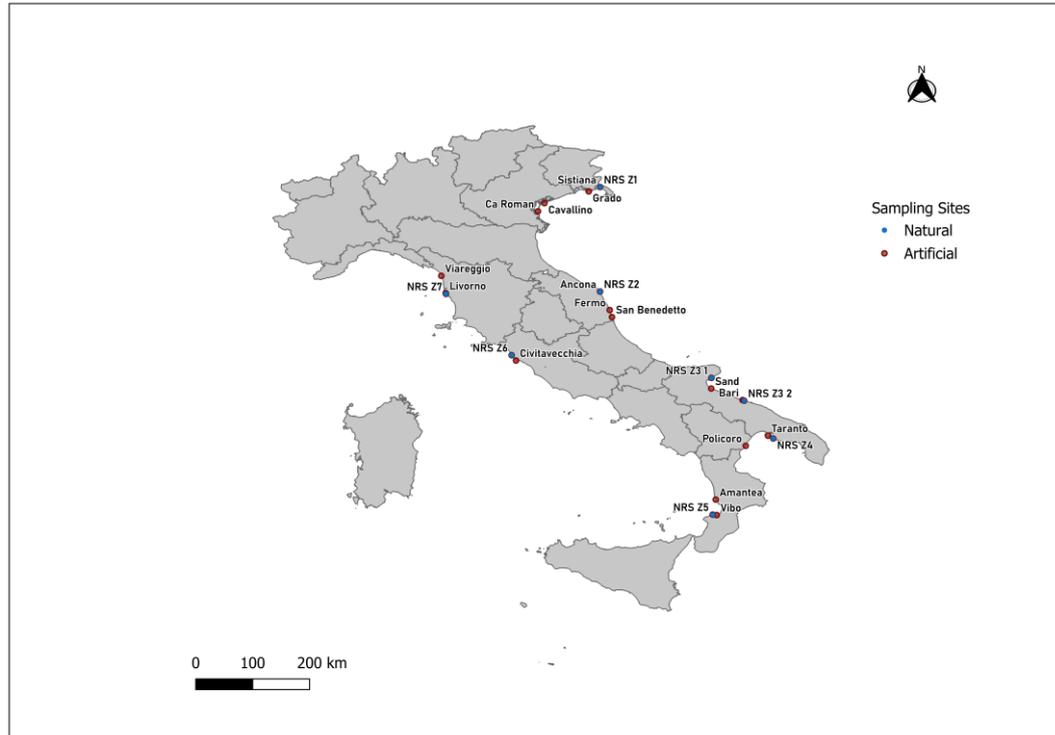
Figure 2 *Map of Italy showing sixteen sampling sites of artificial hard substrates (Sistiana, Grado, Ca Roman, Cavallino, Ancona, Fermo, San Benedetto, Sand, Bari, Taranto, Policoro, Vibo, Amantea, Civitavecchia, Livorno and Viareggio) and eight natural rocky shores (NRS Z1, NRS Z2, NRS Z3 (1), NRS Z3 (2), NRS Z4, NRS Z5, NRS Z6, NRS Z7) distributed across seven biogeographical zones along the Italian coastline.*

2.2. Determination of Island Characteristics of the Structures

For each artificial structure we determined the degree of isolation and the size using Google Earth Pro (Version 7.3.6.9796; Google LLC, 2024). The degree of isolation for each marine urban structure was quantified by measuring the straight-line distance between the structure and the nearest natural rocky shore (NRS), being identified by looking for areas along the coast that had visible rocky features and were not altered by human activities. Using the measurement tool available in Google Earth Pro we drew a straight line from the edge of the structure directly to the nearest point on the NRS. For the second independent variable, the size of the artificial structure sampled, were assessed using the polygon tool in Google Earth Pro, the perimeter of each structure was outlined, and the software calculated the

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enclosed area (m^2). Ethical guidelines and ecological impact minimization were prioritized, with necessary consents obtained from authorities and facility managers at the sampling sites when needed.

2.3. Field Work and Sampling

Sampling took place between 25/08/2023 and 05/10/2023 to avoid extreme weather conditions, ensuring consistency across time. Environmental parameters were monitored during the sampling process to provide ecological context. Water salinity (PSU) was measured at each site to check habitat suitability for marine organisms. Physical characteristics including water temperature (°C) and visibility (m) were recorded, when possible, to understand their influence on species richness and community composition. This ensured that variations in community composition were attributed to natural differences rather than external factors.

Trained divers performed sample collection using 20 cm x 20 cm quadrats to randomly allocate the sampling areas and ensure uniform sampling and then used scrapers to destructively collect both fauna and flora from the substrate (Figure 3). At each site, five replicates were collected aiming for sufficient statistical power to detect spatial variability among sites. In addition, underwater photos were taken for reference and further analysis (Figure 3). Samples were preserved in white, colourless, denatured ethyl alcohol (94°) to prevent degradation and maintain specimen integrity, crucial for laboratory identification. The samples were collected in sterilized containers, which were sealed to ensure optimal preservation.
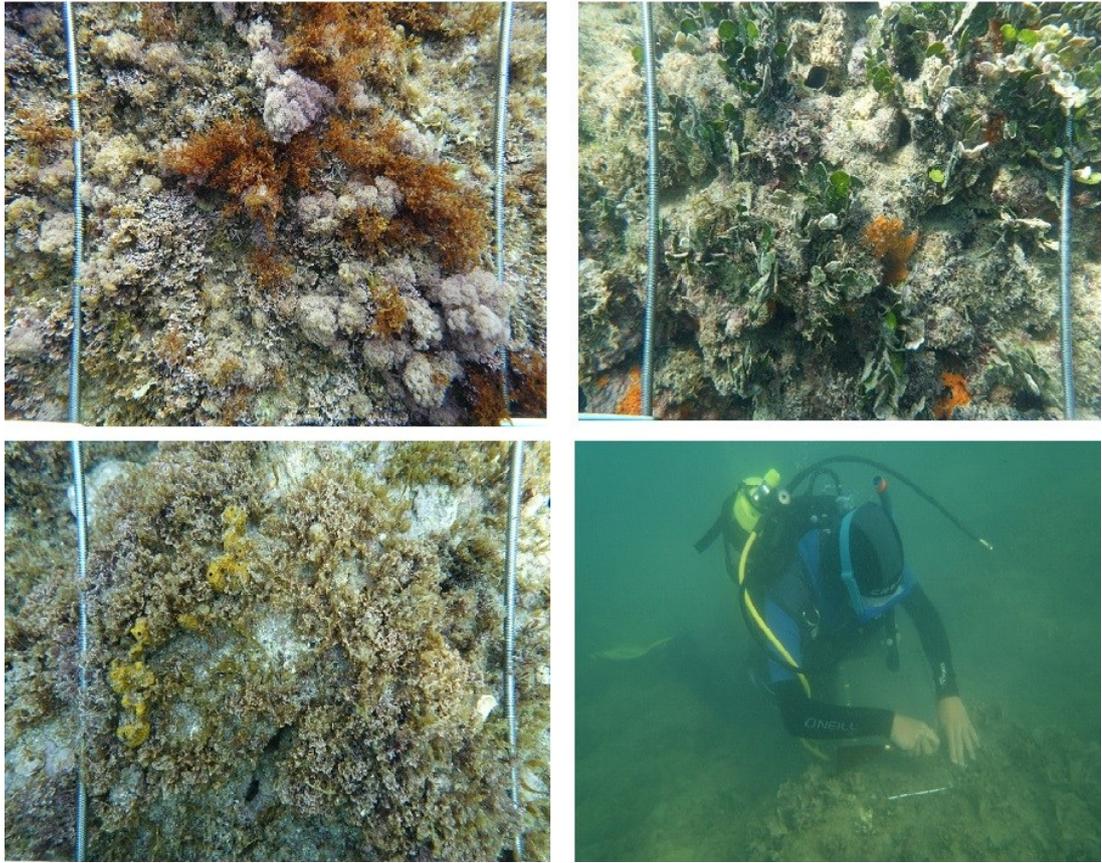
Figure 3 *Field sampling using 20 cm x 20 cm quadrats and scrapers to destructively collect samples.*

2.4. Analysis

2.4.1 Sample Analysis

Samples were randomly selected and analysed in the laboratory at a rate of 3-5 samples per day to mitigate potential biases towards specific samples and to ensure equitable processing over time. Each opened sample underwent sorting, with each specimen identified and documented to the lowest possible taxonomic level using microscopic visual characteristics and referencing relevant literature specific to the sample's geographical origin (Bianchi, C. N., 1981; Brunetti & Mastrototaro, 2017; Hayward & Ryland, 2012; Riedl, 1983; Zabala & Maluquer, 1988). Taxonomic verification was conducted by a qualified taxonomist to confirm the accuracy of species identification. Microscopic identification was performed using a stereo microscope for initial examination of larger structures and a light microscope for

detailed examination of microscopic features. Taxonomic names were cross-checked against the latest updates in taxonomic databases, including the World Register of Marine Species (WoRMS), to ensure accuracy. This process involved taxonomic verification, correction of inconsistencies, and removal of duplicates. First, all identifications were validated using the WoRMS database by verifying spelling, synonymy, and the current accepted names. Next, inconsistencies were corrected to ensure uniform taxonomic classification. Finally, duplicates—potentially resulting from repeated sorting or misidentification—were identified and removed. Additionally, we reviewed our species dataset to identify non-indigenous species (NIS) present in the study areas. The examination was conducted using relevant literature through cross-referencing species lists with existing records of introduced species (Ambrogi, 2000; Ferrario et al., 2018; Gauff et al., 2023; Langeneck et al., 2020; *Marine Non-Indigenous Species in Europe's Seas*, 2022; Massé et al., 2023; Osca & Crocetta, 2020; Ulman et al., 2017; Zenetos & Galanidi, 2020).

Subsequently, samples were dried at 70°C for a minimum of 48 hours, weighted then combusted at temperature between 450°C to 550°C for 6 hours and reweighted to obtain dry mass and ash-free dry mass (biomass), respectively.

2.4.2 Data Analysis

i. Data Analysis, Visualization, Statistical Tests and Significance

All statistical analyses and graphs were done using R (R Core Team (2023), version 4.3.2).

Species richness, defined as the total number of species present, was calculated by counting the number of species based on presence absence data at each sample within our sites and then in total for each site. A Generalized Linear Mixed Model (GLMM) evaluated the effects of the predictor variables (Island size and distance) on species richness per sample. The GLMM was fitted using the *glmer* function from the '*lme4*' package in *R* (version 1.1.35.9; (Bates et al., 2014)), with the following model specification: *Total ~ Distance * logSize + (1 | BGZ)*. Distance

was treated as a continuous variable, while logSize was log-transformed to scale. These predictor variables, Distance and logSize, were included as fixed effects, along with their interaction term Distance * logSize to explore if the effect of Distance on Total depends on the value of logSize and vice versa. Additionally, the model accounts for random variability associated with the grouping factor BGZ by including a random intercept term (1 | BGZ), allowing each level of BGZ to have its own baseline level of Total. This approach acknowledges the potential for different groups (levels of BGZ) to exhibit distinct baseline counts. The distribution model used was set to Poisson, which is appropriate for only positive count data and had the best fit to our data. By fitting this model, estimates for the fixed effects (main effects and interaction) and the random effects were obtained.

To visualize the model and specifically the interaction between Distance and logSize on the response variable (Species richness per sample), we used '*Interact_plot*' function in *R*, from the '*interaction*' package (version 1.1.5; (Long, 2019)). Distance was initially plotted as the predictor variable, with logSize serving as the moderator. This visualization included confidence intervals and data points to illustrate their combined effect on species richness. Additionally, the analysis was reversed, with logSize as the predictor and Distance as the moderator, to explore the reciprocal relationship between these variables.

To evaluate the community composition among sites, the Bray-Curtis dissimilarity matrix was calculated using the '*vegdist*' function from the '*vegan*' package (version 2.6.6.1; (Oksanen et al., 2001)). Then, Principal Coordinates Analysis (PCoA) visualized the dissimilarities among samples based on Bray-Curtis distances for each BGZ. Unlike in the GLMM, Distance was treated as a categorical variable rather than continuous. The PCoA was performed on this matrix using '*wcmdscale*', and the percentage of variance explained by each axis was calculated. The resulting scores were prepared for plotting using '*ggplot2*' (version 3.5.1;(Wickham, 2016)). Ellipses were added around groups of points based on Proximity using '*geom_mark_ellipse*' from the '*ggforce*' package (version 0.4.2; (Pedersen, 2016)), serving to visually highlight and interpret the clustering patterns

and dispersion of samples. Furthermore, we conducted a PERMANOVA test to assess the significance of dissimilarity patterns explained by Distance, using the *'adonis2'* function from the *'vegan'* package (version 2.6.6.1; (Oksanen et al., 2001)). This test evaluated whether the observed dissimilarities among samples were significantly associated with differences in Distance, thereby providing statistical support for the spatial patterns observed in the PCoA plots.

In a similar approach to the GLMM used for modelling species richness, a Generalized Linear Model (GLM) with a Poisson distribution was applied to model the relationship between the predictor variables and introduced species richness observed per sample. Following the GLM analysis and to allow comparison of the abundance of non-indigenous species (NIS) across different proximity levels relative to natural environments, where NIS abundance is typically lowest, a bar plot was generated using the *'ggplot2'* package (version 3.5.1; (Wickham, 2016)) to visually represent the mean proportion of introduced species for each proximity level. The plot included error bars, indicating the standard error, and individual data points were overlaid on the bars to display the raw data.

Prior to statistical analysis, the *Shapiro-Wilk test* was performed using the *'shapiro.test'* function from *base R* to assess the normality of the data distribution. Given that the assumption of normality was not met, we decided to proceed with a non-parametric approach. A *Kruskal-Wallis test* was conducted to evaluate whether there were statistically significant differences in the proportion of introduced species across the different proximity levels. The test was performed using the *'kruskal.test'* function from base *R*, providing an alternative to *ANOVA* when the assumption of normality is not met. To further investigate specific differences between proximity levels, *Dunn's Post-Hoc test* was performed using the *'dunn.test'* package (version 1.3.6; (Dinno, 2014)).

3. Results

3.1. Variability Between Sites

The final dataset comprised 441 species records derived from 80 samples: 16 sites of artificial hard substrate and 8 natural rocky shore (NRS) sites, with 5 samples taken from each site. Among the species identified, 29 were non-indigenous. Mollusca was the most dominant phylum, accounting for 32.9% of the total species observed. This was followed by Rhodophyta (17.8%), Annelida (15.4%), and Arthropoda (7.5%). Chlorophyta represented (6.3%) of the species, while Bryozoa and Heterokontophyta contributed 6.0% and 4.6%, respectively. Other phyla, including Porifera (2.6%), Chordata (2.6%), Echinodermata (2.2%), and Cnidaria (1.4%), were also present, with lower proportions. Minor contributions were noted from Platyhelminthes (0.5%) and Nemertea at 0.2% ([Figure 4])

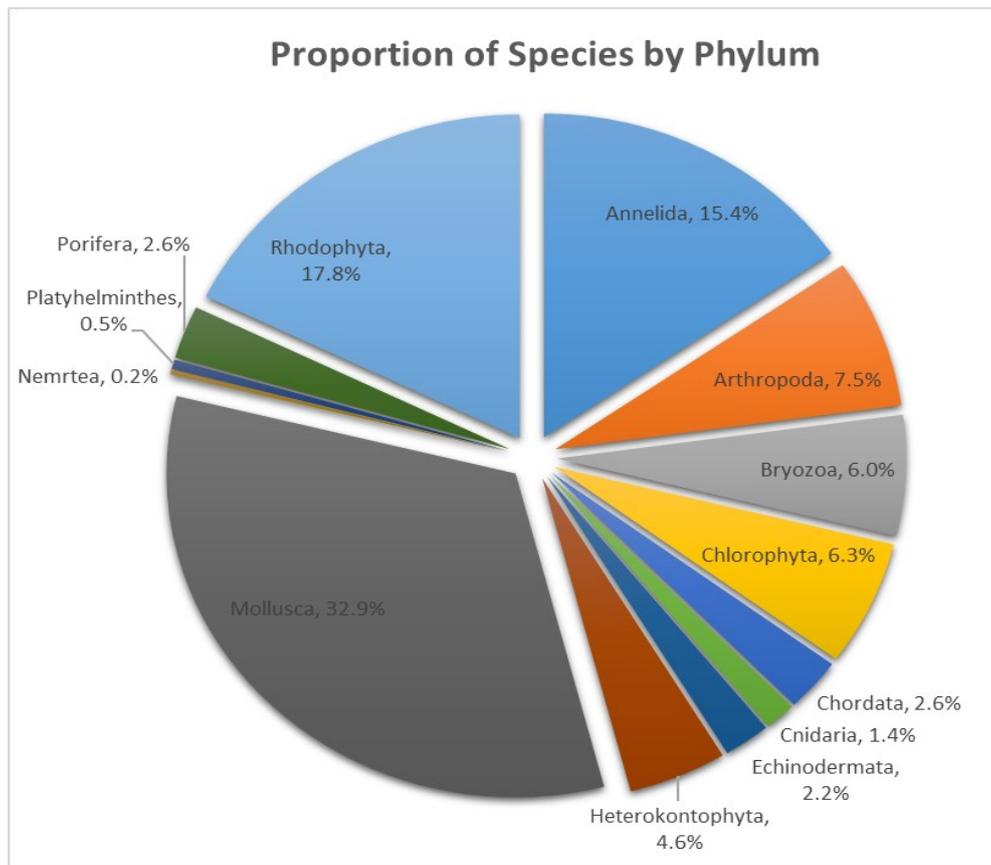*Figure 4 The pie chart illustrates the proportion distribution of 441 identified species by phyla across the sampled locations*

The total number of species identified at each site provided a quantitative measure of species richness. Table 1 (Table 1) summarizes these data, highlighting the variation in species richness across different sites, sampled structures' sizes, and their distances from the nearest natural rocky shore.

Biogeographical Zone (BGZ)	Site_ID	Distance (Km)	Size (m2)	Species richness = Total number of species
Northern Adriatic (BGZ 1)	CA ROMAN	100	23206	**63**
	CAVALLINO	80	30125	**41**
	GRADO	20	7106	**46**
	SISTIANA	0.08	1494	**68**
Mid Adriatic (BGZ 2)	ANCONA	0.075	1057	**54**
	FERMO	45	9861	**32**
	S. BENEDETTO	65	9718	**36**
Southern Adriatic (BGZ 3)	BARI	0.15	7201	**42**
	SAND	25	357	**29**
Lonian Sea (BGZ 4)	POLICORO	45	4977	**48**
	TARANTO	0.2	31760	**76**
Southern Tyrrhenian (BGZ 5)	AMANTEA	40	1957	**9**
	VIBO	7	8708	**29**
Northern Tyrrhenian (BGZ 6)	CIVITAVECCHIA	4	1854	**55**
Ligurian Sea (BGZ 7)	LIVORNO	0.2	2647	**33**
	VIAREGGIO	30	9513	**49**

Table 1 Summary of Study Sites Across Different Biogeographical Zones (BGZs) of the Italian Seas. The table lists the sites surveyed, their respective distances from the nearest natural rocky shore (Km), structures' sizes (in square meters), and the total number of identified species (species richness).

3.2. Species Richness as a Function of Island Size and Distance

The generalized linear mixed model (GLMM) testing for the effect of distance, log(size), and their interaction on species richness showed a significant negative effect of distance *(*** p < 0.001*) on the species richness, indicating that greater distances are associated with lower species richness. The interaction between distance and log(size) also significantly influenced species richness *(*** p < 0.001*), indicating a modifying effect of size on the relationship between distance and species richness, although the main effect of log(size) showed positive effect but was not statistically significant (*p = 0.298*) ([Table 2](#))

The model included 80 observations across 7 biogeographical zones. The marginal R^2 value, representing the variance explained by the fixed effects alone, was 0.240. The conditional R^2, which includes both fixed and random effects, was 0.698. These values indicated that the model explains a good portion of the variance in species richness, particularly when accounting for the random effects of biogeographical zones. The residual variance, or the variance that is not explained by the fixed effects or the random effects in the model was (*σ^2 = 0.06*) and further indicated that the model effectively explains a good portion of the observed variance in species richness

Predictors	Effects of Distance and Log(Size) on Species Richness with Random Effect of Biogeographical Zone		
	Incidence Rate Ratios	*CI*	*p*
(Intercept)	14.12	7.55 – 26.41	**<0.001**
Distance	0.95	0.93 – 0.97	**<0.001**
logSize	1.09	0.93 – 1.28	0.298
Distance × logSize	1.01	1.01 – 1.02	**<0.001**
Random Effects			
σ^2	0.06		
$\tau_{00 \ BGZ}$	0.09		
ICC	0.60		
N_{BGZ}	7		
Observations	80		
Marginal R^2 / Conditional R^2	0.240 / 0.698		

Table 2 Results of the Generalized Linear Mixed Model Analysing the Effects of Distance, Log(Size), and their Interaction on Species Richness. Significant results are denoted by asterisks (p < 0.05, ** p < 0.01, *** p < 0.001)*

3.3. Interaction of Size and Distance

The interaction plot, including confidence intervals and data points and visualizing the interaction between distance and log(size) on species richness showed that for the mean value of log(size), which represents the average of all the size values we have, the total number of species exhibited a clear negative relationship with distance, with species richness decreasing as distance increased. When log(size) increased by one standard deviation (+1 SD), the effect of distance on the total number of species became less pronounced, indicating that larger site sizes moderate the negative impact of distance on species richness. Conversely, at one standard deviation below the mean log(size) (-1 SD), the negative effect of distance on the total number of species was more pronounced, with smaller site sizes exacerbating the negative impact of distance, resulting in a steeper slope of the curve (Figure 5)

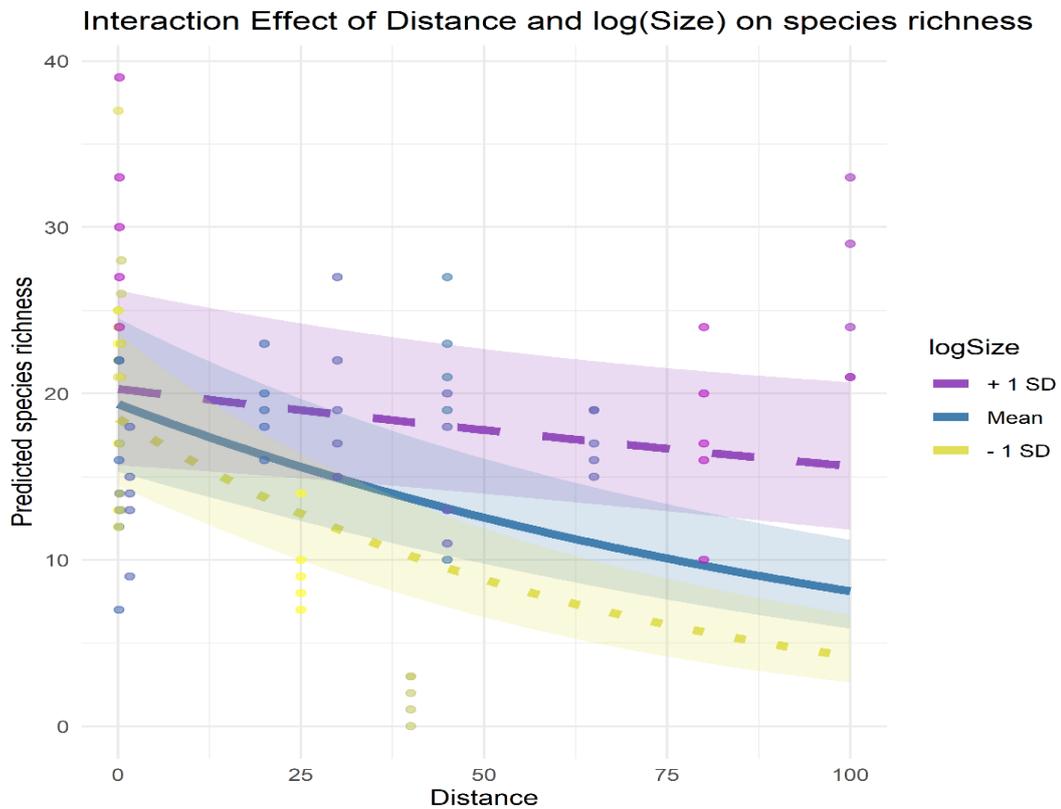*Figure 5 Interaction plot illustrating the relationship between distance and log(size) on species richness. The plot shows how species richness changes with distance at different levels of log(size), highlighting moderation effects. Error bars represent confidence intervals.*

Looking at the interaction plot from the second perspective, with logSize as the predictor and Distance as the moderator we observed that for the mean value of distance, the total number of species increases with log(size). However, at a distance equal to the mean minus one standard deviation (-1 SD), the slope of the line showing the increase in species richness decreased, and it straightened, indicating a diminished effect of log(size) on species richness. In contrast, at a distance equal to the mean plus one standard deviation (+1 SD), the slope remained the same as the mean or became higher, suggesting that at greater distances, the influence of site size on species richness is more pronounced. (Figure 6)
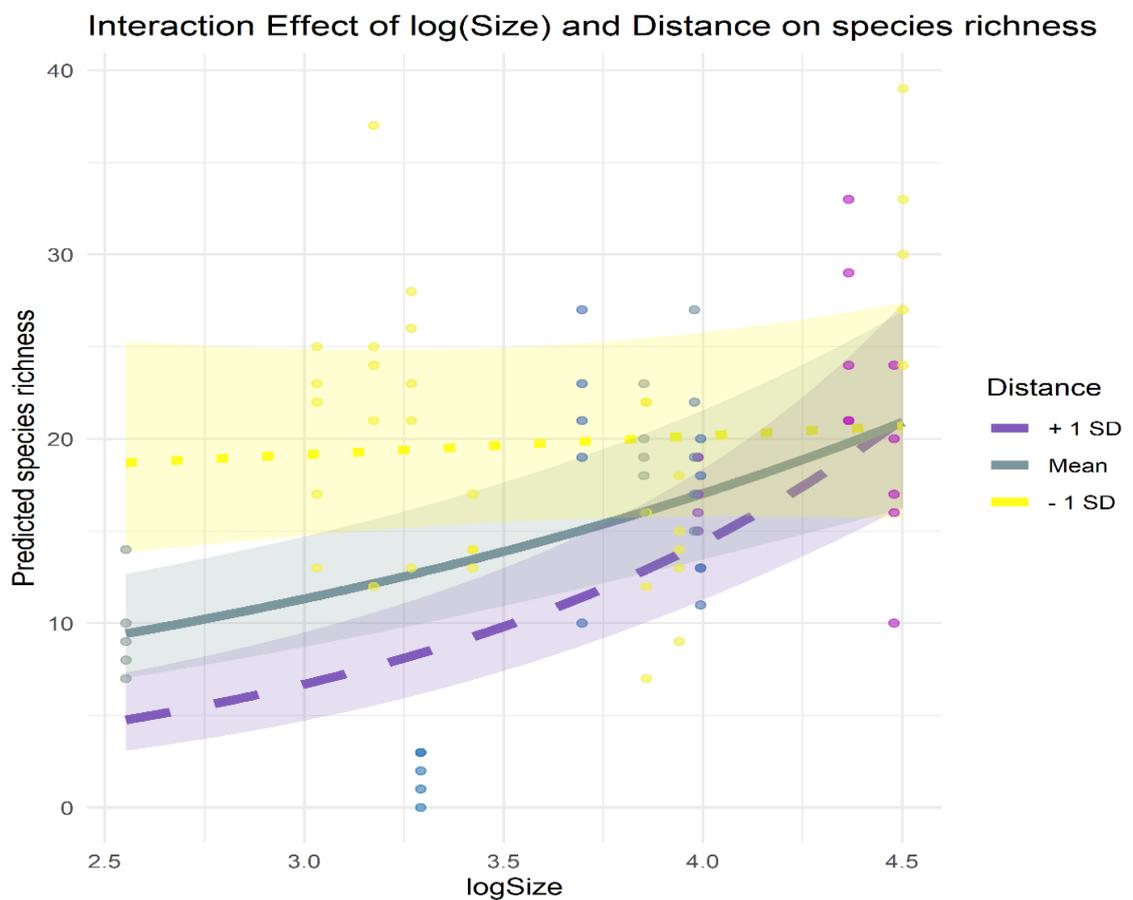

Figure 6 Interaction plot illustrating the relationship between log(size) and total species richness at different distances. The plot shows how species richness varies with log(size) across different levels of distance, highlighting moderation effects. Error bars represent confidence intervals.

3.4. Community Composition of Sites

Across all BGZs, PCoA plots consistently demonstrated that sites categorized as 'Far' and 'Mid-range' from the Natural Rocky Shore (NRS) are distinctly separated from 'Close' proximity sites and the NRS on the PCoA1-axis, which accounts for the majority of the explained variability (23.1% - 44%). Additionally, the PCoA2 axis, which explains between 15.1% and 19.8% of variability, further distinguishes 'Natural Rocky Shore' from 'Close' proximity sites, as well as 'Mid-range' and 'Far' in case of BGZ 1 and 2. This trend is consistently observed in BGZs 1, 2, 4, 5, 6, and 7 (Figure 7).

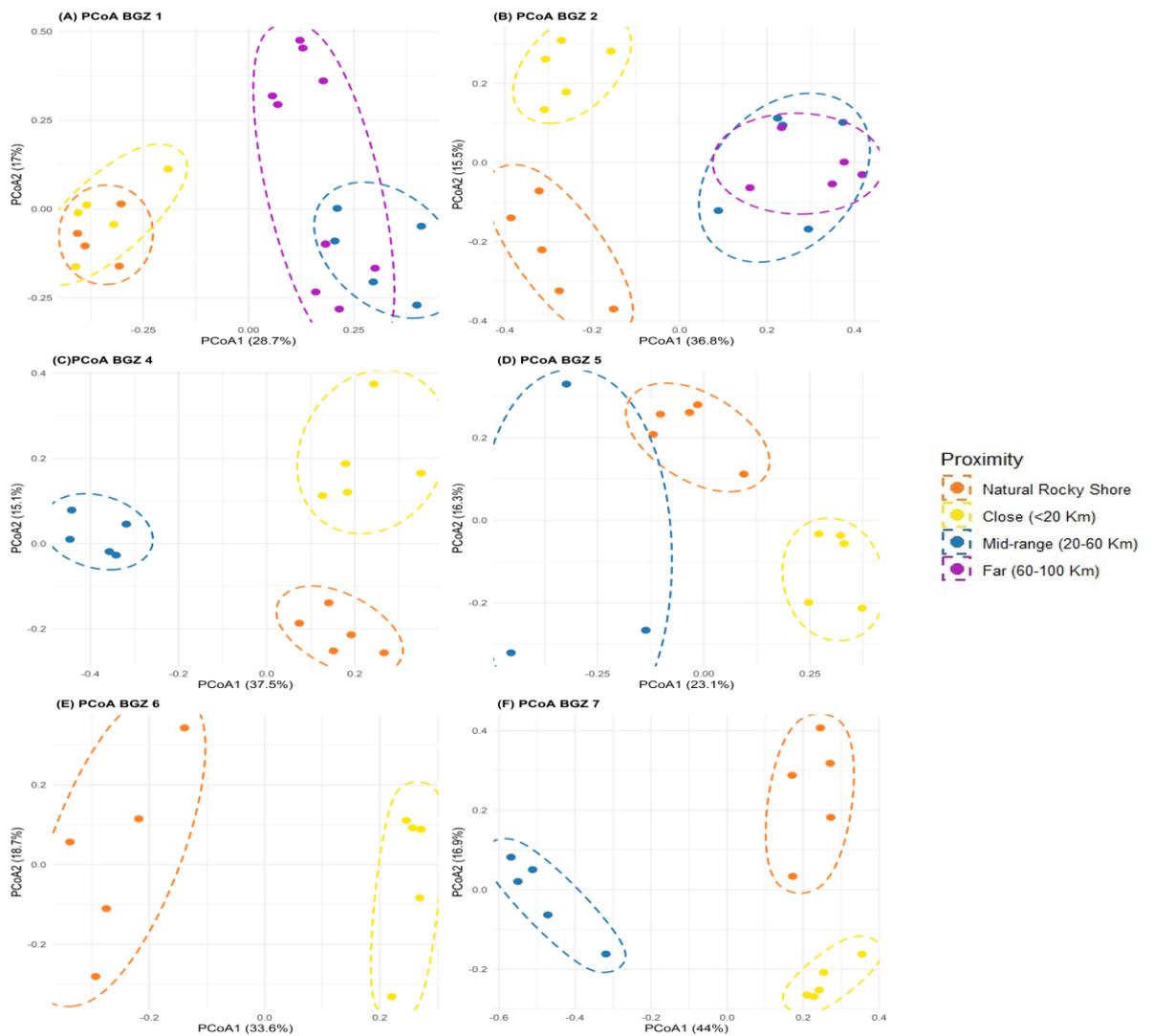*Figure 7 PCoA plots illustrating the clustering of samples from Biogeographical Zone (BGZ) 1,2,4,5,6 and 7 based on Bray-Curtis dissimilarities. Points represent sample locations in the PCoA space, colored by proximity categories (Natural Rocky Shore, Close, Mid-range, Far). Ellipses depict groupings of points around each proximity category, highlighting clustering patterns and dispersion of samples.*

BGZ 3 represent a unique case where there are two distinct natural rocky shores (NRS 1 and NRS 2), the associated sites are specified accordingly, and their respective proximity distances are labelled. The inclusion of two natural rocky shores in BGZ 3 allows for a more detailed examination of site separation based on proximity. The sites associated with NRS 1 and NRS 2, as well as their corresponding 'Close and ' 'Mid-range,' are distinctly represented, further emphasizing the patterns observed in other BGZs. ([Figure 8])
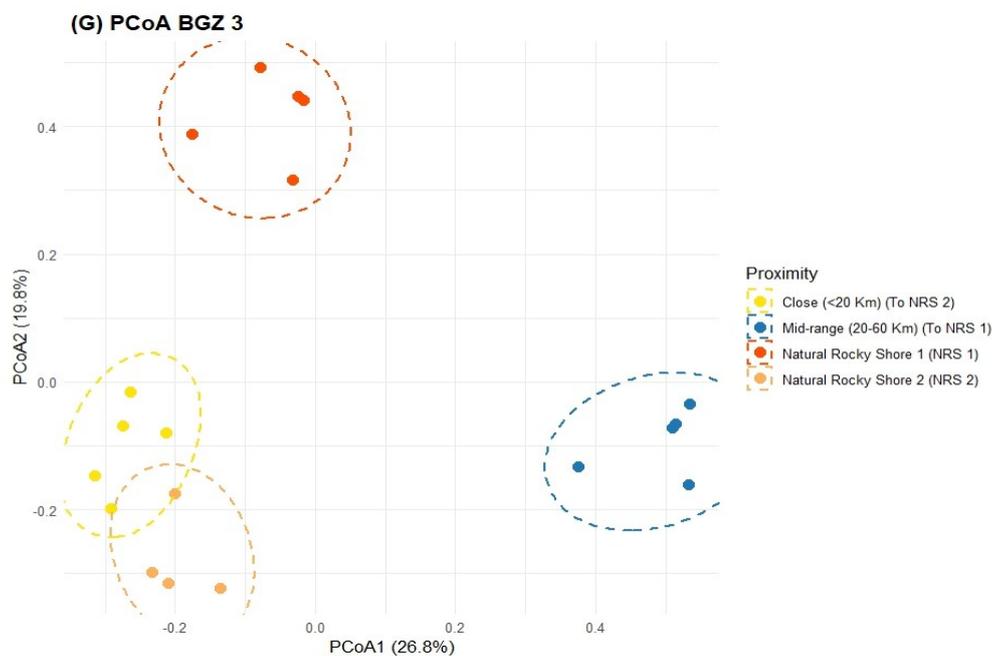
Figure 8 Principal Coordinate Analysis (PCoA) plot showing the distribution of samples from Biogeographical Zone 3 (BGZ 3) based on Bray-Curtis dissimilarity. Points are colored by proximity to different types of rocky shores, with ellipses indicating group dispersion.

The Permutational Multivariate Analysis of Variance (PERMANOVA) employed to assess the significance of species composition differences indicated a significant effect of proximity on species composition across all the biogeographical zones (1 through 7), as evidenced by the obtained p-values. ([Table 3])

PERMANOVA Results

DataSet	Term	Df	SumsOfSqs	R2	F.Model	P.value
BGZ1	Proximity	3	2.84	0.42	4.91	<0.01 **
	Residual	20	3.85	0.58		
	Total	23	6.69	1.00		
BGZ2	Proximity	3	2.44	0.54	6.24	<0.01 **
	Residual	16	2.08	0.46		
	Total	19	4.52	1.00		
BGZ3	Proximity	3	3.71	0.55	6.13	<0.01 **
	Residual	15	3.03	0.45		
	Total	18	6.73	1.00		
BGZ4	Proximity	2	1.53	0.49	5.84	<0.01 **
	Residual	12	1.57	0.51		
	Total	14	3.09	1.00		
BGZ5	Proximity	2	1.55	0.34	2.82	<0.01 **
	Residual	11	3.02	0.66		
	Total	13	4.57	1.00		
BGZ6	Proximity	1	0.65	0.33	3.91	<0.01 **
	Residual	8	1.33	0.67		
	Total	9	1.98	1.00		
BGZ7	Proximity	2	2.40	0.58	8.29	<0.01 **
	Residual	12	1.74	0.42		
	Total	14	4.14	1.00		

Table 3 Results of Permutational Multivariate Analysis of Variance (PERMANOVA) assessing the significance of species composition differences based on proximity across biogeographical zones (BGZs 1-7). Significant results are denoted by asterisks (* p < 0.05, ** p < 0.01, *** p < 0.001).

3.5. Introduced / Non-Indigenous Species

A total of 25 non-indigenous species (NIS), detailed in (Table 4), were identified after the examination of our species dataset.

Species	Kingdom	Phylum	Class	Order	Family
Amphibalanus eburneus	Animalia	Arthropoda	Thecostraca	Balanomorpha	Balanidae
Anadara transversa	Animalia	Mollusca	Bivalvia	Arcoida	Arcidae
Ascidiella aspersa	Animalia	Chordata	Ascidiacea	Phlebobranchia	Ascidiidae
Asparagopsis armata	Plantae	Rhodophyta	Florideophyceae	Bonnemaisoniales	Bonnemaisoniaceae
Branchiomma luctuosum	Animalia	Annelida	Polychaeta	Sabellida	Sabellidae
Bugula neritina	Animalia	Bryozoa	Gymnolaemata	Cheilostomatida	Bugulidae
Caulerpa cylindracea	Plantae	Chlorophyta	Bryopsidophyceae	Bryopsidales	Caulerpaceae
Caulerpa taxifolia	Plantae	Chlorophyta	Bryopsidophyceae	Bryopsidales	Caulerpaceae
Celleporaria brunnea	Animalia	Bryozoa	Gymnolaemata	Cheilostomatida	Lepraliellidae
Cerithium scabridum	Animalia	Mollusca	Gastropoda	Caenogastropoda	Cerithiidae
Clavelina oblonga	Animalia	Chordata	Ascidiacea	Aplousobranchia	Clavelinidae
Codium fragile	Plantae	Chlorophyta	Ulvophyceae	Bryopsidales	Codiaceae
Dyspanopeus sayi	Animalia	Arthropoda	Malacostraca	Decapoda	Panopeidae
Hydroides dirampha	Animalia	Annelida	Polychaeta	Sabellida	Serpulidae
Hydroides elegans	Animalia	Annelida	Polychaeta	Sabellida	Serpulidae
Hydroides nigra	Animalia	Annelida	Polychaeta	Sabellida	Serpulidae
Hypnea musciformis	Plantae	Rhodophyta	Florideophyceae	Gigartinales	Cystocloniaceae
Magallana gigas	Animalia	Mollusca	Bivalvia	Ostreida	Ostreidae
Ophiactis savignyi	Animalia	Echinodermata	Ophiuroidea	Amphilepidida	Ophiactidae
Pinctada radiata	Animalia	Mollusca	Bivalvia	Ostreida	Margaritidae
Ruditapes philippinarum	Animalia	Mollusca	Bivalvia	Venerida	Veneridae
Spirorbis (Spirorbis) marioni	Animalia	Annelida	Polychaeta	Sabellida	Serpulidae
Tricellaria inopinata	Animalia	Bryozoa	Gymnolaemata	Cheilostomatida	Candidae
Womersleyella setacea	Plantae	Rhodophyta	Florideophyceae	Ceramiales	Rhodomelaceae
Xenostrobus securis	Animalia	Mollusca	Bivalvia	Mytilida	Mytilidae

Table 4 list of 25 non-indigenous species (NIS) identified in our dataset, along with their respective taxonomic classifications.

The Generalized Linear Model (GLM) employed to examine the effects of distance and log(Size) on the introduced species richness per sample revealed that log(size) had a significant positive effect on the introduced species richness ($p < 0.001$). In contrast, distance from the nearest natural rocky shore did not have a significant effect ($p = 0.598$) (Table 5).

| Predictors | Effects of Distance and Log(Size) on the introduced species richness | | |
	Incidence Rate Ratios	CI	p
(Intercept)	0.00	0.00 – 0.02	**<0.001**
Distance	1.03	0.93 – 1.13	0.598
logSize	5.57	2.85 – 11.43	**<0.001**
Distance × logSize	0.99	0.97 – 1.02	0.551
Observations	80		
R^2 Nagelkerke	0.558		

Table 5 Generalized Linear Model (GLM) results showing that log(Size) significantly increases introduced species richness (p < 0.001), while Distance does not have a significant effect (p = 0.598).

Our further investigation into the richness of non-indigenous species revealed variation in their proportion, calculated as the number of non-indigenous species divided by the total number of species at a site, across different proximity levels of distance. Specifically, the mean proportion of non-indigenous species tends to increase with the structure's distance from the closest natural rocky shore (Figure 9). Artificial structures located farthest (60-100 km) exhibited the highest mean proportion, with a value of 0.083, followed by those at mid-range distances (20-60 km) with a mean proportion of 0.046, and close proximity (<20 km) structures with a mean proportion of 0.040. Natural rocky shores exhibited the lowest mean proportion of introduced species, with a value of 0.023. The error bars represent standard errors, indicating the variability within each level.
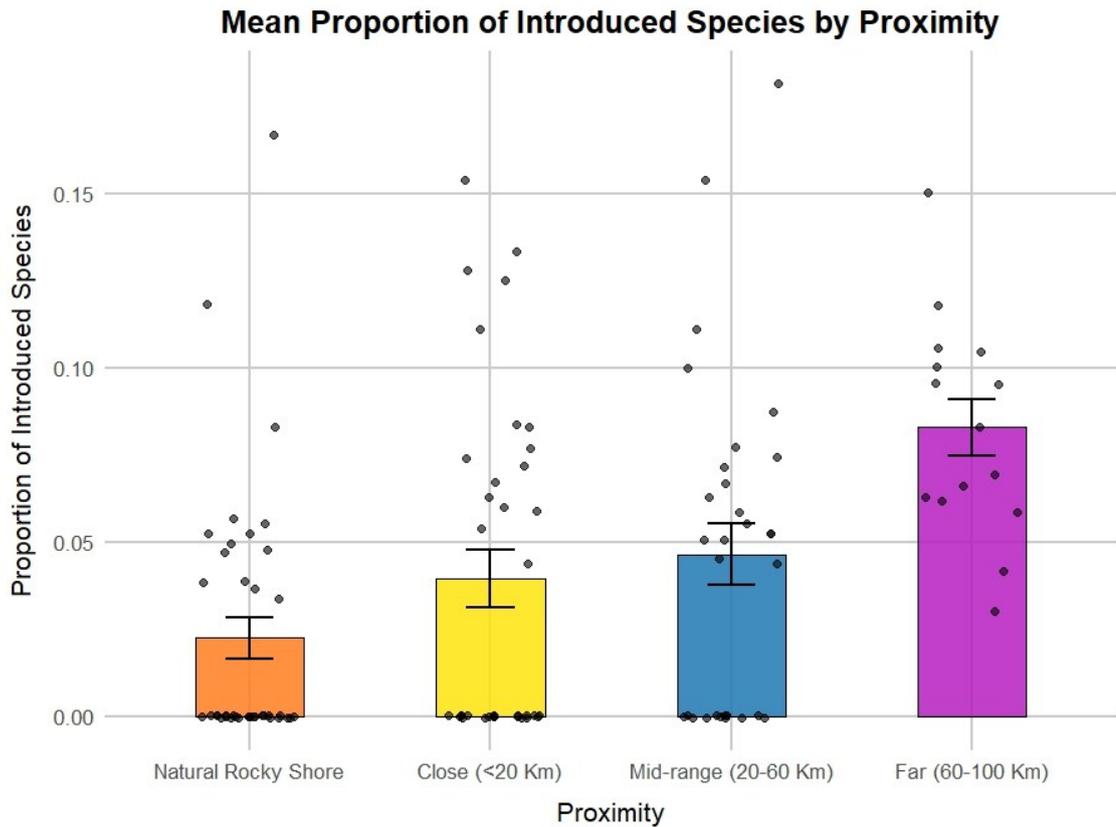
Figure 9 Bar plot showing the mean proportion of introduced species calculated by averaging the proportion of introduced species for samples within each proximity level. Higher values are observed at greater distances from natural rocky shores; error bars indicate standard error.

Kruskal-Wallis test performed to assess the significance of observed differences in the proportion revealed a statistically significant difference among the proximity levels (Kruskal-Wallis chi-squared = 23.19, df = 3, p-value < 0.001). To further investigate the differences between specific proximity levels, Dunn's Post-Hoc test results indicated that the proportion of non-indigenous species at structures located close to the mainland (<20 km) was significantly lower compared to those at far distances (60-100 km) (p-value < 0.01). Additionally, the far structures (60-100 km) showed a significantly higher proportion of non-indigenous species compared to mid-range structures (20-60 km) (p-value < 0.05) and the natural rocky shore (p-value < 0.001). No significant differences were observed between close (<20 km) and mid-range (20-60 km) structures (p-value = 1) or between close structures (<20 km) and the natural rocky shore (p-value = 0.252). The

comparison between mid-range (20-60 km) structures and the natural rocky shore approached significance (p-value = 0.0665) ([Table 6](#))

Kruskal-Wallis and Dunn's Post-Hoc Test Results

Test	Chi-Squared	df	p-value	Comparison	Z-value	Adjusted p-value
Kruskal-Wallis	23.19	3	< 0.001***			
Dunn's Post-Hoc Test				Close (<20 Km) - Far (60-100 Km)	-3.38	<0.01**
Dunn's Post-Hoc Test				Close (<20 Km) - Mid-range (20-60 Km)	-0.62	1
Dunn's Post-Hoc Test				Far (60-100 Km) - Mid-range (20-60 Km)	2.82	< 0.05*
Dunn's Post-Hoc Test				Close (<20 Km) - Natural Rocky Shore	1.73	0.252
Dunn's Post-Hoc Test				Far (60-100 Km) - Natural Rocky Shore	4.76	< 0.001***
Dunn's Post-Hoc Test				Mid-range (20-60 Km) - Natural Rocky Shore	2.29	0.0665

Table 6 Kruskal-Wallis and Dunn's Post-Hoc Test Results for Non-Indigenous Species Proportion Across Proximity Levels. Significant results are denoted by asterisks (* p < 0.05, ** p < 0.01, *** p < 0.001)

4. Discussion

The results of this thesis provided insights into the applicability of Theory of Island Biogeography to marine urban structures along the Italian coasts, examining these artificial environments as potential island-like habitats. We hypothesized that larger structures would harbour higher species richness, and that increased isolation would correlate with reduced species richness and more distinct communities. Additionally, we expected increase in NIS species proportion with both size and isolation of the structure. The results show that species richness increases with structure size, while it decreases with increasing isolation. Whereas for NIS, their richness appears to be significantly correlated with structure size and shows higher proportions at structures farther from natural rocky shores.

4.1 Species Richness-Isolation Relationship

The species-isolation relationship observed in this study demonstrated a significant negative correlation between species richness and the degree of isolation from natural rocky shores. In a study aiming to identify ecologically meaningful metrics and to quantify their relative importance for species richness in a globally representative data set across 453 islands worldwide, isolation of an island was found to be the second most important factor determining species richness (Weigelt & Kreft, 2013). Furthermore, the majority of empirical studies that have investigated the effect of isolation on species richness for various taxa have consistently reported a negative relationship (Kreft et al., 2008; Weigelt & Kreft, 2013). However, different outcomes may be dependent on the spatial scale of the study that could be of a large (landscape) spatial scales or small spatial scale (Jones et al., 2020). Akin to our study, a similar work conducted on artificial structures in China showed a significant negative correlation of species richness with isolation (Dong et al., 2016); however, the continuous artificial shoreline in this study limited the link with island biogeography.

A possible explanation of the negative relationship in our study could be that structures located far from natural rocky shores face higher dispersal illimitations,

and lower habitat connectivity, as spatial extent of connectivity and extent of larval dispersal is strongly influenced by geographic setting (Jones et al., 2009). Marine organisms have variable dispersal capabilities, and their larvae or propagules may not travel long distances limiting their movement from natural rocky shores to artificial structures (Kinlan et al., 2005; Kinlan & Gaines, 2003). Cowen and Sponaugle highlighted how marine larval dispersal is typically limited to biophysical processes (Cowen & Sponaugle, 2009). Additionally, limited gene flow between isolated populations can lead to increased inbreeding and decreased genetic diversity (Palumbi, 2003), making population inhabiting isolated structures more susceptible to environmental changes. This will affect population viability as they lack genetic resilience provided by large interconnected metapopulation (Vandewoestijne et al., 2008) and make them more susceptible to extinction events. Also, as the "rescue effect" ecological theory suggests that population of organisms that receive continuous immigrants, which is not the case if a structure is isolated, should be less vulnerable to local extinction (Brown & Kodric-Brown, 1977). Theoretical framework for the rescue effect was first established by Theory of Island Biogeography (Macarthur & Wilson, 1967) and later evolved by metapopulation theory (Hanski & Simberloff, 1997). All our studied isolated structures were likely more susceptible to connectivity limitations and extinction events. These factors lead to a decreased observed species richness in these structures compared to others close to natural sources of colonizers with a continuous influx and support of immigrants.

4.2 Species Richness-Area Relationship

We observed that larger marine urban structures supported greater species diversity. Area might have influenced species richness directly in several ways: increased surface area of larger structures likely offers more varied microhabitats and shelter, promoting higher biodiversity (Cornell, 2013), larger habitats can reduce competitive exclusion by providing more ecological niches (Holt, 1996) and can buffer populations against local extinctions (Krauss et al., 2010). Studying

wetlands, Brose found that area is surrogate variable for habitat heterogeneity which directly enhances vascular plant species diversity (Brose, 2001).

Plots from the artificial urban structure in Ca Roman, covering 23,206 square meters, exhibited higher species richness (63species) compared to plots from smaller structures such as Grado (7,106 square meters, 46 species) and Livorno (2,647 square meters, 33 species). However, our generalized Linear Mixed Model (GLMM) analysis indicated that the effect of size alone on species richness was not statistically significant. This finding suggests that, although there is a trend towards larger structures supporting more species, other factors play a significant role and species richness is determined by a combination of factors including and beyond size. For oceanic islands, it was found that while habitat diversity and heterogeneity were strong drivers underlying species richness, a collection of smaller, fragmented areas supporting a broader range of habitat variation tended to maintain more species than a few larger areas with a narrower range of habitats (Quinn & Harrison, 1988). Larger structures may interact differently with their surrounding environment and factors such as hydrodynamics and propagule interception can shape species richness patterns. Larger structures can have a stronger stepping-stones effect though a higher chance of intercepting floating propagules and enhancing connectivity between fragmented habitats. This indicates that the relationship between species richness and area is complex and can be strongly influenced by ecological and spatial factors beyond just the size of the habitat, such as the diversity of available niches and the connectivity to other habitats.

4.3 Interaction Between Isolation and Area

One factor affecting the species richness-size relationship, was the proximity of the structures to natural rocky shores, which significantly influenced species richness. Structures closer to natural habitats tended to harbour higher species richness, even when they were relatively small. In island systems, proximity to source of species and propagules facilitate colonization and increase biodiversity (Connell & Glasby, 1999; Macarthur & Wilson, 1967), that might also apply to artificial structures close to natural rocky shores. The interaction from our GLMM analysis provides further

insights into how size and distance jointly influence species richness. The overall trend indicates that species richness increased with size of structure and decrease with its distance from the natural rocky shore; however, the magnitude of these effects is moderated by the other variable respectively. Specifically, species richness was highest in structures closer to natural rocky shores, even for smaller structures. As distance increases, the positive effect of size on species richness becomes more evident. This pattern suggests that while larger structures can support higher biodiversity, their species richness is further enhanced when they are situated closer to natural sources of colonizers. On the contrary, the negative effect of distance on species richness becomes less pronounced as the size of the structure increases. Larger structures show a relatively flatter slope of species decline compared to smaller structures. Larger structures appear to buffer the impact of isolation, likely due to combination of different factors; they offer diverse resources, supporting more species (Cornell, 2013), reduce local extinctions by acting as refuges (Krauss et al., 2010), and enhance connectivity by serving as stepping stones that intercept floating propagules, facilitating species movement (Fowler et al., 2020). For instance, larger habitats have been found to maintain higher biodiversity by providing refuges and facilitating species persistence despite isolation (Krauss et al., 2010). Additionally, the reduced impact of distance on larger structures aligns with the concept that habitat complexity and size can enhance ecological resilience (Olds et al., 2012). Similar results were obtained in a study on the species richness of island floras of a built data of 453 islands, that found the effect of isolation was weaker for large islands, thus suggesting that speciation offsets the negative influence of isolation on immigration in larger islands (Weigelt & Kreft, 2013).

4.4 Non-Indigenous species

In urbanized artificial environments, fouling communities exhibit a distinct composition compared to less disturbed natural habitats, characterized by a significantly greater prevalence of non-indigenous species (NIS) over native species (Airoldi et al., 2015). NIS often flourish in marine urban habitats because these environments provide open space and opportunities for colonization, with

native species either not establishing or struggling to persist, leaving lot of empty spaces, as described by the passenger model (MacDougall & Turkington, 2005). Our findings indicate that natural rocky shores exhibited the lowest proportion of non-indigenous species, with an increase in this proportion toward urban structures at farther distances from these shores.

The generalized linear model used to analyze the effect of distance and log(size) on introduced species' richness per sample was significant for log(size) having a positive impact on the richness of the introduced species ($p < 0.001$). This once again corroborates the findings that larger structures can support higher number of species. In contrast, distance to the nearest natural rocky shore did not significantly influence NIS richness ($p = 0.598$), which may indicate that isolation is not a major driver of NIS richness in these habitats.

However, the bar plot generated to complement the GLM showed that within these urban structures, a trend in the proportion of NIS at varying proximity levels was observed. Specifically, data showed that the farthest structures, which are also the largest in our study, exhibited the highest proportion. This could be explained as increased distance from natural rocky shores likely reduces competition with native species, allowing for the potential establishment of non-native organisms. Isolated structures experience reduced biotic resistance (Kimbro et al., 2013) due to the lower connectivity with natural habitats. Native biotic resistance acts as buffer against the establishment of non-native species (Teixeira et al., 2017) explaining the low proportion obtained in natural rocky shores and structures of close proximity to them as they receive continues flux of species.

Additionally, larger structures are associated with high urbanization levels, reflecting a more intense maritime activity (Ducruet, 2021). This increased activity is associated with a greater frequency of ship traffic, which is a primary vector for the introduction of non-indigenous species though ballast water discharge and biofouling on hulls (Fernandes et al., 2016; Minchin & Gollasch, 2003; Ruiz et al., 2000). The more frequent the ship visits, the higher the likelihood of introducing new species that can thrive in disturbed or altered environments. Furthermore, high anthropogenic disturbances affect natural populations and assemblages by interacting with fundamental ecological processes (Benedetti-Cecchi1 et al., 2001).

The stress from these disturbances, along with the continuous and facilitated introduction of NIS, further aids in their establishment over native species in artificial structures.

4.5   Community Composition Dynamics Analyzed by PCoA

The Principal Coordinates Analysis (PCoA) revealed clear clustering patterns, with PCoA plots consistently showing that sites categorized as 'Far' and 'Mid-range' from the natural rocky shores were distinctly separated from 'Close' proximity sites and the natural rocky shores themselves along the primary axis, which accounts for the majority of the explained variability, highlighting the influence of isolation on community composition. The distinct separation indicates that isolation had a main impact on community composition, with isolated structures possibly exhibited more distinct community assemblages compared to less isolated structures.

This phenomenon is likely driven by the restricted dispersal of marine organisms and the varying environmental conditions across different distances from the natural rocky shores. Community assembly processes determine the composition of biological communities. These processes can be broadly categorized into deterministic (niche-related) processes and stochastic processes as discussed in literature (Chase, 2010; Dornelas et al., 2006; Valdivia et al., 2021). Predation, competition and habitat availability are crucial in determining marine urban community composition (Dayton, 1971; Firth et al., 2014). Different levels of these in isolated structures may influence species composition like observed in the experimental manipulation of consumer presence in a tropical rocky intertidal zone, where changes in predation led to shifts in species dominance, showing that a diverse group of consumers collectively maintained community structure (Menge et al., 1986). Additionally, the limited and often unpredictable arrival of species to isolated structures, coupled with unique local environmental conditions, results in communities that are assembled also by chance, pointing to a possible stochastic nature of these communities. For example, the stochastic model proposed by Hubbell (Hubbell & Borda-de-Água, 2001) discussed that local community dynamics are often influenced by random events and demographic stochasticity,

leading to variations in community composition that are not entirely predictable by deterministic factors alone. Permutational Multivariate Analysis of Variance (PERMANOVA) statistically validated these observations, which showed that proximity significantly affects species composition across all biogeographical zones. The significant p-values from the PERMANOVA analysis support the spatial patterns seen in the PCoA plots, indicating that the differences in community composition are strongly associated with the degree of isolation from natural rocky shores. This further supports how spatial separation influences species assemblages.

4.6   Alignment with Theory of Island Biogeography's Predictions

The principles of Theory of Island Biogeography, as articulated by MacArthur and Wilson provide a framework for understanding the patterns observed in this study. Our findings demonstrated a significant negative correlation between species richness and the degree of isolation from natural rocky shores, with more isolated marine urban structures exhibiting lower species richness. This aligns with the theory's principle that isolation reduces the probability of species colonization, thereby decreasing overall species diversity. Furthermore, larger marine urban structures were found to support greater species diversity, consistent with the species-area relationship, another foundational principle of the theory.

Both geographical and biological definitions characterize what is considered an island, giving it its unique identity. For a marine environment to be correctly labelled as island-like, it should meet both these definitions: a geographical definition as a place or habitat that is well-defined and geographically isolated, and a biological definition as possessing species endemism, island rule, species-area relationship, and species isolation relationship (Dawson, 2016; Foster, 1964; McClain et al., 2009). Urban structures placed in the marine environment introduce hard substrates that serve as new habitats for colonization. The characteristics of these structures, mimicking rocky shores, make them anchor points for fauna and flora specific to natural rocky shores. The areas where we collected samples are characterized by the topography of the coastal and continental regions, with a dominant alternation between hard substrates and soft sediments. This causes

geographical isolation of marine urban structures, in many cases, from nearby natural rocky shores. Thus, marine urban structures meet the first criterion of geographical isolation (Bulleri & Chapman, 2010; Connell, 2001).

This study provides evidence of biogeographical isolation, as our results align with the species-area relationship, species isolation relationship and patterns of community differentiation across isolation gradients (Chase et al., 2011; Macarthur & Wilson, 1967; Whittaker, 1972). Although these structures are not entirely isolated from the surrounding reference sources— given the connectivity in the marine environment is different from the stronger isolation experienced by terrestrial biota on an island—the results are consistent with what is described in the Theory of Island Biogeography. It is also evident the interaction between area and isolation, that was translated in our results in change of outcome depending on the interplay between these two factors. Here, we observe not a pure species-area relation, and not a pure species-isolation relationship, but an interaction of both which defines how diversity changes over studied structures. MacArthur and Wilson made clear that Theory of Island Biogeography is not limited to only true island, but also to any kind of isolated habitat. Giving flexibility in the testing of Theory of Island Biogeography on different systems (Macarthur & Wilson, 1967). Plenty of this system is discussed by Dawson (Dawson, 2016) to witch is evident to add marine urban structures, as they fit the description both geographically and biologically, to a considerable extent, and gives deeper understanding of marine perspective of biogeography.

4.7 Understanding Biodiversity Patters in Urban Marine Environments

Understanding the biodiversity patterns of marine urban environments requires an in-depth analysis of how these structures function as ecological systems within the aquatic environment. This involves examining the interactions between artificial substrates and marine biota, considering factors such as habitat complexity, resource availability, and connectivity with natural habitats. It has been previously shown that urban areas have broad ecological footprint on biodiversity and community structure (Bulleri & Airoldi, 2005; Chapman, 2007), species interaction (Klein et

al., 2011) and spread and settlement of non-indigenous species (Bulleri & Airoldi, 2005; Gauff et al., 2023). Furthermore, efforts have been made to mitigate these impact through ecological engineering, showing how simple enhancement methods can be cost-effective measures to manage local biodiversity (Firth et al., 2014). Recent studies have reinforced the importance of habitat complexity in promoting biodiversity. For example, eco-engineered tiles on seawalls have been shown to enhance biodiversity by providing varied microhabitats, which support a greater variety of species (Bishop et al., 2022; Chapman & Underwood, 2011). Additionally, the structural complexity and connectivity of seagrass meadows have been found to play crucial roles in shaping biodiversity, with more complex habitats supporting more diverse assemblages of species (Henderson et al., 2017). Our findings suggest that urban structures follow to ecological patterns predicted by Theory of Island Biogeography. Hence, incorporating a new component that involves the strategic placement of these structures to consider isolation factors, alongside habitat complexity and design, could enhance their resilience and productivity as artificial ecosystems.

Additionally, exploring the relationships between various urban seascape, such as the size, location, shape, and human usage of marine urban structures, can offer valuable insights into how connectivity influences the dynamics of native and non-native species, ultimately contributing to biodiversity preservation and an increase in native species richness. This knowledge could be used to mitigate negative effects of isolation, such as the spread of non-native species, and even be exploited for bioenhancement or restoration objectives. Connectivity plays a critical role in promoting gene flow and dispersal, thereby mitigating the impacts of fragmentation and isolation within artificial hard substrate habitats (Roberts et al., 2003).

Marine urban structures located in close proximity to one another and to natural rocky shores can form metapopulations, where individual structures exhibit distinct population dynamics. Within these metapopulations, local extinctions can be mitigated through recolonization by nearby populations, ensuring population persistence despite extinction events. This highlights the role of connectivity in maintaining colonization and preventing regional habitat losses (Hanski, 1999). To further enhance the ecological role of marine urban structures and support

biodiversity, strategies to improve connectivity can be implemented. Eco-friendly, modular reef units could be deployed between structures to serve as stepping-stones, facilitating movement and colonization across a fragmented landscape. Additionally, strategically placing multiple structures in networks that bridge gaps between isolated structures could promote genetic exchange, enhance habitat connectivity, and optimize larval dispersal by considering prevailing currents. These efforts would support long-term species persistence and population dynamics, ensuring effective connectivity across artificial habitats and increasing their ecological role.

5. Limitations

It is essential to acknowledge the limitations of this thesis to guide future research and improve future study designs.

First, a broader range of isolation levels and sizes across different biogeographical zones in Italy and beyond would benefit the study. The expansion would allow for deeper understanding of the interaction between isolation and size on species richness. The current study design included a limited combination of these factors in all the biogeographical zones, which may have constrained our ability to fully capture the variability in communities. Second, testing stochasticity of species composition on these substrates, compared to the source species composition, would have required more than one sampling site with the same level of isolation from the same source. This replication would enable us to differentiate between stochastic and deterministic processes driving species richness and composition. Third, the study could not test for the effect of the age of the sampled structures on species richness and community composition, as it was challenging to obtain accurate data on age of these structures. While age of structures can influence colonization patterns and species composition dynamics (Horsák et al., 2012; Macarthur & Wilson, 1967), studies suggests that assemblage on artificial structures remain distinctive regardless of age (Miller et al., 2009).

Future studies should consider study design that include wider range of variables, proper distribution of levels combinations, and include manageable number of sampling structures with well documented histories.

6. Conclusion

The primary objectives of the thesis were to check for the applicability of the Theory of Island Biogeography to artificial marine hard substrates along the Italian coastline and to assess if these structures can be considered island-like environments if isolated from other rocky substrates. The study specifically aimed to investigate if species richness on studied structures followed the species-area relationship, where larger structures have greater species diversity, and the species-isolation relationship as there is a negative correlation between species richness and degree of isolation from natural rocky shores.

The main finding showed that marine urban structures, like natural islands, have significant patterns of species richness and composition that is affected by their size and degree of isolation. Species-isolation relationship demonstrated significant negative correlation between species richness and degree of isolation from natural rocky shores. More isolated structures exhibited lower species richness, which align with the principle of Theory of Island Biogeography. This highlights the importance of connectivity and proximity to species natural source in maintaining biodiversity on artificial structures. For the species-area relationship, there was a trend that bigger marine infrastructure supported greater species diversity. However, distance significantly influenced how size affected species richness, with very close structures showing a diminished effect of size due to their proximity to natural propagule sources. Furthermore, the analysis of community composition indicated that isolation affects community dynamics on marine urban structures. Structures farther from natural rocky shores showed distinct communities compared to those closer to natural habitats, suggesting that isolation not only affects species richness but also leads to unique community assemblages. Additionally, the farthest and largest structures exhibited the highest proportion of non-indigenous species (NIS). While the size of these structures is a significant factor in supporting greater NIS richness, the influence of distance is less pronounced, as methods of introduction such as maritime activities and urbanization, are pervasive and can facilitate the establishment of NIS across various locations regardless of proximity to natural habitats. This finding underscores the potential role of marine urban structures in

fostering the establishment and spread of non-native species, particularly in environments where the influx of native species is limited by isolation.

The application of the TIB to marine urban structures emphasizes their potential role as island-like environments. These structures meet both the geographical and biological criteria for being considered island-like, given their isolation and distinct species compositions. The findings of this study contribute to the broader understanding of how artificial habitats can mimic natural island systems, providing valuable insights for conservation and management efforts.

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