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TESI DI LAUREA

Assessing Habitat Suitability for Pacific Oyster *(Magallana gigas)* in the Venice Lagoon

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Abstract

Oysters have an important role in protecting coastal-marine ecosystems, by providing several benefits such as filtering water, creating habitat, reducing eutrophication, controlling coastal erosion, absorbing carbon, and supporting biodiversity. The Pacific oyster, or *Magallana gigas*, is one of the most important bivalve species cultivated worldwide. *Magallana gigas* were brought for aquaculture to the Venice lagoon. This species finds a good home in the brackish water conditions of the lagoon, which are characterized among other things by salinity oscillations and the tidal currents. This species then naturally occurred in the lagoon, coexisting in wild populations with the local species. But pollution, climate change, and human activity all pose serious threats to natural environments, potentially affecting their survival. This study aimed to investigate the habitat suitability for *Magallana gigas* in the Venice lagoon, that is, which are the ideal conditions for *Magallana gigas* to grow, reproduce, and survive. This study focuses on environmental indicators such as water temperature, salinity, and depth to evaluate habitat suitability. MaxEnt is particularly useful for habitat suitability models. A key element of habitat suitability models is the selection of environmental characteristics that are assumed to be important for the target species. This study uses the Venice lagoon to test a suitability model for the *Magallana gigas* habitat. The allometrics of the Pacific oyster in the Venice Lagoon were also examined in the study. The habitat suitability model map is a useful tool for illustrating the implications of climate change and altering ecosystem conditions on oyster habitat suitability.

Keywords: habitat suitability, MaxEnt, allometries.

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1. Introduction

1.1 The Venice Lagoon ecosystem

The largest lagoon in Italy, the Venice Lagoon, plays a crucial role in the ecology and is an excellent case study for research looking at the adequacy of the environment for the Pacific oyster, or *Magallana gigas* (Thunberg, 1793) The biggest lagoon in the Mediterranean basin is the Venice Lagoon, which is located in the Northern Adriatic Sea and spans an area of around 550 km^2 (Fig. 1). Large, shallow areas that make up roughly 75% of the entire surface (Molinaroli et al., 2009; Zucchetta, 2009) are connected by a network of channels, most of which are less than 2 meters deep (Solidoro et al., 2002; Zucchetta, 2009). This ecosystem is a shallow coastal lagoon with an average depth of 1.2 meters (Molinaroli et al., 2007; Zucchetta, 2009). With a range of around ±50 cm during spring tides, deeper channels are linked to three broad mouths (Lido, Malamocco, and Chioggia) that preserve lagoon–sea contact and let tidal flows to reach the lagoon (Umgiesser et al., 2004; Zucchetta, 2009).

Figure 1. The Venice Lagoon (Source: Google Earth, 2024).

On every tidal cycle, on average, around one-third of the water (390 × 106 m^3) is exchanged (Gacic et al., 2004). However, weather also has a significant impact on water flows and properties (Cucco and Umgiesser, 2006). Two watershed divides split the basin into three major sub-basins (Fig 1.) (Solidoro et al., 2002). With a mean mud content of almost 80% in dry weight and a decreasing trend from north to south, the basin's bottom sediments are mostly composed of clayey silt (Molinaroli et al., 2007). With an annual mean inflow of 35.5 m^{3}s^{-1} (Zuliani et al., 2005), freshwater inflows have an impact on salinity, with the northern sub-basin accounting for more than half of the freshwater inflows (Zonta et al., 2005; Zuliani et al., 2005).

A contemporary illustration of a tidal environment in peril from severe degradation processes brought on by the combined effects of climate change and human activity is the Venice Lagoon. Since the 15th century, the lagoon has undergone major morphological changes as a result of the Serenissima Republic of Venice, the ancient Venetian state, diverting the main rivers that had previously debouched into the lagoon to the Adriatic Sea to prevent the lagoon from silting up; such trend has been exacerbated by more recent human actions altering the lagoon hydrodynamics and promoting widespread tidal form erosion (Tommasini et al., 2019). The Venice Lagoon is an example of a particular type of ecosystem where anthropogenic and natural dynamics coexist and are intimately linked, where complex global transformation processes (like climate change and sea level rise) are coupled with intense local human pressures (like water pollution and altered hydrodynamics) (Vergano, L. and Nunes, P., 2007).

1.1.1 Importance of the Venice Lagoon

The history and future of the largest brackish body of water in the Mediterranean, the Venice Lagoon, are intimately intertwined with those of the City of Venice and the other urban settlements that make up the lagoon. Venice and its lagoon have been UNESCO World Heritage Site since 1987, and are closely linked since when Venetian inhabitants are thought to have fled to the northern lagoon islands for shelter from Barbarians in the fifth century. They are a unique illustration of how humans and landscape, as well as natural and constructed settings, have coevolved (D'Alpaos, C. and D'Alpaos, A, 2021).

Even though the lagoon fishing has gradually decreased since the 18th century, it still has some economic value today. Although the boats, equipment, and methods of the past have been replaced by new ones or adapted, it is still one of the most traditional occupations of the local community (e.g. Brunelli, 1940; Rallo, 1992). There are many different species of fish found in lagoons, but only a small number are used for commercial purposes, such as: the European eel (*Anguilla anguilla*), sea bass (*Dicentrarchus labrax*), and gilt-head bream (Sparus auratus). There are also five types of mullets—*Mugil cephalus, Chelon labrosus-chelo, Liza aurata, L. ramada, and L. saliens*—. Additionally, the lagoon is home to the grass goby (*Zosterissessor ophiocephalus*) and the big-scale sandsmelt (*Atherina boyeri*). Several flatfish species inhabit this area as well, alongside the invertebrate species, common cuttlefish (*Sepia officinalis*). Being euryhaline, these species travel between the lagoon and the sea to finish their life cycle. The migration period varies according to the species' temperature and dietary requirements, although they usually spend the summer in the lagoon, where food is plentiful. The best fishing seasons are late summer and early fall when the fish go to the sea after reaching commercial size.

In addition to fish, bivalve mollusks are an important resource, producing 50,000 tons annually (Pellizzato, 1996; Ravera, 2000). The most important bivalves in terms of commerce are *Mytilus galloprovincialis, Ostrea edulis, Magallana gigas, Crassostrea angulata, Tapes decussatus, T. philippinarum, and Cerastoderma glaucum.* A few cephalopods (*Sepia officinalis* and *Eledone moschata*) and gastropods (*Bolinus brandaris and Aporrais pes-pelicani*) are important in the region was successfully introduced in 1966–1967. In 1983, an Asiatic clam (*Tapes philippinarum*) was introduced. Other allochthonous mollusk species introduced to the lagoon did not provide the expected results (Cesari and Pellizzato, 1985). The lagoon is home to farms of blue mussels (Mytilus galloprovincialis). In recent years, both the Decussatus and Philippine species of clams have been collected using hydraulic dredges. Research indicates that this strategy negatively affects benthic organisms and significantly alters the chemical exchange between sediments and water (Ravera, 2000).

The Venice Lagoon is made more complex by the numerous economic activities that take place there now, which operate as catalysts for change with differing degrees of (un)sustainability. Tourism, fishing, aquaculture, ports and maritime transport, industrial operations, urbanization and related activities, and agriculture (in its catchment) are the most important of these. The lagoon ecology is threatened by several issues that originate from a mix of present activity, physical forcing functions, and previous interventions. These include the previously discussed morphological changes, pollution and nutrient loads (and the ensuing eutrophication events), loss of biodiversity, relative sea level rise, and an increase in the frequency and severity of extreme tides or "high water" occurrences (Ravera, 2000; Solidoro et al., 2010).

1.2. Oysters as a key organism

1.2.1 The ecological role of oysters

As important members of the marine food web and major contributors to nutrient cycling, water quality, and habitat structure, oysters are essential to the health, stability, and biodiversity of the lagoon ecosystem. In Ehrich et al. (2014), Newell (1988) states that oysters filter water at an average rate of 0.12 $m^3g^{-}1$ dry weight (DW) day−1, eliminating suspended organic and inorganic particles to influence nutrient cycling and water column clarity. Oysters are autogenic engineers that build reefs by building up shells (Wilberg et al., 2013; Ehrich et al., 2014). This shell serves as both a habitat for other creatures and a substrate for the establishment of oyster larvae (Newell, 1988; Ehrich et al., 2014). This natural filtration process enhances water clarity and quality, benefiting other marine organisms and promoting a balanced aquatic environment (Mazur et al., 2024). By reducing turbidity, oysters indirectly aid in light penetration, which benefits submerged aquatic vegetation (SAV), essential for carbon sequestration, and provides habitats for juvenile fish (Piehler and Smyth, 2011). Oysters indirectly contribute to light penetration by lowering turbidity, which promotes submerged aquatic vegetation (SAV), which is necessary for sequestering carbon and supplying habitat for young fish (Porter, Cornwell, and Sanford, 2004).

Additionally, oyster reefs are essential for establishing and maintaining habitats for a wide range of marine species. For many species, including fish, crabs, shrimp, and other invertebrates, their reefs offer intricate three-dimensional structures that act as refuges, feeding grounds, and breeding grounds (Peterson et al., 2003). By establishing a physically complex ecosystem, these reefs provide shelter to young creatures from predators and encourage biodiversity, with some regions home to up to 300 species (Grabowski and Peterson, 2007). This increase in biodiversity strengthens ecosystem resilience, making coastal ecosystems more resilient to external stresses, including pollution, storms, and temperature fluctuation.

To comprehend the ecological relevance of oysters, it is essential to see them as "ecosystem engineers". Oysters change the physical environment by producing reefs, which maintain shorelines, affect sedimentation rates, and create confined zones of intense biological activity (Jones et al., 1994). By promoting the recruitment and retention of sediment and supporting various assemblages of flora and fauna, this engineering role improves habitat complexity, which in turn reduces erosion and shields coastal regions from wave and storm surge energy. Oysters contribute to the nitrogen and carbon cycles in addition to their structural and water quality advantages. Their shells retain carbon, which aids in carbon sequestration, and their diet and nutrient excretion help transform nitrogen into forms that other species may use. Therefore, conservation and restoration activities are essential because the health and functionality of the entire ecosystem are seriously threatened by the collapse of oyster populations in the Venice Lagoon (Beck, 2011), whether as a result of overharvesting, pollution, habitat loss, or climate change.

1.2.2 Economic value

The Lagoon of Venice is a location for oyster and mussel farming, shipping young mollusks to other Italian agricultural locations, particularly those in Sardinia and Liguria—the Western Mediterranean area (Prioli,2008). Oysters have stimulated local economies by generating jobs in harvesting, processing, and distribution in addition to directly generating cash. The region's cultural ties to seafood are particularly noteworthy; oysters are central to Venice's culinary legacy, and seafood-themed events provide seasonal tourism income (Béné et al., 2016). Shellfish reefs play an important role as habitat for other species; the fish produced on oyster reefs have significant value to coastal economies (Grabowski and Peterson 2007).

Oyster cultivation, also known as aquaculture, has become more economically significant in the lagoon than conventional harvesting. By encouraging sustainable methods that allow oyster populations to flourish without reducing natural stocks, this strategy has supported environmental stewardship and helped preserve local jobs. In addition to promoting ecological balance, sustainable aquaculture practices including habitat restoration and selective breeding significantly increase oyster harvests' resilience and productivity over time (Pérez-Ruzafa et al., 2011). Oysters' economic worth is shown by the rising demand for them both domestically and abroad, which encourages investment in sustainable aquaculture methods. Aquaculture is a vital undertaking for the region both economically and environmentally, and this change towards sustainable aquaculture is crucial for satisfying consumer demand while guaranteeing minimal environmental effect (FAO, 2018).

Oysters have economic worth that goes beyond the fishing and aquaculture industries. The environmental services that oyster reefs offer, such habitat creation and water filtering, are important and have a big economic impact. Oysters support the tourist sector by fostering a more wholesome and aesthetically pleasing marine environment by filtering contaminants and excess nutrients from the water. Oyster filtration produces more clear water, which facilitates boating, diving, and other ecotourism activities that draw tourists (Newell, 2004). Furthermore, by establishing habitats that sustain a variety of fish species, oysters indirectly enhance the resilience of other fisheries in the lagoon, which in turn increases local fishery production (Beck et al., 2011). Oyster population restoration and maintenance in the Venice Lagoon are essential for maintaining the local economy as well as the ecological health of the area because of these numerous economic advantages. Future generations may be guaranteed that the lagoon's oyster populations will continue to contribute to the fishing, tourism, and aquaculture sectors via investments in conservation projects and habitat restoration, backed by laws encouraging sustainable farming.

1.3. *Magallana gigas* (Thunberg, 1793)

Magallana gigas have similar characteristics with other oysters, such as irregularly shaped valves. The growing environment has a significant impact on the shell's form. For example, the shell might be flat and less ridged on soft substrate, rounded, domed, and fluted on hard substrate, and narrower when crowded (Quayle

1969). The lower right valve may be deeply cupped. The outside surface of both valves is covered with concentric growth layers or lamellae; however, the left (upper) side has fewer and more robust ridges. Strong ripples form ridges and spines along the lamellae's margins (Langdon and Robinson, 1996). Shells can range in color from white to gray to off-white, with the ridges occasionally being brown or purple. There is a purple muscle scar on the smooth, white inside of the shell (Quayle 1969; Coan et al. 2000). Although it is said to occasionally reach 400–450 mm, *Magallana gigas* develops at around 80 mm (Carriker and Gaffney, 1996). Quayle (1969) illustrates the larvae. Late larvae of this and other oysters are characterized by the asymmetrical umbo, whereas early veligers are almost round. About 300 µm is the length at which they settle (Quayle, 1969).

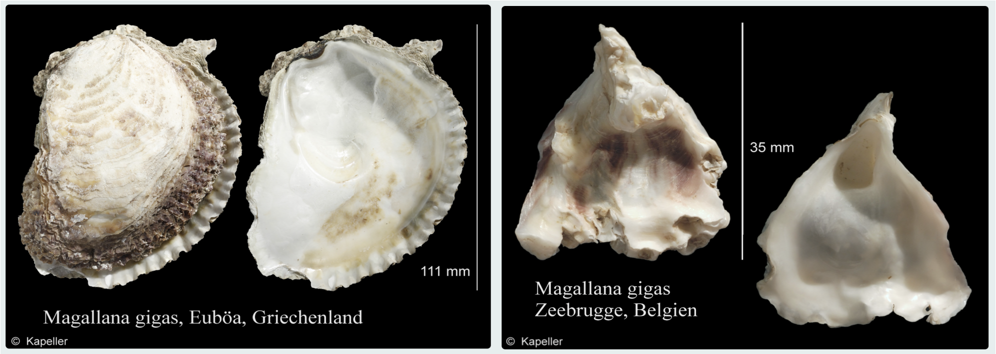

Figure 2. *Magallana gigas* (Source : https://www.rkapeller.eu/).

The species *Magallana gigas* is genetically diverse. Different strains with varying growth patterns and ecological preferences are grown in various regions of Japan. The Miyagi strain, which is huge and grows quickly, is the most often planted kind and comes from Japan's central Pacific coast (Quayle, 1969). The Northwest and Indo-West Pacific areas also have a large number of closely related species. They are closely related to the Portuguese oyster, *Magallana angulata*, which was brought to Europe in the 16th century (Reece et al., 2008).

Like other oysters, *Magallana gigas* is a protandric hermaphrodite, meaning that it matures as a male at first and frequently changes to a female in later seasons. In the water column, where fertilization takes place, males discharge sperm and females release eggs. The fertilized egg develops into a shelled veliger larva after initially becoming a ciliated trochophore larva. The larva develops a foot and becomes a pediveliger, capable of settling, after feeding on phytoplankton. Larval settlement in laboratory culture took place between 11 and 30 days at 16 to 30°C (Quayle, 1969; His et al., 1989). At 80 mm, gonads can form in *M. gigas* (National Research Council 2003). Adult *M. gigas* have a retention effectiveness of almost 100% while feeding on 6-32 µm phytoplankton, but they are less effective when feeding on smaller species (Nielsen et al., 2016). Oysters typically reach a maximum length of 300 mm, however, adult oysters have been seen to reach 450 mm (Carriker and Gaffney, 1996). In China and Japan, protected coastal waters are home to *Magallana gigas*. This oyster may withstand brief exposures to salinities as low as 5–10 PSU, although it typically develops at 23–28 PSU (Carriker and Gaffney, 1996). Although temperatures above 30°C are stressful, it can withstand a fairly broad temperature range, from -1.8 to 35°C (Shpigel et al., 1992; Carrasco and Barón, 2010).

Water temperatures of around 20° C are usually the trigger for Pacific oyster spawning (Quayle, 1969). Following fertilization, larvae spend a few weeks floating in the water column before landing on hard ground. Although it has been demonstrated that larvae may live at considerably lower temperatures, the optimal temperature for their survival and settling at this time is around 27° C (Villa et al., 2009). According to Villa et al. (2009), larvae raised at 17° C had a survival rate of above 80%. The minimum need for larval survival to complete reproduction is degree days above 10.55° C. The mean summer water temperature from all records utilized throughout our study period was 14.5° C, well below the average spawning threshold of 20° C. Historically, water temperatures in south Puget Sound have not reached the temperature threshold for spawning (Villa et al.,2009).

One of the most significant species of shellfish cultivated globally is *Magallana gigas* (Lallias et al., 2015). The Food and Agriculture Organization (FAO) (2009) reports that *M. gigas* was the most produced aquaculture species in the world in 2003, with a total production of 4.38 million tons, or $3.69 billion USD. However, the lagoon also hosts a native oyster species, *Ostrea edulis* (European flat oyster), which is considered a key part of the region's historical marine ecosystem. While *M. gigas* has become widespread due to its resilience and rapid growth, *O. edulis* faces threats from overfishing, habitat loss, and competition with non-native species like *M. gigas* (Beck et al., 2011). Despite being brought to Italy in the 1970s small-scale Pacific oyster aquaculture has only lately begun in Italy, particularly along the Adriatic coastline, the Po delta, Sardinia, Sicily, and the Liguria region (Mosca et al., 2021).

1.4. Habitat suitability model

Models that are referred to as resource selection function or habitat suitability models, forecast the geographical distribution of species (Guisan and Zimmermann, 2000; Manly et al., 2002; Pearce and Boyce, 2006). These models are increasingly attracting more attention. Their use has been particularly encouraged to address conservation issues, such as managing species distribution, assessing ecological impacts of various factors (e.g., pollution, climate change), risk of biological invasions, or endangered species management, since they frequently aid in both understanding species niche requirements and predicting species potential distribution (Scott et al., 2002, Guisan and Thuiller, 2005; Hirzel, 2006).

Prediction of species distribution is an important element of conservation biology. Management for endangered species (Sanchez-Zapata and Calvo, 1999), ecosystem restoration (Mladenoff et al., 1997), species re-introductions, population viability analyses (Akc¸akaya and Atwood, 1997) and human-wildlife conflicts (Le Lay et al., 2001) often rely on habitat-suitability modeling. Multivariate models are commonly used to define habitat suitability and, combined with geographical information systems (GIS), allow one to create potential distribution maps (Guisan and Zimmermann, 2000; Hirzel, 2006).

Researchers may determine the geographic regions most suited for a species' survival and expansion by using habitat suitability models, which offer crucial insights into the ecological requirements of species. Because it allows for targeted interventions to be done in places that have the highest potential of sustaining fragile species, this skill is essential for conservation efforts (Guisan et al., 2013). These models are being used more and more in practical conservation tasks, such as determining which habitats should be protected first, restoring ecosystems, and creating corridors to lessen habitat fragmentation (Elith and Leathwick, 2009). To determine areas of vital habitat, forecast population viability, and evaluate the possible effects of habitat loss or modification, for example, management strategies for endangered species frequently depend on habitat suitability models.

Applications of habitat suitability models extend to ecosystem restoration, species reintroductions, and human-wildlife conflict management, where models help predict suitable sites for reintroduction, forecast population growth, and evaluate potential conflicts (Le Lay at al.,2001). In places like distant or severely fragmented ecosystems, where direct monitoring is difficult or impossible, their utilization is crucial. Habitat suitability models give resource managers a proactive approach to conservation planning by offering predictive skills that allow them to foresee and reduce biodiversity problems before they become fully apparent.

In summary, habitat suitability models are essential tools in conservation biology that support a variety of conservation goals, from predicting the effects of climate change and planning interventions for invasive species to evaluating extinction risk and directing restoration (Elith and Leathwick, 2009). The use of these models has proven crucial for sustainable and well-informed conservation efforts, especially in light of the intricate problems that ecosystems face today.

1.4.1 Maximum Entropy Modeling

The maximum entropy (MaxEnt) by Phillips et al. (2006), approach has been extensively employed to simulate the distribution of species (Elith et al., 2011; Merow et al., 2013). By determining the probabilities that suggest the most dispersed distribution or the closest to uniformity (i.e., maximum entropy), this technique seeks to estimate the distribution probability of the species being studied (Phillips et al., 2006; Phillips and Dudík, 2008). Due to the absences being projected from the background (thus the term "pseudo-absences"), it is feasible to work with less information, such as presence-only datasets, thanks to this assumption. MaxEnt, like other modeling approaches, is grounded in the ecology principle that the distribution of a target species (response variable) is influenced by other variables, often environmental parameters. By generating a set of modifications for the predictors, MaxEnt offers a way to measure this link (Elith et al., 2011; Phillips et al., 2006). The modeling program finds an appropriate collection of these mathematical modifications, or features, using six categories: hinge, threshold, quadratic, linear, product, and automated.

The regularization value controls the degree to which the projected distribution probability closely resembles the observed data for each of these feature groups. It may be altered to improve model fit and smooth it out. In order to produce an estimate as near to the likelihood that a species is present depending on the environment as is practicable, MaxEnt then provides three different forms of output: raw, cumulative, and logistic (Elith et al., 2011; Phillips et al., 2006; Phillips and Dudík, 2008). The collection of tiny non-negative probabilities given to every pixel in the research area is known as the "raw" result. These raw probabilities are used to produce the "cumulative" and "logistic" results. The estimated likelihood of species occurrence is represented by the first one, which is derived by cumulatively accumulating raw output values that are subsequently rescaled between 0 and 1. Rather, the logistic output is the result of the logistic function converting the raw numbers into probabilities between 0 and 1. The latter is the most well-thought-out of the three since it is simpler to use and understand across a range of research settings.

Additionally, the program performs several statistical studies that help assess the model that is produced. In particular, it uses a jackknife test of regularized training gain and computes ROC curves to examine the contributions of the variables to the model (Phillips, 2017). Although MaxEnt is user-friendly and has shown encouraging outcomes in presence-only studies, caution is necessary (Yesson et al., 2012). The program specifically assumes that there is no sampling bias and that the data supplied for calibration and validation are independent. The input data must be carefully selected to provide a solid background dataset that may be used to extract pseudoabsences and perhaps dispersed occurrences in the sample region (Phillips, 2009).

1.4.2 Environmental degradation

Oyster habitats are essential to preserving marine biodiversity, enhancing water quality, and stabilizing coasts, especially in delicate coastal areas like the Venice Lagoon. In addition to providing ecosystem services including nitrogen cycling and habitat for other marine animals, these habitats sustain ecological processes (Beck et al., 2011). However, pollution, climate change, and human activity pose serious challenges to oyster reefs and beds in these regions. The worldwide problem of protecting coastal ecosystems in the face of environmental degradation is best shown by the Venice Lagoon, a distinctive but increasingly damaged ecosystem (Solidoro et al., 2010).

One of the main causes of the degradation of oyster habitats in the Venice Lagoon is still pollution. Heavy metals, excess nutrients, and other pollutants are introduced via industrial discharge, agricultural runoff, and untreated municipal trash, among other sources of pollution. Eutrophication is the most prevalent ecological problem in coastal lagoons (Bricker et al. 2007). The strain from the growing population of the surrounding land region is the primary source of the issue in Venice Lagoon. In addition to the increased amounts of nutrients from growing agricultural activity needed to meet the demands of the expanding population, domestic and industrial discharges of nitrogen and phosphorus from nearby urban centers also enter the lagoon (Çevirgen et al., 2020). The local economy and oyster business may be impacted by the buildup of heavy metals like for example lead and cadmium in oyster tissues, which can also be harmful to human health. (Ravera, 2000).

Climate change intensifies these challenges, adding additional stressors to the already fragile oyster habitats in the lagoon. According to Sehlinger et al. (2019), oyster life is impacted by localized genetic adaptations, environmental variables including food supply and hydrology, and physical factors like temperature and salinity change. The main stressors affecting oyster survival are generally thought to be low salinity and high sea temperatures (Muranaka and Lannan, 1984). Sea temperature and salinity are important factors in regulating oyster survival, even if measuring their effects is difficult (Sehlinger et al., 2019). Oyster development and mortality have been demonstrated to be adversely affected by low salinity exposure, and these effects are exacerbated when high temperatures and low salinity levels are coupled (Rybovich et al., 2016). Additionally, studies have shown that higher temperatures can cause oyster hematocyte death, whereas lower salinity levels have been linked to oyster cellular mortality (Gagnaire et al., 2006). Additionally, high temperatures cause changes in the body composition of oysters, such as higher saturated fatty acid and lower protein content, which puts additional stress on the oyster (Flores-Vergara et al., 2004).

The stresses on oyster ecosystems have been exacerbated by human activities such as tourism, coastal development, and dredging for navigation. Specifically, dredging changes the hydrodynamics of the lagoon, reduces appropriate substrates for oyster attachment, disrupts sedimentation patterns, and destroys habitat (Solidoro et al., 2010). Restoring oyster habitats' biological functions and halting future deterioration require addressing the combined effects of pollution, climate change, and human activity in the Venice Lagoon. The goal of this study is to investigate these urgent environmental concerns in order to provide guidance for sustainable management strategies that give oyster population restoration and conservation first priority. By examining the distinct effects and interactions of these elements, this thesis will advance knowledge about how to prevent habitat loss and carry out successful conservation initiatives in threatened coastal areas.

1.4.3 Oyster population decline

Oyster population declines in the Venice Lagoon are a growing ecological concern that reflects the complex interactions between human activity and environmental changes. The lagoon was known in the past for its abundant oyster populations, especially the native species *O. edulis*, and its varied marine life. This alarming trend highlights the urgent need for understanding the contributing factors to ensure the sustainability of this vital ecosystem.

The loss of oyster populations in the Venice Lagoon has been attributed to a number of important issues, including habitat deterioration, which has had a significant influence on the natural habitats where oysters flourish, mostly as a result of coastal development and pollution. Oyster production will be impacted directly by climate change, as well as indirectly by a variety of changes in precipitation patterns, salinity, and the intensity of extreme weather events (Brugère and De Young, 2015; Frost et al., 2012; Neokye et al, 2024). One of the biggest issues facing the twenty-first century is climate change (Neokye et al, 2024). According to De Bruijn and van Dijk (2006), one of the main factors influencing the majority of oyster species and their distribution worldwide is climate change. Furthermore, climate change has several effects on oyster habitats. Oysters use less food when temperatures are higher than ideal because they are less effective at filtering (Matsuyama et al., 1999). According to the United States Environmental Protection Agency (USEPA), rising water temperatures, excessive nutrient levels, and climate-related changes may all be factors in the occurrence and severity of harmful algal blooms (HABs). By obstructing sunlight and reducing the oxygen needed by other creatures, including those that directly or indirectly contribute to oyster food supplies, the excessively prevalent toxic algal blooms can impact aquatic ecosystems (U.S. EPA, 2014). Furthermore, oyster mortality may rise as a result of hazardous algal blooms becoming more frequent or severe (Pierce and Henry, 2008).

With anomalous death events of *Magallana gigas* as adults observed in the majority of French oyster-producing regions, which are often connected to the oyster herpes virus, oyster output has decreased in recent years (Martenot et al. 2011). The bacterial pathogens *Vibrio splendidus* and *V. aestuarianus* are now believed to be more important in mortality events, and the severity of losses may be influenced by pathogen-to-pathogen interactions and the development of some resistance by previously infected stocks (Vezzulli et al. 2015; Petton et al. 2015). Similar deaths have recently occurred in the UK, Jersey, Ireland, and the Netherlands (Renault 2011; Bostock et al, 2016). To effectively restore oyster populations and protect the ecological integrity of the Venice Lagoon, conservation methods must take into account the intricate relationships between these variables.

1.5 Objectives of the study

This study's main goal is to use the Maxent (Maximum Entropy) modeling technique to evaluate the spatial distribution and habitat appropriateness for the Pacific oyster (*Magallana gigas*) in the Venice Lagoon. Effective management and conservation methods for *Magallana gigas*, an invasive species with significant ecological and economic implications, depend on knowledge of its preferred habitats and potential range. To achieve this objective, the study is structured around several key aims:

1. Identify Environmental Predictors by ascertaining which environmental factors—such as temperature, salinity, and water depth—have the most bearing on forecasting the lagoon's habitat suitability for *Magallana gigas*.

2. Spatial Analysis of Habitat Suitability creates maps of *Magallana gigas'* possible habitats to identify places that are either at danger of colonization or would benefit from focused management initiatives.

3. Temporal Variability and Model Robustness, by using monthly averages of important environmental elements to analyze variations over time in habitat suitability throughout various months. This will guarantee a thorough comprehension of how the seasons affect the appropriateness of the habitat.

4. Direct Conservation and Management, based on findings on habitat appropriateness, offer data-driven suggestions for the management of

Magallana gigas in the Venice Lagoon, including the identification of priority sites for monitoring and possible conservation measures.

2. Materials and Methods

2.1 Study area

The study was conducted in Venice Lagoon especially between the lagoon's middle and southern regions. Substantial seawalls surround the majority of the islands in the lagoon, also referred to as coastal barriers or flood barriers, in this region. Furthermore, wooden pilings define the boundaries of each lagoon's canal. According to seatemperature.info, the average temperature of the lagoon system is 9.8°C in the summer and 25.2°C in the winter, with an average salinity between 33–34 psu (seatemperature.info).

Figure 3. The locations of the 30 seawall's samples taken from Lusenzio, Pellestrina and Lido.

The intertidal assemblages developing atop seawalls and pilings were the primary focus of the investigation. The subtidal sections of these formations were too murky and too dim for us to sample. Seawalls and pilings from several lagoon sections were sampled to reflect the various degrees of human pressure that the lagoon experiences. Lusenzio, Lido di Venezia, and Pellestrina. Seawalls, signified high, medium, and low degrees of urbanization, respectively (Figure 3. All locations had concrete seawalls, except for three (Pellestrina sites 14, 15, 16; Figure 3.) where seawalls were constructed out of limestone. The geographical distribution of *Magallana gigas* was likewise strongly correlated with depth, with oysters being found mostly in locations within the intertidal zone (ranging from +32 cm to -27 cm AMSL) with the optimum locations for colonization and survival are those shielded from wave exposure (Teschke et al., 2020).

According to Figure 4., Chioggia's urbanization levels were categorized as high, medium, and low for pilings in the lower and higher central lagoon zones. Several places were selected to reflect varying degrees of urbanization and human impacts on maritime environments. With a population density of 4,672 people per km^2, Lido di Venezia is thought to be more urbanized than Pellestrina, which has a population density of 3,391/km² (https://www.citypopulation.de/).

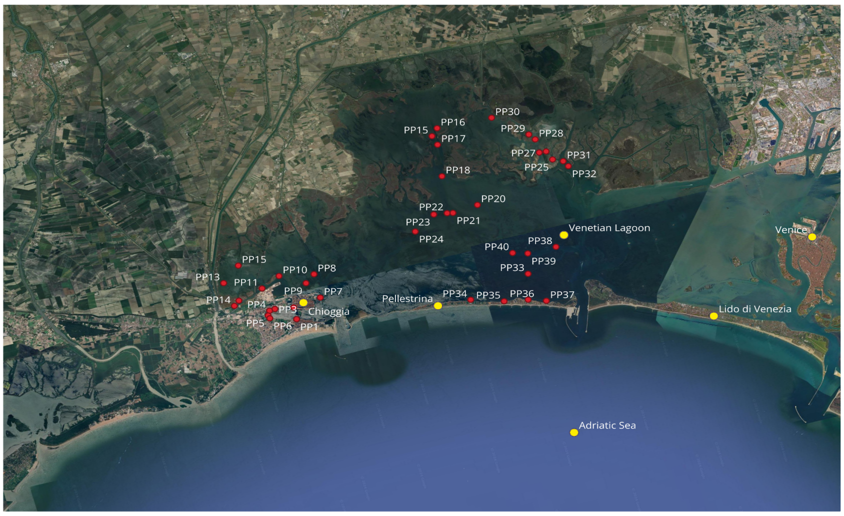

Figure 4. The locations of the 42 pilings samples taken from Chioggia, Lower Central Lagoon (LCL), and Upper Central Lagoon (UCL) represent high, medium, and low urbanization levels.

Regarding the different piling locations, Chioggia is most urbanized due to its vicinity to harbours and human populations, whilst the upper central lagoon area was the least urbanized due to its proximity to salt marshes. Lusenzio, the confined area inside the town of Chioggia, is where some of the analyzed pilings were located (6 pilings total). The level of urbanization in the lower central lagoon is regarded as medium urbanized. In the lower central lagoon area, the majority of the pilings were located in front of Pellestrina, which is urbanized, but not as urbanized as Chioggia (Figure 4).

For every kind of structure, a sample of the intertidal assemblages was taken from the earlier work by Kassar (2023). For sea walls, ten samples were taken at ten distinct locations for every degree of urbanization, for a total of thirty samples. 42 samples—14 for the high urbanization level, 12 for the low urbanization level, and 16 for the medium urbanization level—were randomly selected for the pilling in order to cover the whole research region. 72 samples in all were therefore gathered for the investigation. According to Kassar (2023), seawalls were sampled from April 18 to April 28, 2023. A 10 × 10 cm quadrat was used for each sample, and it was positioned at random on the seawall's intertidal zone. All living things within the quadrat were scraped out and stored in the refrigerator for subsequent analysis. Species were recognized to the lowest taxonomic level feasible and sorted within a day or two of collections.

Figure 5. Field sampling of pilings (Kassar, 2023).

2.2 Oyster's allometries

2.2.1 Analysis of oyster's allometric relationship

Oyster specimens (*Magallana gigas*) were collected from intertidal zones within the Venice Lagoon for a one-year period from April 2020 to April 2021, a period selected to capture seasonal growth conditions for the species (Fabioux et al., 2005). Sampling sites represented varied salinity and temperature levels, using the Venice Lagoon model in 2019, providing a key environmental context for the study of allometric relationships (Helm et al., 2004).

Figure 6. The locations of 8 oyster samples on Venice Island.

The collected oyster samples were placed in plastic bags, each labeled with a unique code for each station. We took allometric measurements on each specimen, including shell length (L), width (W), height (H), and both wet and dry mass (M). These measurements were recorded using Vernier calipers with a precision of 0.01 mm for length and an electronic balance accurate to ±0.01 g for mass, ensuring measurement consistency (Gosling, 2003).

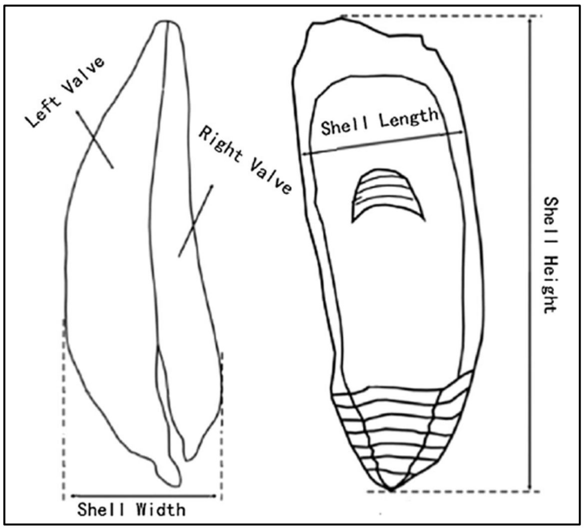

Figure 7. Diagram showing method of measuring the height, length, and width of oyster valves (Dong et al,. 2018).

We weighed each oyster to determine its Total Wet Weight. Following this, we opened the oysters and separated the tissue from the shell. To measure Tissue Wet Weight, we randomly selected tissues from 30 oysters per bag and placed them into sample containers.

Figure 8. Process of *Magallana gigas* allometric measurements.

After removing the soft tissues, we weighed the sample container with the oyster tissue and then subtracted the weight of the empty container to obtain the tissue weight. The shells were dried at 60°C for 48 hours to obtain their dry weight, following standard protocols in oyster allometry studies (Bayne & Newell, 1983). After drying, we weighed the tissue again and subtracted the empty container's weight to calculate the Total Dry Tissue Weight. This procedure was carried out at ISMAR-CNR (Institute of Marine Sciences of the Italian National Research Council) in Venice under the supervision of Dr. Guarneri.

Figure 9. Processed of weighting and drying *Magallana gigas*.

2.2.2 Oyster Conditional Index

The oyster condition index (CI) was calculated to evaluate the physiological status and health of *Magallana gigas* specimens from the Venice Lagoon. This index is widely used in bivalve research as it indicates the relationship between tissue mass and shell volume, reflecting factors such as food availability, temperature, and salinity, which can significantly impact oyster health. According to Lawrence and Scott (1982), the Conditional Index can be calculated with equation 1:

$$\text{Conditional Index} = \left(\frac{\text{dry weight of meat (g)}}{\text{shell cavity volume (ml)}}\right) \text{X } 100$$

The conditional index provides an indication of the energy reserves of the oyster, reflecting its overall fitness and growth potential in a given environment. The result of the Conditional Index helps in understanding variations in oyster health and can be linked to environmental factors affecting oyster growth, also provides a standardized ratio that facilitates comparisons across specimens and sampling periods (Lucas & Beninger, 1985).

2.2.3 Statistical analysis

To analyze the allometric relationship between shell size and mass, a power-law model with equation 2:

$$\text{Power} - \text{Law Model}$$

$$\mathrm{M} = \mathrm{a}\ \cdot \mathrm{L}^{\mathrm{b}}$$

was applied where M represents mass, L represents shell length, a is the scaling coefficient, and b is the allometric exponent (Powell & Stanton, 1985).

To express the linear relationship between height (Y) and length (X) of *Magallana gigas* may be understood from the results of the linear regression analysis. The regression equation 3:

Linear Regression

$$Y = a + bX$$

represents this relationship, where a, the intercept, denotes the estimated height when length is zero, establishing a baseline for the height variable. The slope b indicates the rate of height increase per unit increase in length, thus providing an assessment of proportional growth (Lucas & Beninger, 1985). Regression analysis was conducted in MATLAB (version R2023a).

2.3 Habitat suitability model with MaxEnt Modeling approach

2.3.1 Environmental variables

To accurately model the habitat suitability for *Magallana gigas* (Pacific oyster) in The Venice Lagoon, three key environmental variables were selected based on their biological relevance to oyster distribution and growth: bathymetry, salinity, and temperature. We used the average yearly temperature and salinity, average monthly temperature and salinity values along with the 99% and 1% percentiles, to analyze the typical and extreme environmental conditions at intertidal depths in the Venice Lagoon and align with Oyster Conditional Index (CI). This alignment enabled analysis of environmental influences on oyster presence and condition, as previous research indicates that factors like temperature and salinity can significantly affect oyster metabolic processes and, consequently, condition (Shumway, 1996). These associations were evaluated for the year included in the research using the Venice Lagoon model created by Dr. Marco Bajo (ISMAR-CNR Venice). With the use of this model, the effects of seasonal changes in temperature and salinity as well as other environmental factors on the *Magallana gigas* over the research period could be thoroughly assessed. The study primarily focused on circumstances in 2019, a year preceding the sampling activities behind the data presented in this work, and Dr. Marco Bajo provided the data for the model.

The SHYFEM (Shallow Water Hydrodynamic Finite Element Model), created by ISMAR-CNR in Venice, Italy, was used to construct the dataset, which was referered to year 2019 Time. This dataset, created on September 2024, was intended to examine residency durations and other hydrodynamic processes for the Venice Lagoon during 2019. The SHYFEM model, well-known for its use in shallow and intricate water systems, offered information on important environmental factors necessary to comprehend circulation patterns, water renewal, and ecosystem dynamics in general.

Figure 10. Bathymetry depth profile in meter of the Venice Lagoon (ISMAR,2024).

Both MATLAB and Python were used in this study's data processing because of their strong analytical and computational powers. For effective data manipulation and analysis, MATLAB was used because of its sophisticated matrix operations, data visualization, and numerical techniques. These tasks were enhanced by Python's flexible modules, including x-array and pandas, which were crucial for managing big datasets, especially for the study of time series and environmental variables. When MATLAB and Python were used together, extensive data processing was made possible, improving accuracy and enabling in-depth investigation of environmental factors in the model simulations.

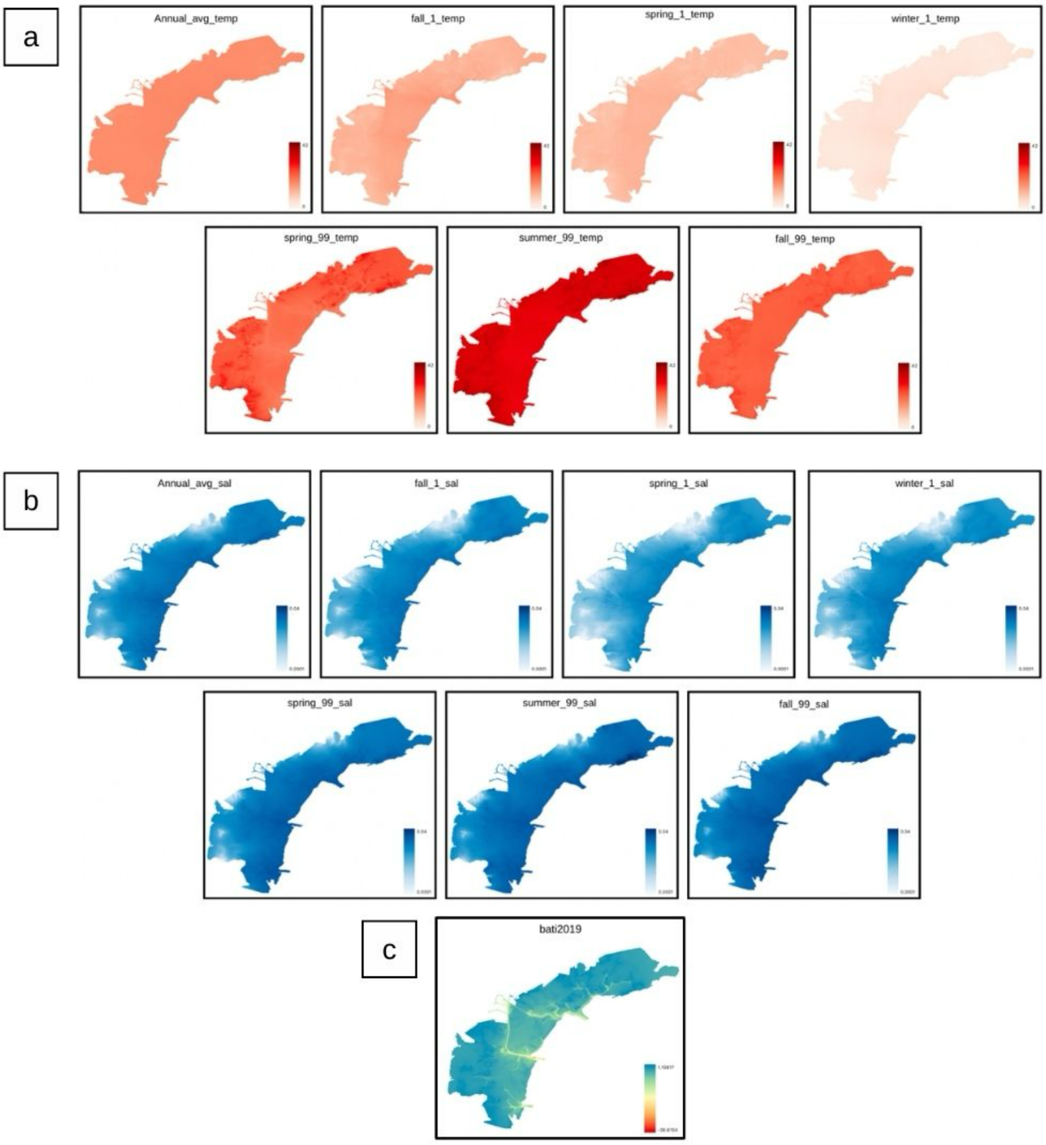

Figure 11. Spatial distribution of selected environmental variables used for mapping and habitat suitability modeling of *Magallana gigas* in the Venice Lagoon (11a. salinity, 11b. temperature, 11c. bathymetry).

Table 1. List of 15 variables used for habitat suitability model development for *Magallana gigas* in the Venice Lagoon.

Code	**Variable**	**Unit**	**Min**	**Max**
annual_avg_temp	Annual average temperature	Degrees Celsius	13.177994	17.539104
annual_avg_sal	Annual average salinity	PSU	0.0000999924	0.03678876
spring_1_sal	1st percentile of monthly salinity on spring	PSU	0.0000999959	0.035887962
fall_1_sal	1st percentile of monthly salinity on fall	PSU	0.0000999886	0.03685644
winter_1_sal	1st percentile of monthly salinity on winter	PSU	0.0000999853	0.036044179
spring_1_temp	1st percentile of monthly temperature on spring	Degrees Celsius	5.25684593	12.3271289
fall_1_temp	1st percentile of monthly temperature on fall	Degrees Celsius	7.12212599	18.1580683
winter_1_temp	1st percentile of monthly temperature on winter	Degrees Celsius	1.10863703	8.30833262
spring_99_sal	99th percentile of monthly salinity on spring	PSU	0.0001	0.03877779
summer_99_sal	99th percentile of monthly salinity on summer	PSU	0.0001	0.04650721
fall_99_sal	99th percentile of monthly salinity on fall	PSU	0.0001	0.04003595
spring_99_temp	99th percentile of monthly temperature on spring	Degrees Celsius	15.2595964	35.2829063
summer_99_temp	99th percentile of monthly temperature on summer	Degrees Celsius	26.7428177	42.4870926
fall_99_temp	99th percentile of monthly temperature on fall	Degrees Celsius	18.787367	29.6583074
bati2019	Bathymetry of the Venice Lagoon	Meter	2.2121317	-35.851997

2.3.2 Sampling bias and spatial filtering

Oyster presence data obtained in the field may be subject to sampling bias because of a variety of human and environmental disturbances. The accuracy of the model may be jeopardized by such biases, especially in cases when the sampling points are not evenly distributed. To overcome these problems, sampling should ideally follow a planned regime that minimizes bias and covers the whole spatial breadth of the research region (Barry et al., 2006). Zero spatial inaccuracy is still difficult to achieve in real-world datasets, nevertheless.

To mitigate this, a spatial filter allowed for the preservation of just one presence point per grid cell and had a grid size of 2000 m × 2000 m. By dividing occurrences equally throughout the research region, this method served to lessen the impacts of spatial autocorrelation and provide a more trustworthy dataset.

2.3.3 Modeling and mapping

We predicted the possible appropriate habitat of *Magallana gigas* in the Venice Lagoon using Maxent software, version 3.4.1. A probability distribution model is the end result of Maxent, a machine learning program based on maximum entropy that takes as input a set of environmental characteristics specific to a certain place as well as presence-only data (Merow et al. 2013).

Following the results of the mapping and distribution models, we evaluated the model's performance. Most modeling work generates distinct datasets for model validation by dividing the field data into training and test/validation datasets (Guisan and Zimmermann, 2000). The extremely small number of samples, however, may make it impossible to separate data sets for validation when modeling endangered and vulnerable species. To investigate the significance of individual variables for model prediction, as suggested by Pearson et al. (2007), we employed a Jackknife approach in this work.

For three distinct scenarios—without variables, with only one variable, and with all variables—Jackknife forecasts the significance of the environmental covariates based on area under curve (AUC) gains. In addition, we assessed the model's goodness of fit using the AUC technique and the receiver operating characteristic (ROC). The model that performed the best was the one with the greatest AUC value. AUC, which ranges from 0 to 1, compares the model's predictive performance to random prediction (Phillips et al., 2006). For interpretational purposes, the final suitability map's values, which ranged from 0 to 1, were further divided into four classes: 0–0.2 indicates unsuitability, 0.2–0.4 indicates low, 0.4–0.6 indicates moderate, and 0.6–1 is high suitability (Ansari and Ghoddousi, 2018).

3. Results

3.1 Allometric relationship

3.1.1 Power Law of *Magallana gigas* Allometric Relationship

Several physiological and morphological characteristics of *Magallana gigas* scale reliably with oyster body size, according to our analysis of the power-law allometric relationships in this species. In particular, shell length, weight, and volume measurements follow a consistent allometric scaling pattern with a power-law relationship and exponents for bivalves. This relationship demonstrates how oysters' metabolic and structural needs rise nonlinearly with growth, reflecting the species' physiological limitations and environmental adaptations.

In addition to being biologically significant, our analysis reveals that these scaling exponents shed light on the resource allocation and growth dynamics of oyster populations. These results can help develop oyster growth prediction models, which are crucial for managing aquaculture and conducting ecological evaluations.

Table 2. Power Law fitted value.

Parameter		Fitted Value
Spring	a	0.00039534
	b	2.9502
Summer	a	0.0010423
	b	2.7094
Fall	a	0.00051921
	b	2.8457
Winter	a	0.0035051
	b	2.3025

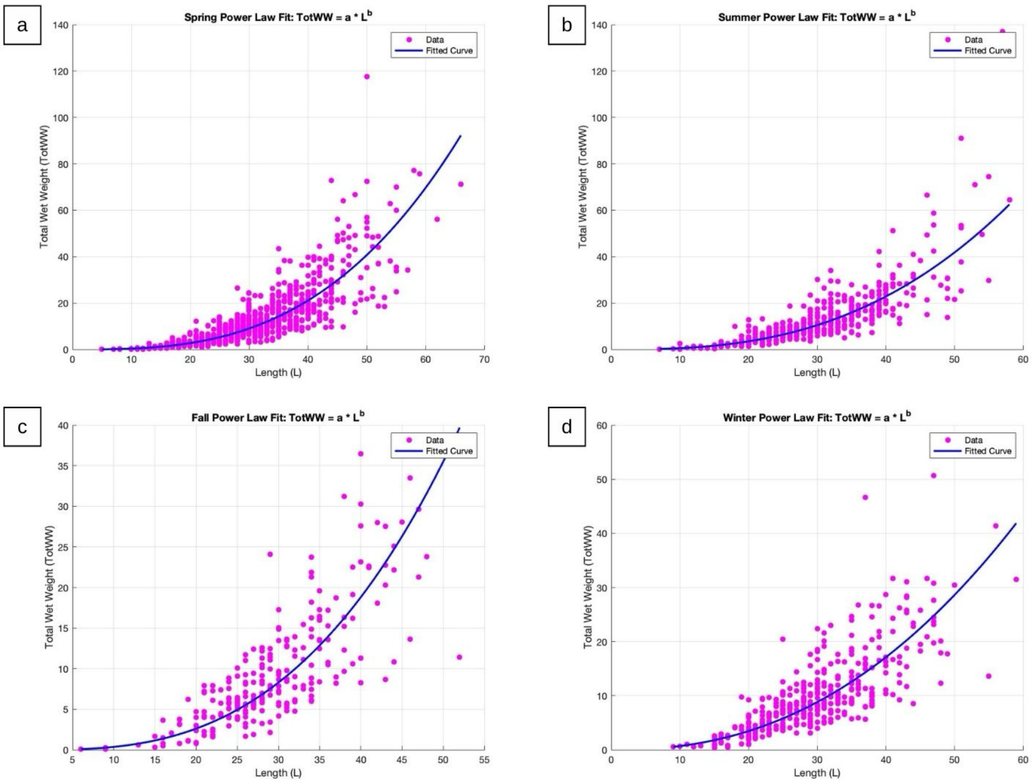

Figure 12. The power law of *Magallana gigas* is categorized based on the season (12a. Spring, 12b. Summer, 12c. Fall, and 12d. Winter).

3.1.2 Linear regression of *Magallana gigas*

The link between *Magallana gigas'* height (Y) and length (X) may be understood from the results of the linear regression analysis. The regression equation captures this relationship, where a, the intercept, represents the estimated height when the length is zero, establishing a starting point for the height variable. The slope b reflects the rate at which height increases per unit increase in length, providing a measure of proportional growth. In the context of *M. gigas*, a positive b suggests that as the oysters grow in length, their height increases accordingly, implying consistent growth patterns across size classes. This relationship is key for understanding how physical dimensions correlate in these oysters, as well as for assessing how environmental or physiological factors might influence growth trends. Thus, this linear model offers a valuable foundation for interpreting size metrics in *M. gigas* and supports further analysis of growth variations across different habitats or conditions.

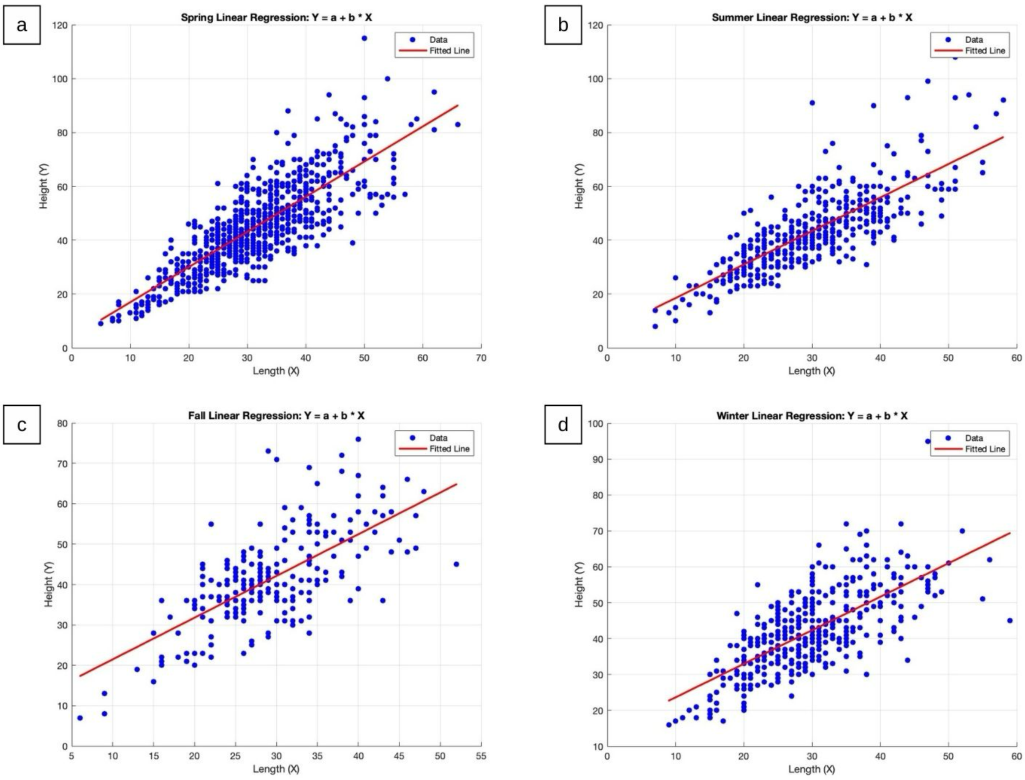

Figure 13. Linear Regression of *Magallana gigas* is categorized based on the season (13a. Spring, 13b. Summer, 13c. Fall, and 13d. Winter).

Table 3. Linear Regression

Season	Predictor	Coefficient (Estimate)	Standard Error (SE)	t-value	p-value	Sig.
Spring	Intercept	3.9086	1.1081	3.5274	0.00044567	***
	Slope	1.3053	0.03392	38.481	2.7346.E-178	***
Summer	Intercept	6.0764	1.4438	4.2087	3.1084.E-05	***
	Slope	1.2446	0.046283	26.891	2.6505.E-95	***
Fall	Intercept	11.141	2.1722	5.1289	6.1855.E-07	***
	Slope	1.0326	0.07221	14.301	1.2927.E-33	***
Winter	Intercept	14.301	1.4911	9.5903	1.154E-19	***
	Slope	0.93404	0.048042	19.442	4.5499E-59	***

3.2 Environmental parameters

3.2.1 Intertidal temperature in Venice Lagoon

We created several visualizations for the whole Venice Lagoon with intertidal temperature analysis in 2019 to show the monthly, seasonal, and overall temperature trends in this dynamic environment.

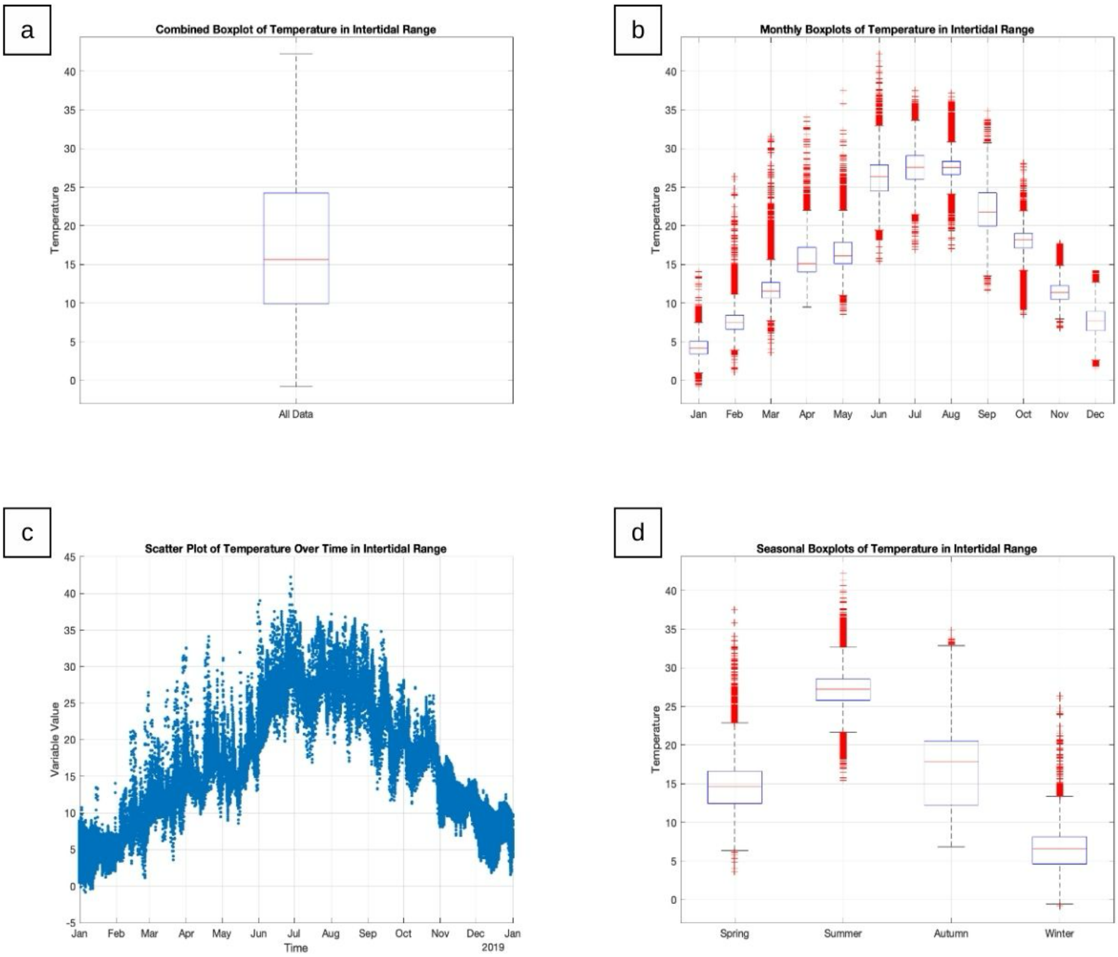

Figure 14. The intertidal temperature in Venice Lagoon 2019 (14a. Combined boxplot of temperature, 14b. Monthly boxplot of temperature, 14c. Scatter plot of temperature over time, and 14d. Seasonal boxplot of temperature).

Magallana gigas in this area are subject to environmental fluctuations, as demonstrated by a combined boxplot of intertidal temperatures that showed the central trend and variability throughout the year. A more thorough understanding of temperature variability for each month was offered by monthly boxplots, which showed notable seasonal variations with warmer summer temperatures peaking and lower winter values. The extent and regularity of temperature variations within the intertidal zone were further highlighted by the scatter plot of intertidal temperatures, which displayed individual data points across time. Comparisons between spring, summer, fall, and winter were made possible by seasonal boxplots, which showed clear seasonal trends that are essential to comprehending the environmental stresses on oyster habitats. These findings offer a thorough picture of the temperature conditions in the Venice Lagoon's intertidal zones, offering important new information about the potential effects of temperature variability on oyster physiology and distribution.

3.2.2 Intertidal salinity in Venice Lagoon

We developed a number of visualizations to show monthly, seasonal, and overall salinity patterns for the Venice Lagoon's intertidal salinity analysis in 2019. To demonstrate the salt levels oysters are exposed to in this habitat, a combined boxplot of intertidal salinity values showed the overall distribution and year-round variability of salinity.

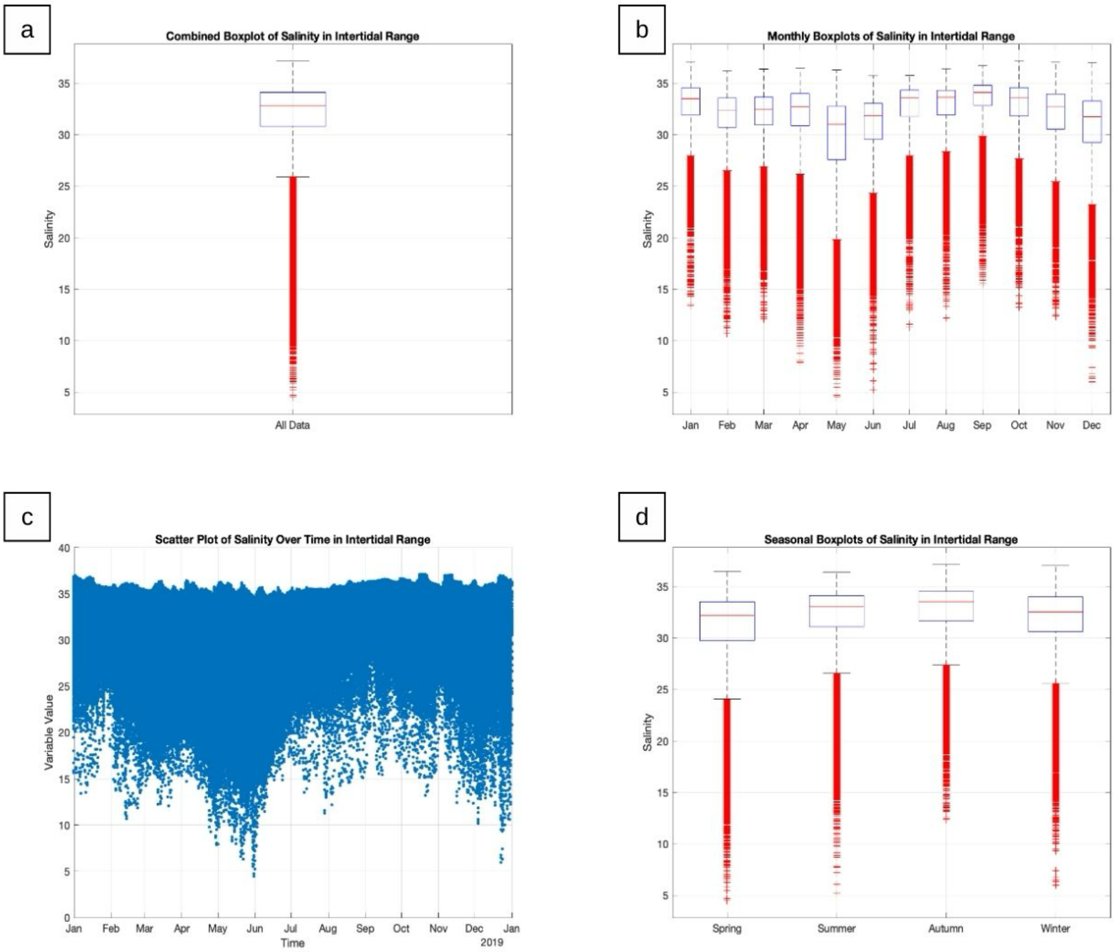

Figure 15. The intertidal salinity in Venice Lagoon 2019 (15a. Combined boxplot of salinity, 15b. Monthly boxplot of salinity, 15c. Scatter plot of salinity over time, and 15d. Seasonal boxplot of salinity).

A thorough analysis was given via monthly boxplots, which revealed clear variations with lower salinity values in the cooler, wetter months and higher values during warmer or drier months, possibly as a result of greater evaporation and lower rainfall. Individual data points were shown over time in an intertidal salinity scatter plot, providing information on daily fluctuations and sporadic extreme values. Comparisons between spring, summer, fall, and winter were made possible by seasonal boxplots, which showed distinct seasonal patterns that might have an effect on oyster physiology and habitat selection. This thorough understanding of the salinity dynamics in the intertidal zone of the Venice Lagoon supports more research on oyster dispersal and resilience to salinity fluctuations by illuminating the environmental conditions that oysters face.

3.3 Habitat suitability model

3.3.1 Importance of environmental variables within each model

The receiver operating characteristic (ROC) curve for the identical data, once more averaged across the replicate runs, is shown in the following image. It should be noted that predicted area, not true commission, is used to define specificity. For the replicate runs, the standard deviation is 0.067 and the average test AUC is 0.792.

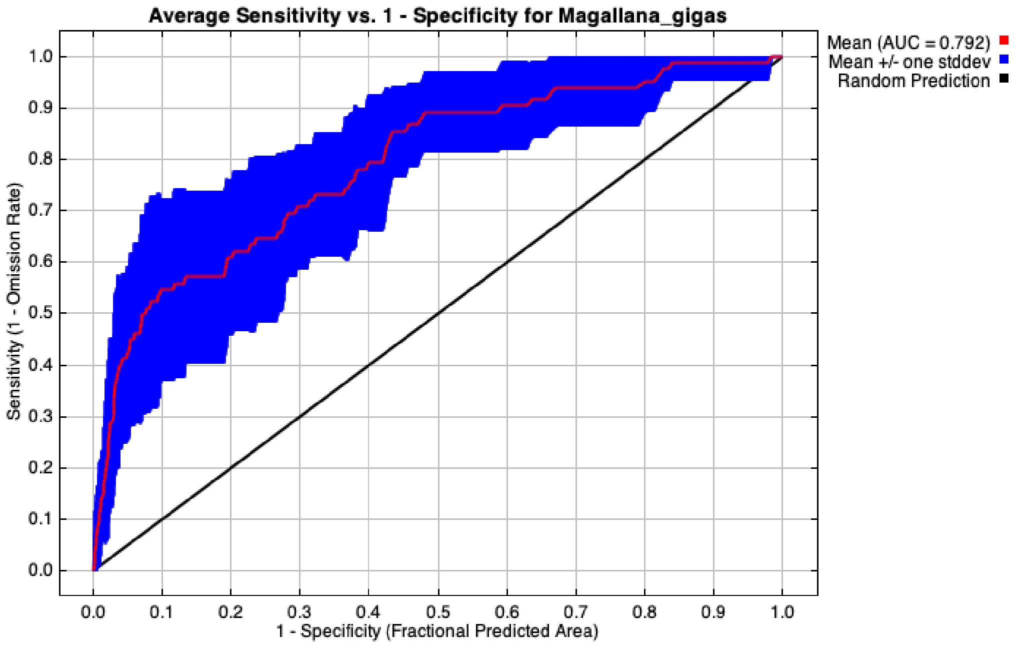

Figure 16. Receiver operating characteristic (ROC) curve for *Magallana gigas*.

With an AUC score of 0.792, the Maxent model provided a good prediction of the possible appropriate habitat for *Magallana gigas*. According to the internal Jackknife test of the Maxent model, "spring_99_temp" and "annual_avg_salinity" were the variables that were most important in predicting habitat suitability (Fig.16). The most useful information was contained in these two environmental factors because they showed the greatest gain when compared to the others. Likewise, the model's response to each variable yielded results that were consistent with the internal Jackknife test. Spring_99_temp (28.9%), annual_avg_salinity (17.4%), fall_1_salinity (10.5%), annual_avg_temp (10%), and spring_1_temp (9.7%) were the factors that contributed the most in the habitat suitability model.

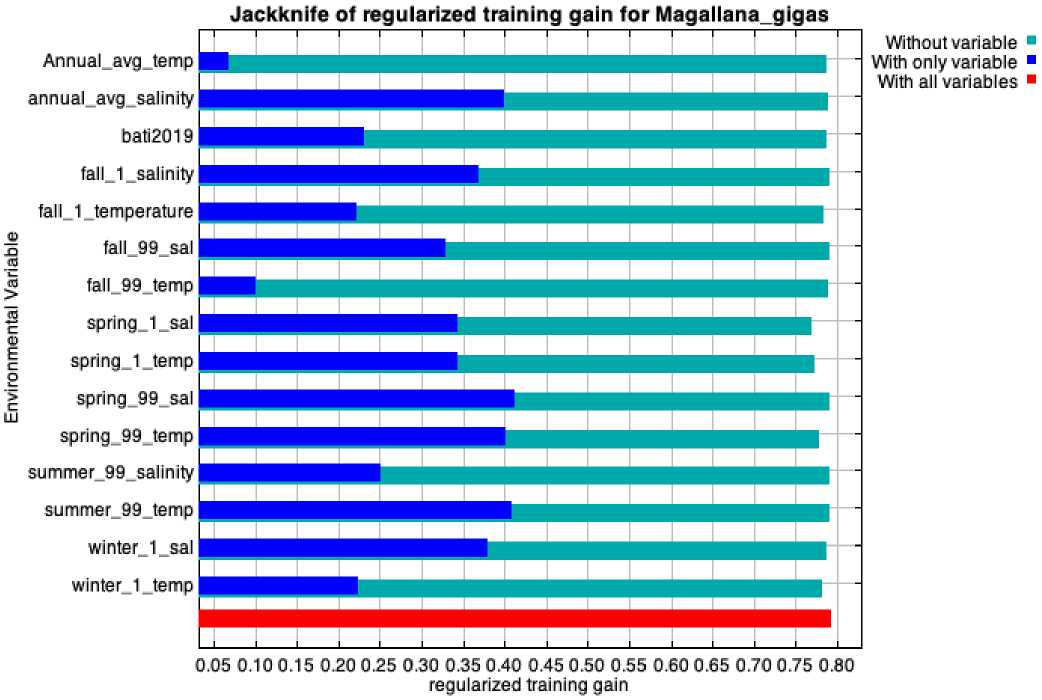

Figure 17. Jackknife of regularized training gain of *Magallana gigas* in Venice Lagoon.

Estimates of the relative contributions of the environmental variables to the Maxent model are provided in the following table. The initial estimate is calculated by adding the rise in regularized gain to the contribution of the related variable in each iteration of the training procedure, or subtracting it if the change in the absolute value of lambda is negative. The values of each environmental variable on training presence and background data are permuted at random for the second estimate. The training AUC decline that results from reevaluating the model on the permuted data is displayed in the table, and normalized to percentages. When the predictor variables are associated, variable contributions should be evaluated cautiously, just like with the variable jackknife. Values shown are averages over replicate runs.

Table 4. Environment variable percent contribution for *Magallana gigas* in Venice Lagoon.

Variable	Percent contribution	Permutation importance
spring_99_temp	28.9	32
annual_avg_salinity	17.4	0.6
fall_1_salinity	10.5	0.1
annual_avg_temp	10	2.4
spring_1_temp	9.7	26
spring_1_sal	6.5	4.2
spring_99_sal	5.3	6.2
fall_99_temp	4.9	1.2
winter_1_temp	2.8	8.2
fall_1_temperature	1.8	7.5
winter_1_sal	1.2	7.1
summer_99_temp	0.5	0
bati2019	0.3	2.1
fall_99_sal	0.2	2.3
summer_99_salinity	0	0

3.3.2 Potential distribution of *Magallana gigas* in Venice Lagoon

The MaxEnt-derived projected distributions were extended around the Venice Lagoon (Figure 18).

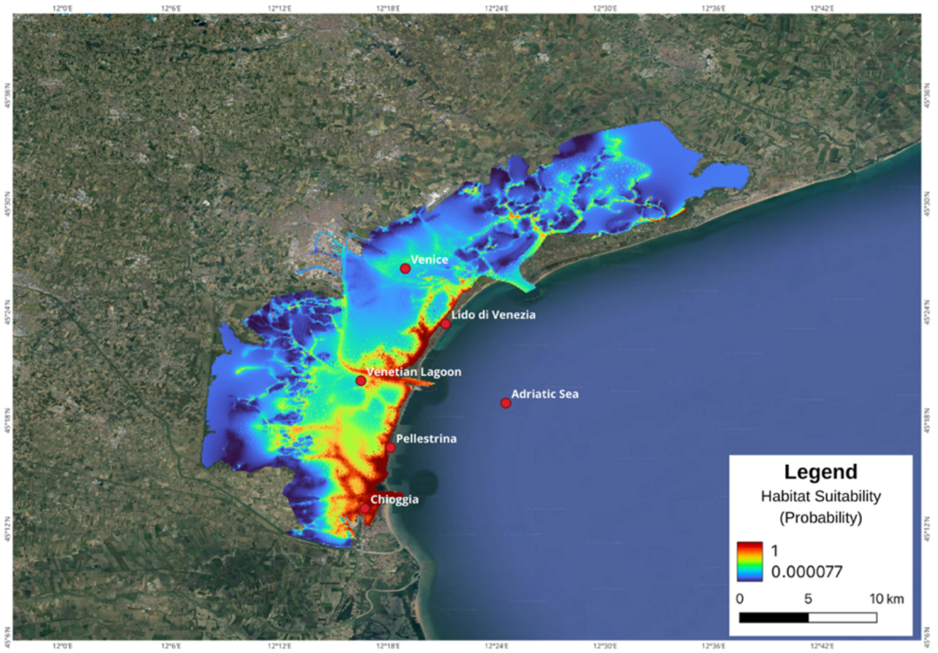

Figure 18. Predicted potentially suitable habitats of *Magallana gigas* in the Venice Lagoon using Maxent modeling.

Overall, the probabilities of occurrence were higher in the Chioggia and Lower Central Lagoon (LCL) area and were more or less spread on the Upper Central Lagoon (UCL). The *Magallana gigas*, as expected, had a widespread predicted distribution (Fig 18.) which is however more concentrated on the inner seaside part of the lagoon.

4. Discussion

4.1 Allometries for *Magallana gigas*

The need for sustainable aquaculture is increasing worldwide, which has accelerated research into new species with great ecological resilience and adaptation. The Pacific oyster, or *Magallana gigas*, has become a viable option because of its capacity to flourish in estuarine and intertidal environments, its quick development, and its resistance to a variety of environmental factors (Troost, 2010; Shatkin et al., 1997). After being introduced as a sustainable substitute for native species due to overfishing and environmental changes, *M. gigas*, which was first cultivated in Asia, is now extensively grown in Europe and North America (Boudry et al., 2003). Beyond its function in seafood production*, M. gigas* enhances water quality and promotes biodiversity through its capacity to construct reefs, which contributes to ecosystem services (Ruesink et al., 2005).

In addition to its potential in aquaculture, *M. gigas* has significant biological effects in non-native settings, frequently resulting in intricate relationships with nearby marine ecosystems. Through its reef-building tendency, *M. gigas* can drastically change the structure of an area once it is introduced. This improves local biodiversity by giving different aquatic creatures a place to live and a substrate (Troost, 2010). However, this structural change can also lead to competition for resources with native species, which can sometimes cause changes in the composition of the community (Boudry et al., 2003). Because oysters are effective filter feeders that can lower phytoplankton levels and improve light penetration, the introduction of *M. gigas* may have an impact on nutrient cycling and water clarity in the Venice Lagoon, where environmental variability is significant (Ruesink et al., 2005).

Building on *Magallana gigas'* ecological responsibilities and habitat appropriateness, power-law analyses of allometric relationships provide insight into the species' growth patterns and resource allocation, which is crucial for efficient management and sustainable aquaculture techniques. The growth connection between the Total Wet Weight (TotWW) and length (L) of *Magallana gigas* in the Venice Lagoon is described by a power law model (Table 2), and the table shows seasonal fluctuations in fitted values for parameters a and b. The scaling relationship between these two dimensions is revealed by the power law relationship, where b denotes the kind of scaling. Whereas a sub-linear scaling ($b < 1$) suggests that total wet weight grows more slowly than length, a super-linear scaling ($b > 1$) suggests that total wet weight grows more rapidly than length. Seasonal variations in b values demonstrate how environmental conditions affect oyster growth patterns throughout the year.

When examining the power law connection between *Magallana gigas* length (L) and total wet weight (TotWW) across seasons, a consistent super-linear scaling is seen in each case, with b values approaching 3. According to this near-cubic scaling, the oysters' total wet weight nearly triples in proportion to their length as they become longer. Given their high scaling exponent, bigger oysters appear to be accumulating body mass at a remarkably high pace in comparison to their linear development. This pattern highlights an effective development strategy, whereby gaining weight in relation to length may benefit resistance in dynamic intertidal settings, energy storage, and reproductive production. The non-linear character of biological growth—where an organism's biomass builds substantially faster than its linear dimensions—is reflected in a super-linear relationship. In line with findings in other bivalve species, the discovery of this scaling trend across the spring, summer, fall, and winter seasons suggests a robust and season-independent growth dynamic for *Magallana gigas* (Bayne and Newell, 1983). Larger individuals tend to have bigger energy reserves, which further promotes quicker weight gain relative to size. These growth patterns are usually associated with changes in metabolic processes and energy storage (Lucas and Beninger, 1985).

Assessing the growth efficiency and biomass output of shellfish populations in ecological and aquaculture research requires a knowledge of the scaling relationship between length and weight (Lucas and Beninger, 1985; Bayne and Newell, 1983). Because larger oysters may accumulate biomass more quickly, which might have an impact on harvest dates and marketability, the observed super-linear scaling in *Magallana gigas* highlights the significance of size-based management tactics in oyster agriculture. The steady super-linear trend also supports the widely held belief that as marine mollusks, such as oysters, grow larger, they accumulate more biomass due to a combination of genetic and environmental factors, including temperature and food availability (Sehlinger et al., 2007).

Modeling and forecasting the growth and productivity of oyster populations depends on this connection, and such results offer important information for managing oyster farms and wild populations efficiently. Additional investigation may be necessary to determine if the observed super-linear growth is consistent across different ecological situations and for additional bivalve species, as well as how environmental factors such as temperature and salinity affect this scaling behavior.

4.2 Environmental Variables

An overall overview of temperature variations within the intertidal range can be found in the boxplot of annual temperature (Fig 14a.). The majority of the recorded temperatures are moderate, according to the median temperature, which is located in the middle of the data range. Extreme values are occasionally represented by outliers. Outliers both above and below the interquartile range indicate occasional extreme temperature events, indicating a significant level of variability in the data. This comprehensive investigation reveals a broad range of temperatures, which may affect the intertidal species' year-round tolerance levels.

With noticeable variations between the summer and winter seasons, the monthly boxplots (Fig 14b.) show a clear seasonal trend in temperature. The period from June to August makes this the warmest time of year. This suggests that summer temperatures are higher. This unpredictability might be a sign of exposure to extreme heat episodes, which could affect intertidal creatures like oysters physiologically. The range of temperatures significantly drops from December to February, which is indicative of colder and more consistent weather. Because these temperature fluctuations can have a substantial impact on species behavior, growth, and survival, this cyclical pattern of temperature changes emphasizes how crucial it is to take seasonality into account when interpreting environmental data in the intertidal region.

The seasonal trend in temperature variability within the intertidal range is highlighted in the daily temperature scatter plot (Fig 14c.) throughout the entire year. This figure unequivocally demonstrates how temperatures rise gradually starting in the early spring and peak in midsummer, around July and August, before progressively falling towards winter. Additionally, the scatter pattern points to daily temperature variations, particularly in the warmer months when the range of values is wider. Intertidal animals live in a dynamic thermal environment, with potentially difficult conditions during the hottest summer months due to the high temperatures, as seen by the seasonal and daily temperature variations.

The seasonal boxplots (Fig 14d.), which divide temperature data into spring, summer, fall, and winter categories, provide more evidence of the trends that have been noticed. Both the high average temperatures and the frequency of severe temperature events are reflected in the summer's highest median temperature. Winter, on the other hand, indicates more stable and colder weather because it has the lowest median temperature. With moderate median temperatures and fluctuation, spring and fall are considered transitional seasons as the climate changes from cooler to warmer months and vice versa. These seasonal patterns show how different temperatures affect intertidal species, which may have an impact on their rates of metabolism, cycles of reproduction, and general survival.

The thermal environment in the intertidal range is influenced by significant seasonal variations in temperature, but salinity patterns show a distinct but no less significant dynamic. A crucial layer to our research of habitat appropriateness and species resilience in this zone is added when we comprehend how salinity changes with the seasons and months, giving us more insight into the environmental circumstances intertidal creatures confront. An overview of salt levels over the year is given by the combined boxplot of salinity in the intertidal region (Fig 15a.). The majority of the data is densely grouped above and below the median salinity level, which is around 32.9 PSU. The interquartile range exhibits moderate change, suggesting that the intertidal zone's salt levels are comparatively constant. A considerable number of outliers, with values as low as 5 PSU, are seen below this range, indicating sporadic occurrences of rainfall or freshwater intrusion e.g. due to riverine and tide effects. A rather steady marine salinity environment with sporadic interruptions probably caused by external variables like precipitation or freshwater runoff is shown by this constant median level and lower outliers.

A thorough temporal representation of salinity variations throughout the year may be seen in the scatterplot of daily salinity over time (Fig 15c.). Salinity does not go above normal marine levels, as indicated by the steady upper barrier at about 35 PSU. The frequency and breadth of lower salinity levels, however, sharply rise during warmer months, with daily variations occasionally falling noticeably. These dips are a sign of recurring freshwater intrusions into the intertidal zone, which are probably caused by riverine discharges or rainfall. According to the scatter plot, intermittent freshwater pulses are a regular occurrence, even though the intertidal zone typically experiences marine salinity.

According to this study, the intertidal range's salinity data shows a constant median value of about 32.9 PSU over all months and seasons, indicating a mostly stable saline environment. The statistics also show notable monthly and seasonal variations. This salinity fluctuations indicate that intertidal species—like oysters—are frequently subjected to varying salinity conditions, which may have an impact on their capacity to osmoregulate and the appropriateness of their habitat.

4.3 Maxent Modeling results

4.3.1 ROC and Jackknife

The Maxent model's prediction accuracy in locating appropriate habitats for *Magallana gigas* is revealed by the ROC curve displayed (Fig 16). The model performs significantly better than random prediction, which would have an AUC of 0.5, as indicated by the mean Area Under the Curve (AUC) value of 0.792 (Phillips et al., 2006; Elith et al., 2011). While values near 0.5 suggest performance comparable to random chance, an AUC near 1.0 implies great model accuracy (Elith et al., 2006). Although more/different environmental variables or model parameter modifications might improve accuracy, the model's AUC of 0.792, in this case, indicates that it has good prediction potential for habitat appropriateness (Merow et al., 2013).

The red line represents the mean ROC curve, capturing the model's overall sensitivity and specificity across runs. The blue shading around the mean line denotes one standard deviation, highlighting variability due to cross-validation splits or data uncertainty (Wenger & Olden, 2012). This variability band is essential for understanding the robustness of the model: while the central tendency is strong, some variation across validation samples suggests that there may be room to improve input precision or feature selection to ensure stable predictions (Hernandez et al., 2006). This ROC analysis indicates that the Maxent model performs well for *Magallana gigas*, affirming that environmental predictors such as temperature and salinity contribute valuable information for modeling its distribution (Phillips & Dudík, 2008). However, further calibration of the model might yield even higher predictive accuracy, which could improve conservation or management efforts for this species (Franklin, 2010).

Significant variations in the contributions of different predictors to the model are shown by the variable importance analysis (Table 4). With the largest contribution of 28.9% and a permutation significance of 32, the spring_99_temp variable is very noticeable and has a significant impact on the model's output. With a 9.7% contribution and a permutation significance of 26, spring_1_temp comes in second. Other significant variables include spring_99_sal, which contributes 5.3% and has a permutation importance of 6.2, and annual_avg_salinity, which contributes 17.4% but has a very low permutation importance of 0.6. On the other hand, variables like summer_99_temp and summer_99_salinity, which have respective contributions of 0.5% and 0%, have very little permutation relevance. These results are supported by the jackknife analysis, which quantifies the model's sensitivity to each variable by methodically eliminating them. Fall_1_salinity and fall_99_sal are much less important variables in model prediction than spring_99_temp and spring_1_temp. The permutation relevance is generally supported by the jackknife findings (Fig 17.), which emphasize the significant environmental factors while indicating that certain predictors, such as specific seasonal salinities and temperatures, have a negligible impact on the model.

The geographical distribution of *Magallana gigas* and similar bivalve species is severely limited by salinity and temperature since these factors directly affect physiological processes necessary for survival, development, and reproduction. Salinity largely influences oyster distribution; optimal development typically occurs within a moderate range, whereas exceptionally high or low salinity levels might result in physiological stress or even mortality. Higher salt levels, often seen in coastal and estuary habitats with limited freshwater inflow, are advantageous for *M. gigas* because they provide consistent osmotic conditions that are adverse for many competing species (Troost, 2010). Oysters tend to expand to locations where salinity remains within a stable, favorable range since their establishment and growth are often limited in areas with low or fluctuating salinity (Boudry et al., 2003).

According to prior research, the 25–35 PSU range is best for *M. gigas* development and reproduction (Shatkin et al., 1997). This geographical trend is consistent with research by Troost (2010), who observed that *M. gigas* formed robust populations in regions with intermediate salt levels in estuary systems throughout Europe. Additionally, *M. gigas* can withstand fluctuations, but drastic salinity changes, such as those seen close to freshwater inputs or in isolated lagoon parts, may make it more difficult for it to survive and spread, according to Colombo and Turchini (2021). The distribution of the species is also greatly influenced by temperature, which affects reproductive time and metabolic activity. Habitat suitability peaked at mean temperatures of 15 to 25°C. Conversely, winter extremes may limit northern ranges, while overly hot summer temperatures can cause physiological stress, particularly in the intertidal zones. The appropriateness of the habitat is also influenced by the depth of the water; moderate depths offer the best circumstances for balancing nutrient availability and light penetration.

According to our suitability model (Fig 18.), the best habitats for *M. gigas* are found in the Chioggia and Lower Central Lagoon areas of the Venice Lagoon, especially those with steady salinity and moderate depth. More than 70% of the lagoon's expected appropriate habitat is located in this center region, supporting historical accounts of oyster settlements in comparable estuarine habitats (Ruesink et al., 2005). On the other hand, locations with significant depth changes or substantial salinity variability have lower habitat appropriateness, indicating that *M. gigas* may find it difficult to develop there.

Lower habitat suitability was also detected by the model mostly in sections of the lagoon with large salinity or temperature swings caused by freshwater intake and seasonal variations. This is consistent with Jackson (1994) findings that *M. gigas* needs consistent temperature and salinity levels to grow throughout time. Although the lagoon's environmental variables capture the main elements affecting the spread of *M. gigas*, habitat suitability is also impacted by non-climatic factors including substrate type and competition with other species (like mussels). As long as temperature and salinity are within their tolerance range, *M. gigas* appears to have some flexibility in selecting its environment.

The suitability model for *M. gigas* may overestimate possible habitats since Maxent forecasts the basic niche rather than the actual niche (Kumar and Stohlgren, 2009). Notwithstanding these drawbacks, our model provides a useful instrument for directing conservation and management initiatives in the Venice Lagoon. In particular, where *M. gigas* may support ecosystem services like habitat structuring and water filtering, the high-suitability regions that have been identified might be the focus of conservation or aquaculture initiatives. Since *M. gigas* is a crucial ecological filter feeder, its distribution is probably going to have an effect on biodiversity, nutrient cycle, and local water quality.

5. Conclusion

The thorough examination of *Magallana gigas* in the Venice Lagoon produced several important conclusions that shed light on the distribution, growth, and ecological dynamics of the species. The oysters favor particular environmental parameters that enable their development and survival because environmental factors like temperature and salinity vary significantly across the lagoon. The distribution of oysters was shown to be strongly correlated with seasonal and annual averages of salinity and temperature, with some regions exhibiting consistent salinity and mild temperature variations being more conducive to oyster growth.

The variables affecting oyster population dynamics were brought to light by applying MaxENT modeling to data from 70 sample locations spread over 15 environmental layers. The distribution and abundance of *Magallana gigas* were shown to be significantly influenced by temperature variations, yet the species also flourishes in regions with steady salinity levels.

Furthermore, the growth patterns of *Magallana gigas* showed a power-law allometric connection. These discoveries not only advance our knowledge of the ecology of *Magallana gigas* but also offer vital information for the species' management and cultivation in the Venice Lagoon. They highlight the necessity of closely monitoring environmental conditions to guarantee the long-term viability of the species.

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Appendix

Analysis of omission/commission

The test omission rate and projected area are displayed in the following figure as a function of the cumulative threshold, averaged across the replicate runs. Due to the specification of the cumulative threshold, the omission rate ought to be around the anticipated omission.

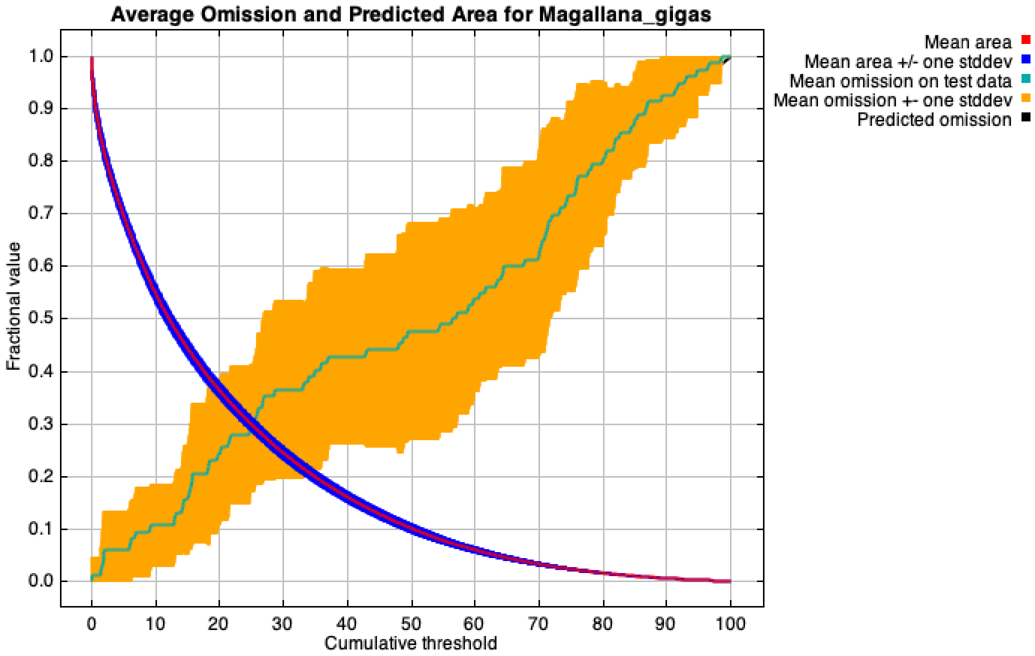


Figure 1. Average omission and predicted area for *Magallana gigas*

The following picture shows the results of the jackknife test of variable importance. The environmental variable with the highest gain when used in isolation is spring_99_sal, which therefore appears to have the most useful information by itself.

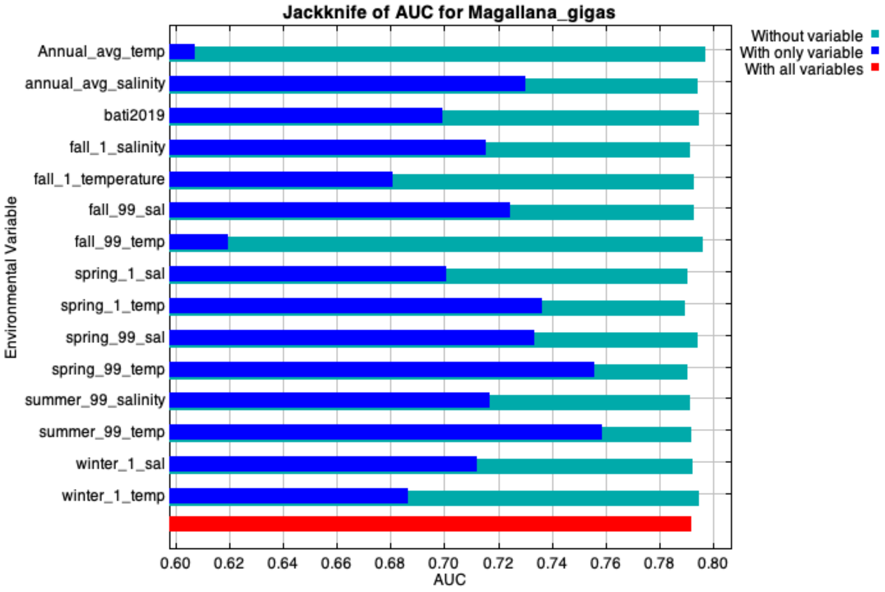


Figure 2. Jackknife of AUC for *Magallana gigas*

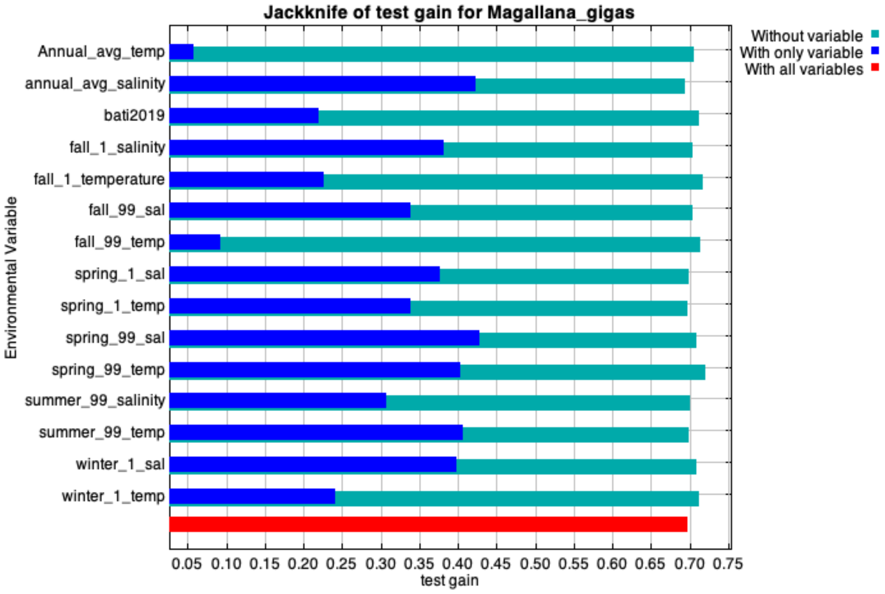


Figure 3. Jackknife of test gain for *Magallana gigas*

Picture of the model

The point-wise mean, standard deviation, minimum, maximum, and median of the ten output grids.

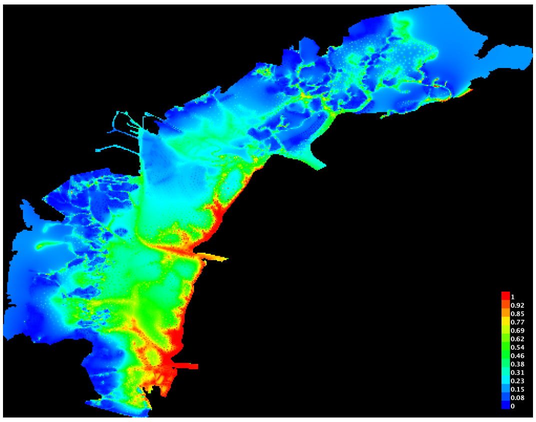


Figure 4. Picture of the mean model of the ten output grids.

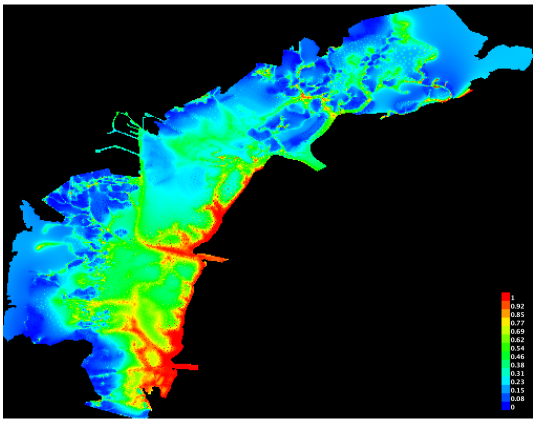


Figure 5. Picture of the maximum model of the ten output grids.

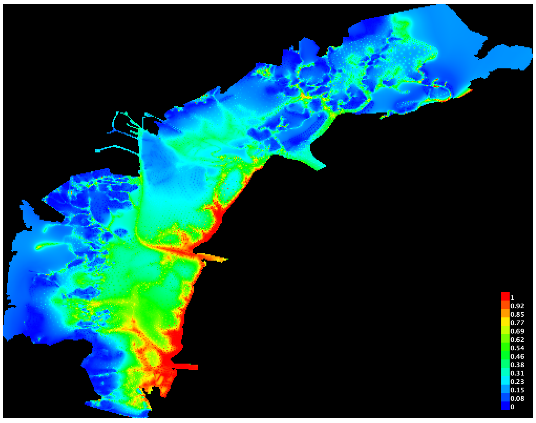


Figure 6. The median model of the ten output grids.

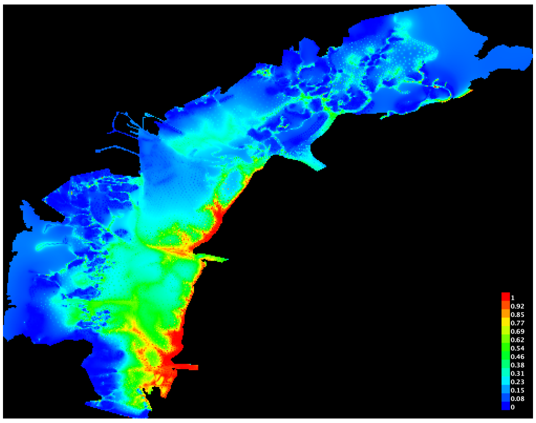


Figure 7. The minimum model of ten output grids.

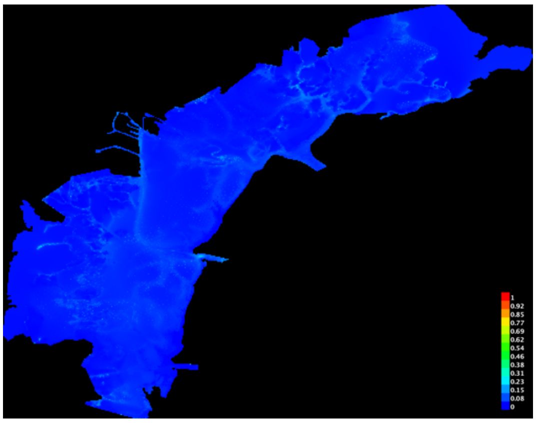
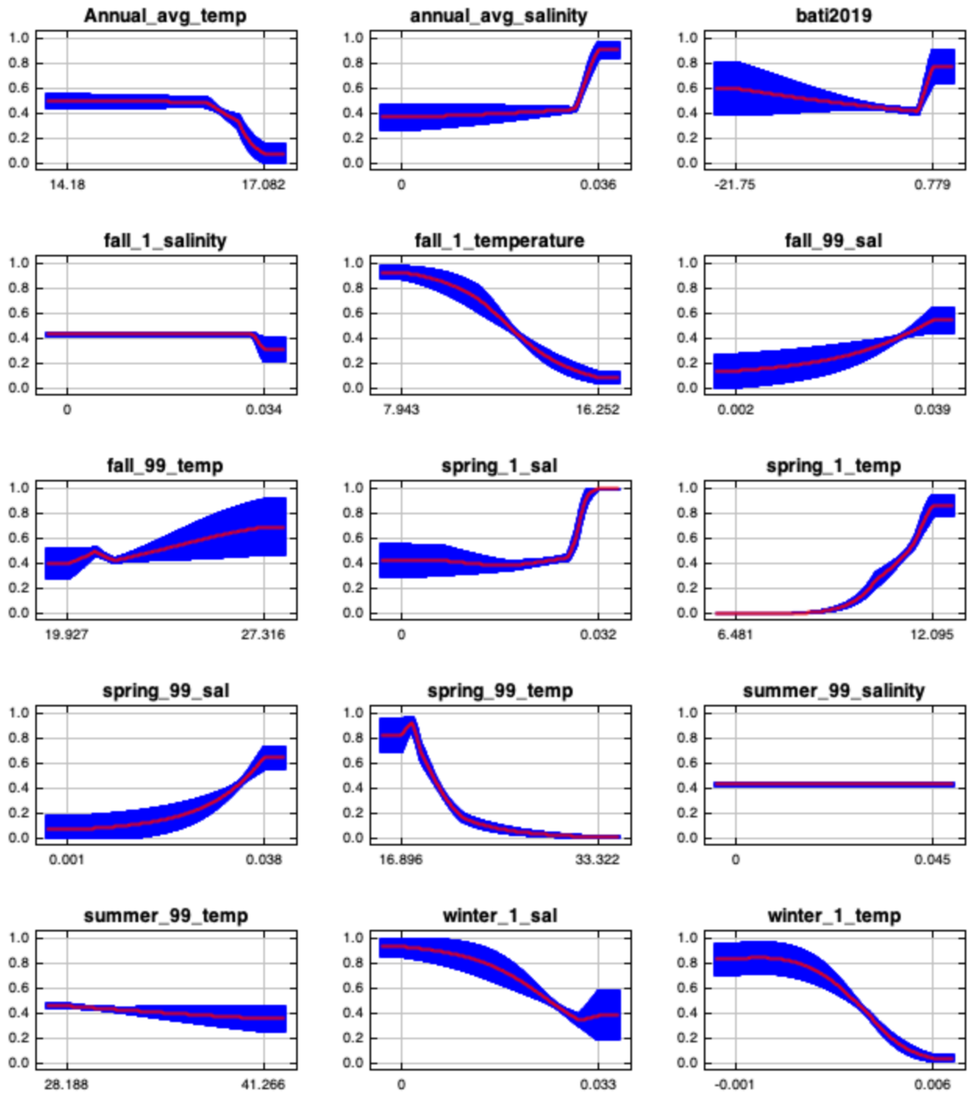


Figure 8. The standard deviation model of the ten output grids.

Response curves

The impact of each environmental variable on the Maxent forecast is displayed by these graphs. The graphs illustrate how, while maintaining the average sample value for all other environmental factors, the estimated probability of presence varies when each variable is changed. To view a bigger representation of a response curve, click on it. Because the model may rely on the correlations in ways that are not visible in the curves, it might be challenging to understand the curves if your variables are highly linked. Stated differently, the curves illustrate the marginal impact of altering a single variable, whereas the model may benefit from altering groups of variables together. The graphs display the mean +/- one standard deviation and the mean response of the ten replicate Maxent runs (red). (blue, two shades for categorical variables).



Each of the following curves, in contrast to the marginal response curves above, represents a distinct model—that is, a Maxent model made using just the relevant variable. The dependency of expected appropriateness on the chosen variable as well as dependencies brought about by correlations between the chosen variable and other factors are depicted in these figures. If there are significant correlations between the variables, they could be simpler to understand.