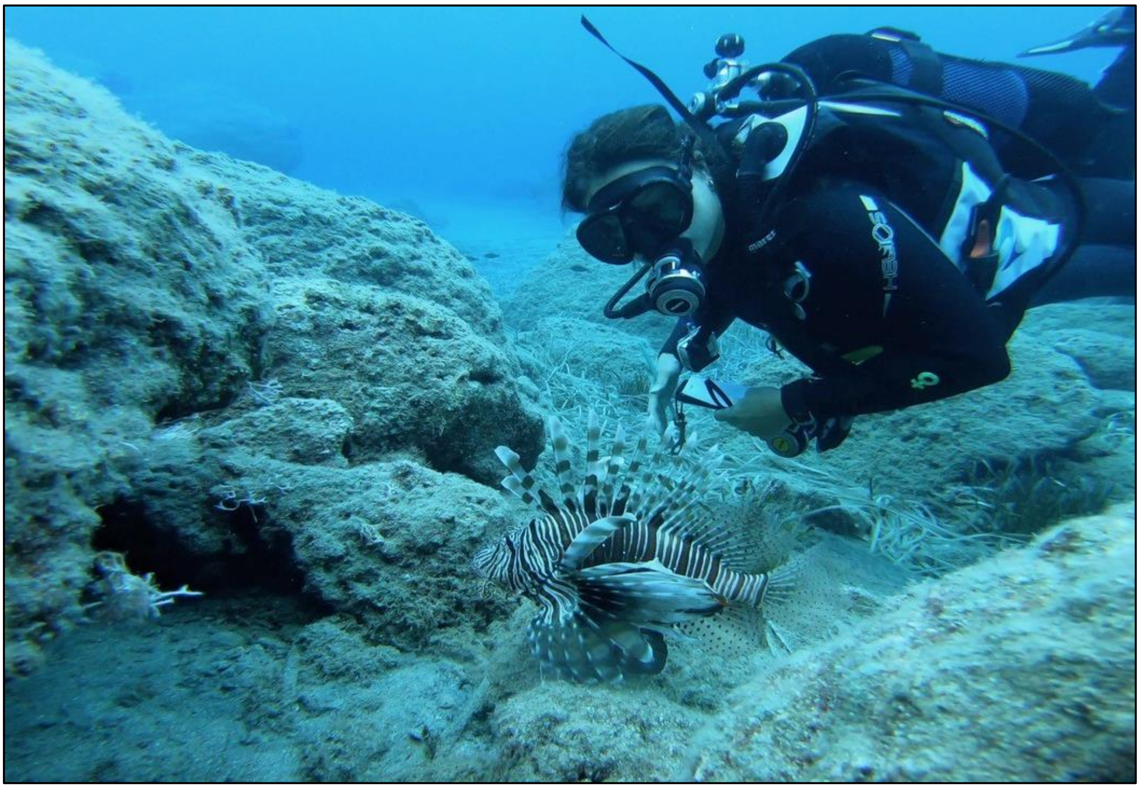
Lionfish Labyrinth: Untangling the relation between lionfish (*Pterois miles*) abundance, habitat complexity and prey biomass in the Mediterranean Sea



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June 2024

Abstract

Alien species are considered invasive once they establish in non-native areas, leading to the disruption of the local ecosystem. The adaptability of an invasive species to new habitats is thought to be a key factor in their invasion success. Lionfish (*Pterois miles*), native to the Red Sea, have successfully invaded the Mediterranean Sea, extending their range as far as Sardinia, Italy. With their high adaptability, rapid reproduction, and generalist carnivorous diet they exert significant pressure on the Mediterranean fish communities. Despite their habitat versatility, lionfish appear to prefer complex substrates in their Indo-Pacific invasive range. However, studies on the relationship between lionfish abundance and habitat characteristics in the Mediterranean are currently lacking. In this study, I examined the correlation between habitat complexity, prey availability and lionfish density at 12 sites along the southern coast of Crete, Greece. Habitat complexity was assessed using two methods, and both lionfish abundance and prey fish abundance were measured using Underwater Visual Census. Here, I show a positive correlation between lionfish abundance and habitat complexity. The interaction between complexity and prey biomass shows a trend, hinting that the effect of complexity on lionfish density decreases with increasing biomass. However, the two methods of measuring habitat complexity yielded substantially different results. I discuss the possible methodology of accurately measuring habitat characteristics. These findings highlight the importance of habitat complexity and prey availability on lionfish occurrence patterns, providing valuable insights into the ecology of this invasive species. This knowledge can inform targeted control strategies aimed at managing the rapid lionfish invasion.

Key words: Invasive species, habitat complexity, lionfish, Mediterranean Sea, *Pterois miles*

Introduction

When non-native or alien species colonize new areas, resulting in ecological and economic harm, they are classified as invasive (Valéry et al., 2008). The successful invasion of an alien species has been recognized as the second major cause of biodiversity loss worldwide (Vitousek et al., 1997). The introduction and establishment of invasive species pose a significant threat to the structure and function of marine ecosystems, such as the irreversible loss of species (Otero et al., 2013). Marine ecosystems are heavily impacted by climate change and anthropogenic pressures, with the introduction of invasive species aggravating these existing challenges. Rising temperatures and the increasing global trade amplify the invasion rates, further threatening underwater ecosystems worldwide (Papacostas et al., 2017; Young et al., 2017). Moreso, a global meta-analysis shows that the invasion of a predatory species in aquatic ecosystems accounts for a decline in species richness of 21% (Mollot et al., 2017). These invasive marine predators cause a decline in commercially important species (Grosholz et al., 2000), including populations of fish important for the aquarium trade (Ballew et al., 2016; Rocha et al., 2015). This reduction of herbivorous fish species leads to increases in macroalgae, which causes decreases in coral cover (Eaton et al., 2016; Lesser & Slattery, 2011). Consequently, human livelihoods are negatively impacted by these predatory invaders (Grosholz et al., 2000). Besides the direct economic impact on fisherman, all people that are directly and indirectly dependent on healthy, functioning marine ecosystems are affected by such an invasion of predatory marine species (Albins & Hixon, 2008). Effective management requires empirical data on ecological impacts, emphasizing the need for further research.

The devil firefish (*Pterois miles)* (Bennet, 1828), hereafter referred to as lionfish, is a species of lionfish native to the Indian Ocean and the Red Sea. It has recently invaded the Mediterranean Sea and is spreading at an alarming rate (Hall-Spencer et al., 2016). The first sighting in the region was documented in Israel in 1991 (Golani & Sonin, 1992). However, a notable increase in sightings began in 2012, with specimens found in Lebanon and Cyprus (Bariche et al., 2013; Jimenez et al., 2016), and later in Turkey in 2014 (Turan et al., 2014). Following this, the *P. miles* population rapidly expanded along the coasts of Cyprus and Turkey (Cemal et al., 2017; Turan, 2020), followed by the Aegean Sea (Dailianis et al., 2016; Turan & Öztürk, 2015). The invasion continued, with sightings reported on the Greek Ionian coast in 2020 (Phillips & Kotrschal, 2021; Vavasis et al., 2020) and reaching as far as Croatia, Malta, Sicily, and Sardinia by 2022 (Bottacini et al., 2024). Predictions indicate that the expansion will continue, potentially encompassing the entire Mediterranean Sea (Poursanidis et al., 2020). Genetic analyses suggest that *P. miles* likely invaded through the Suez Canal with few individuals, demonstrating their resilience even with low initial numbers (Bariche et al., 2017). Lionfish are considered among the most successful invaders (Rocha et al., 2015), especially following the rapid and successful invasion of the Western North-Atlantic and the Caribbean Sea by *P. miles* and the related *P. volitans* (Albins & Hixon, 2008; Isabelle M Côté et al., 2013; Côté & Smith, 2018; Whitfield et al., 2002). This invasion has caused great harm to native communities, causing decreases in biodiversity, fish abundance and biomass, with up to 97% loss of fish abundance where lionfish density was highest (Benkwitt, 2015). Subsequently, it has caused deterioration of reefs and socio-economic losses (Andradi-Brown, 2019; Côté & Smith, 2018). Given these consequences, concerns arise regarding about the current Mediterranean invasion, since it will likely have similar negative impacts on the ecosystem (Kletou et al., 2016). The public awareness regarding the issue remains low (Kleitou et al., 2019), and despite the necessity for EU legislation, progress in this area has been slow (Kleitou et al., 2021).

The high success rate of lionfish as invaders is generally attributed to several key life history traits and morphological characteristics (Isabelle M Côté et al., 2013). These traits include high fecundity, broad environmental tolerances, habitat adaptability, and a versatile, generalist diet (Côté & Smith, 2018; D'Agostino et al., 2020; Peake et al., 2018). Stomach content analyses in the Aegean Sea demonstrate their opportunistic carnivorous diet, which includes a wide variety of teleost fish and crustaceans (Batjakas et al., 2023). One study identified 167 different species of vertebrates and invertebrates in their stomachs, highlighting their broad dietary range and adaptability (Peake et al., 2018). Furthermore, lionfish exhibit local dietary specialization, further showcasing their efficiency as both generalists and specialists (Zannaki et al., 2019). They demonstrate one of the highest hunting successes recorded in animals, with a success ratio up to 88% (Green et al., 2011). Consequently, *P. miles* are reducing native species biomass and diversity, as indicated by preliminary assessments (Turan & Doğdu, 2022). Furthermore, *P. miles* exhibits a high fecundity, with Mediterranean females showing prolonged oocyte development and summer and autumn-limited spawning. The rising temperature due to climate change is likely to extend this period, enhancing fecundity and promoting the invasion (Mouchlianitis et al., 2022). The sex ratio in the Mediterranean population is in favour of females, heigthening overall species fecundity (Savva et al., 2020). The absence of natural predators in invaded areas further facilitates the increase in *P. miles* abundance (Cemal et al., 2017), as does the lack of competition from other lionfish species (Lee et al., 2011). Collectively, these factors make lionfish a significant threat to the Mediterranean ecosystem. The expanding invasion range underscores the urgent need for effective management, which relies on comprehensive research into lionfish biology and their ecological impacts (Periklis et al., 2021).

Thus far, several studies have examined the ecology of lionfish in the Mediterranean. Typically, lionfish are observed either individually or in small groups (Cure et al., 2012), sheltering in caves and crevices during daylight hours. They become active during dusk and dawn, when they venture onto the reefs to hunt (D'Agostino et al., 2020; Gavriel et al., 2021; McCallister et al., 2018). Notably, a significant variability was found among individuals regarding depth distribution and diel activity patterns (Gavriel et al., 2021). Despite this daily variation, lionfish exhibit high site fidelity (Bos et al., 2018; Phillips et al., 2024). A study conducted in Cyprus revealed that a substantial majority (98.7%) of lionfish sightings (n=202) occurred on hard substrates, including rocky reefs, caves, and artificial reefs, while a negligible proportion (1.1%) was observed on sandy substrates, with an even smaller fraction (0.2%) recorded in seagrass meadows (Savva et al., 2020). This suggests a strong preference for rocky substrates, though no further studies were done to elucidate the habitat characteristic preferences or complexity within these rocky reefs. In their native range, lionfish are habitat generalists, that typically inhabit various environments (Cure et al., 2012). In the Atlantic, some studies show a strong preference for complex habitats (Biggs & Olden, 2011; Claydon et al., 2012; Lee et al., 2011), while others show no positive correlation between habitat complexity and lionfish abundance (Anton et al., 2014). With their invasion into Mediterranean waters, it becomes imperative to understand their habitat adaptations and local preferences in order to gain insights into their occurrence patterns (Poursanidis et al., 2020). Both their native range and the invaded terrain in the Western Atlantic are coral dominated, while the Mediterranean is characterized by rocky reefs, which are inherently less structurally complex. This offers a unique opportunity to investigate the invasion ecology of this species in a different ecological context. Despite the pressing need, empirical data on the habitat preferences of *P. miles* in the Mediterranean remains scarce (Savva et al., 2020), posing a critical bottleneck in developing adequate management strategies (Tiralongo et al., 2022). Additionally, the role of resource availability in relation to habitat preferences has not been studied in the Mediterranean. Investigating these factors is crucial for understanding the mechanisms driving lionfish density patterns in their invasive range.

In this study, I investigate the correlation between lionfish abundance, habitat complexity and prey fish biomass. Specifically, I predict that lionfish density positively correlates with habitat complexity because complex habitats offer better hunting conditions such as increased crypsis. I further predict that lionfish density positively correlated with prey fish biomass, since I expect higher resource avalibility to attract these predators. Additionally, I predict that complexity and prey biomass may depend on each other when determining lionfish density because more complex habitats are expected to harbour more prey fish. By elucidating the relationships between habitat complexity, prey abundance and lionfish density I aim to gain insight in lionfish occurrence patterns which can advance management strategies aimed at mitigating the impacts of the invasion.

Materials and Methods

Study sites

We collected data at 12 sites along the southern coast of Crete, Greece (Figure 1), from September to November 2023. The first lionfish sighting on the island was in 2016 (Phillips & Kotrschal, 2021), after which the lionfish infestation expended rapidly. More detailed information on the sites is represented in Table A, Appendix 1. The sites were selected based on local lionfish abundance and the distance between sites.

During scouting, we excluded potential sites with a lionfish count below 12 specimens or with an inter-site proximity of less than 250 meters. To facilitate the collection of data at two sites per day, we strategically paired the locations of the sites. While the selected sites have a minimum approximate length of 100 meters, they exhibit considerable variations in shape and depth. The maximum depth per site ranged from 10 to 31 meters. Each site was measured twice throughout the fieldwork period. Sites were either reached from the shore, using a Diver Propulsion Vehicle (Suex VRX scooter), or from a boat.

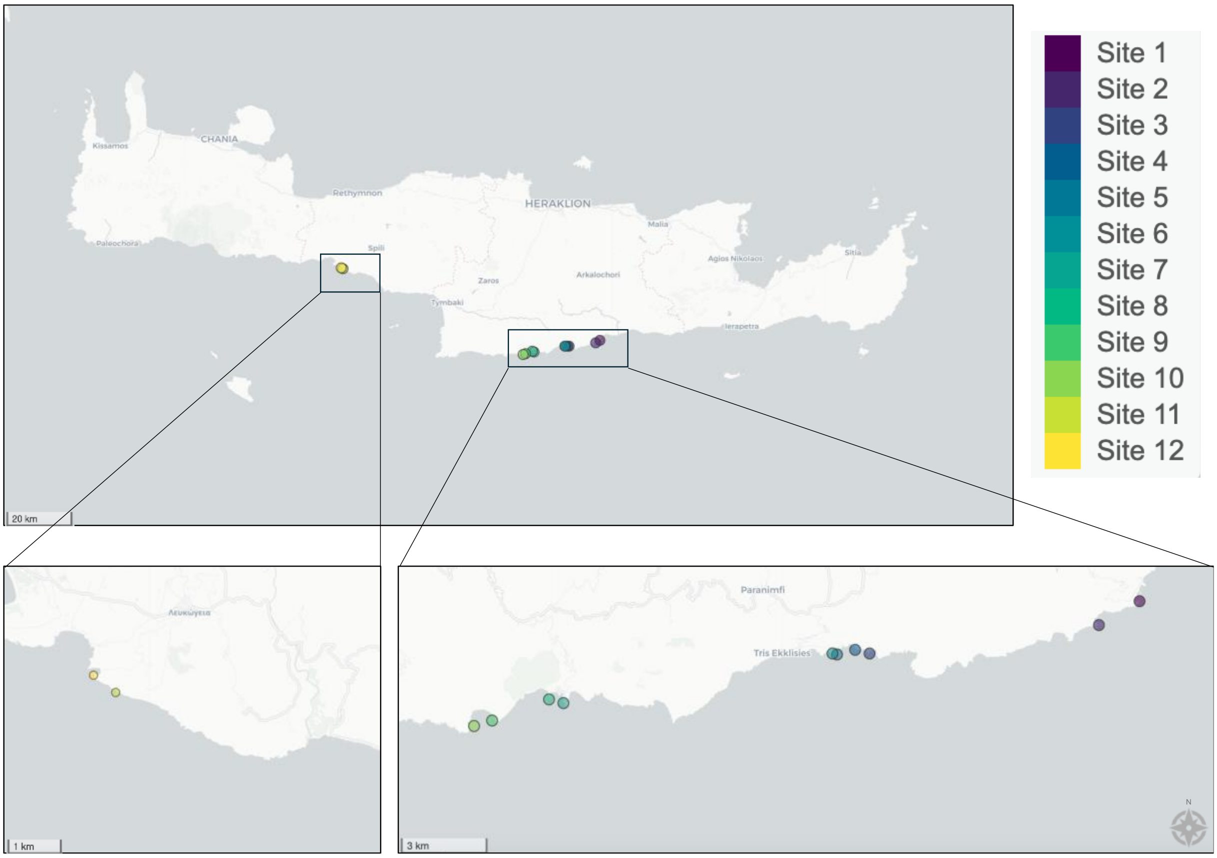

Figure 1. Locations of the dive sites along the south coast of Crete, Greece, in the Mediterranean Sea

Fish surveys

To quantify diversity and abundance of the sites fish community at the sites, we used Underwater Visual Census (UVC) (Bortone et al., 1991; Ward-Paige et al., 2010). Three members of the research team swam a 25-meter transect while documenting the observed quantity and body size (as total length, TL) of all fish encountered, classified at the lowest taxonomic level. The transects observational frame spanned 2 meters bilaterally and 2 meters above the substrate, totalling a two-dimensional surface area of 100 square meters. Per dive, two divers conducted 3 transects, yielding 6 transects and 12 transects per site in total. The divers deployed a spool, tied at the 25-meter mark, as a non-intrusive means of measuring distance while swimming, minimizing disturbance to the fish. During the UVC, the divers maintained a swimming speed of 10 meters per minute. The transects functioned as replicates for the statistical analysis.

In preparation for data collection, underwater size estimation techniques and fish identification skills were sufficiently practised, with individual success rates above 80%. To systematically document fish assemblages, a standardized table featuring the most prevalent fish species was used, including the following size classes: <1 cm, 1-6 cm, 6-11 cm, 11-16 cm, 16-21 cm, 21-25 cm, and >25 cm (Table B, Appendix 1). Throughout all dives, water temperature ranged between 24 and 26°C. Minimal to no current was encountered during data collection, and visibility remained consistently high, with a minimum of 20 meters. Metadata collected per transect included site, date, name of the diver and start and end depth.

The prey fish biomass variable for the analysis was determined using the length-weight relationship equation $W = a \cdot L^b$, with a and b being species specific parameters which were sourced from FishBase. Fish exceeding 15 cm in length were excluded from the analysis, as they have not been documented as lionfish prey (I. M. Côté et al., 2013; Peake et al., 2018). All species, except for lionfish, were considered as prey due to the lionfish's generalist diet. The total transect biomass was converted to grams per square meter for the statistical analysis.

Lionfish observed within the transects were documented to determine their local density, which was later converted to a standardized measure of density (number of individuals per hectare). This data was used as the proxy of lionfish abundance in the statistical analysis.

Habitat complexity

Habitat complexity was expressed in terms of substrate rugosity, thus abiotic complexity, which was measured through video analysis of randomly recorded transects. I captured 8 one-minute videos per site, using a Gopro Hero 7 Black camera in perpendicular position to the substrate. A cross-shaped device (50cmx50cm) was attached to the camera with a rope of 2 meters in length. The cross functioned as a measuring device, enabling size estimation of the recorded substrate. Per video, I took 6 snapshots, one every 10 seconds, which I analysed and scored using the seascape scoring approach (Di Franco et al., 2021; Giakoumi et al., 2019). This method uses an index with scores between 1 and 5, with 5 indicating the highest level of complexity, based on the size of boulders and the depths of holes and crevices (Table 1). I scored a total of 48 images per site, of which I took the average value to characterize the complexity of each site. To avoid bias, randomisation of the snapshots was employed before the scoring process.

Table 1. Habitat complexity index: Definitions of the scores for complexity of habitats in the Mediterranean Sea, with an example snapshot per score to visualize the scoring definition.

Complexity score	Definition	Visual reference
1	Very low structural complexity: flat bottoms without holes/crevices, no rocky boulders	
2	Low structural complexity: few holes/crevices (<50 cm deep) or small rocky boulders (<50 cm) scattered over flat surface, little height difference	
3	Medium structural complexity: small holes/crevices, some less than 100 cm deep, or presence of medium rocky boulders (50-100 cm)	
4	High structural complexity: large holes/crevices (50-100 cm deep), some more than 100 cm deep, or presence of large rocky boulders (>100 cm)	
5	Very high structural complexity: large number of deep holes, crevices and overhangs (>100 cm deep), or high presence of assemblages of large rocky boulders (>100 cm)	

Adjacently, I applied another scoring method, based on expert knowledge. The three divers of the research team individually and independently assigned a score to each site, drawing upon their accumulated experience. Scores were given after a thorough explanation of the complexity index, of which I took the means for the analysis. To assess the inter-observer reliability among the divers, I calculated the Intraclass Correlation Coefficient (ICC). This two-way model yielded an ICC of 0.62, showing substantial agreement between the divers ($F(11, 23) = 6.49$, $p < 0.001$), supporting the use of this variable in the analysis. Subsequently, I compared the outputs of the two different scoring methods, which are shown in Figure I, Appendix 1.

Statistical analyses

All statistical analyses, including the generation of graphs and maps, were conducted using Rstudio (Version 2024.04.1+748). I used the packages "tidyverse" and "dplyr" to clean and summarize the data, "cor.test" and "corrplot" to identify correlations, "glmmTMB" to fit and test the models, "ggplot2", "sjPlot" and "ggeffects" to visualize the data, make graphs and visualize the model outcomes and "DHARMa" to test the model assumptions.

To analyse the influence of habitat complexity and prey biomass on lionfish density, I used two generalized linear mixed models (GLMMs). Both models were fitted using a negative binomial distribution (family = "nbinom2"), suitable for overdispersed and non-normally distributed count data. Additionally, I incorporated zero inflation into each model (ziformula = ~1) to address the excess zeros in the lionfish data, as many transects contained no lionfish. Due to the lack of full independence among transects, I accounted for random factors (Site, Diver, Date) to control for grouping effects.

The first model (Model 1, Table 2) incorporated the habitat complexity scores obtained from the video analysis. I modelled a GLMM with Lionfish density as the response variable (family = "nbinom2"), including fixed factors for Complexity and Biomass, along with their interaction term. The random effects included Site, Diver, and Date. The second model (Model 2, Table 2) incorporated the habitat complexity score as established by the divers. I fitted this model using the same negative binomial distribution and maintained the same formula as in Model 1 to enable direct comparison between the two scoring methods. Fixed factors were considered significant based on their associated p-values ($\alpha = 0.05$).

Table 2. Overview of the model components and fit statistics.

	Dependent variable	Fixed factors	Random factors	Family	AIC	Dispersion test
Model 1	Lionfish abundance	Complexity_video * Biomass	Site + Diver + Date	nbinom2	1154.9	p-value = 0.46
Model 2	Lionfish abundance	Complexity_diver * Biomass	Site + Diver + Date	nbinom2	1150.1	p-value = 0.49

Prior to the GLMM analyses, I conducted a correlation analysis, to assess the relationship between the variables (Figure 2). This preliminary analysis helped to identify potential multicollinearity issues that could affect the GLMMs. The two different scoring methods for habitat complexity showed no correlation ($|\rho| = 0.07$, p-value = 0.39), as seen in Figure 2. I based model selection on Akaike's Information Criterion (AIC). Residual diagnostics showed no significant deviation from model assumptions, showing no departures from homoscedasticity or normality. After fitting, none of the models showed overdispersion of the residuals ($p > 0.05$).

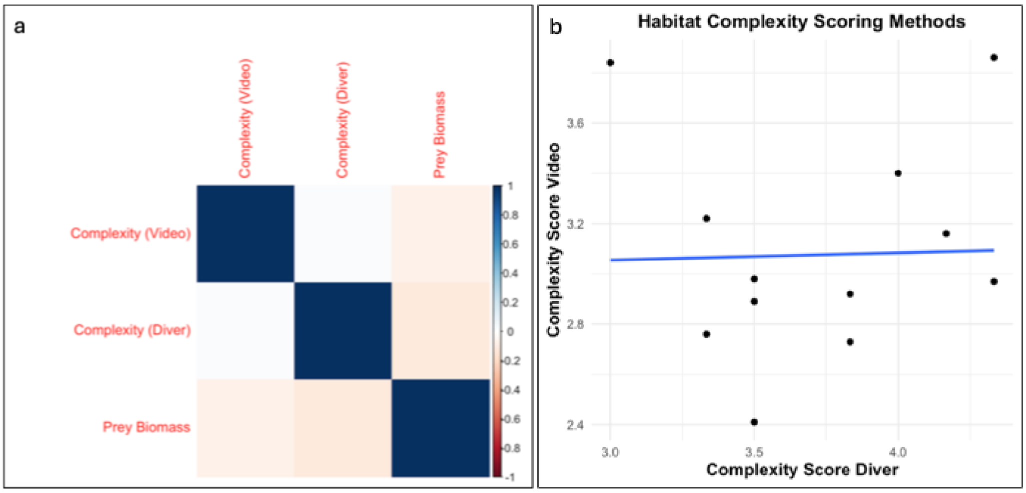

Figure 2. Correlation diagnostics: **a.** The correlation matrix of the fixed effects used in both models, showing minimal correlation between any variables. **b.** The lack of correlation between the habitat complexity scores as obtained by the video analysis and the scores as established by the divers.

Results

Complexity score by video analysis

Lionfish density does not seem to be impacted by either habitat complexity or prey fish biomass (Figure 3). Also, the combined effect of habitat complexity and prey biomass seems to have no impact on the abundance of lionfish. When looking at the figure, all three lines (for low, medium and high biomass) overlap and only slightly increase or decrease with increasing complexity score. These effects are considerably low and show no statistical significance (Table 3). The random effects variance components are 0.029 for Site, 0.014 for Diver, and 0.034 for Date. This indicates that temporal variation has the highest influence on the variability in lionfish density, though site-specific factors also contribute to determining the lionfish density.

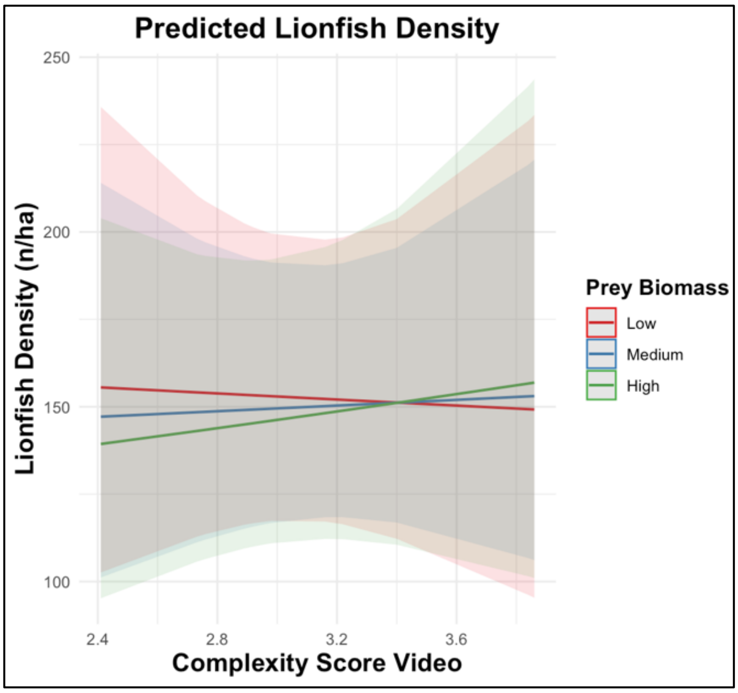

Figure 3. The predicted lionfish density in number per hectare, as a function of habitat complexity (as scored through the video analysis) and prey biomass, in grams per square meters (low = 0.31, medium = 0.94, high = 1.56).

Complexity score by divers

When considering the diver-derived scores for habitat complexity, lionfish density seems to be positively correlated with habitat complexity. Predicted lionfish density is significantly higher at sites with higher habitat complexity (Table 3). Higher prey fish biomass also seems to positively impact lionfish abundance, though this is only indicated by a positive trend. The interaction between complexity and biomass also shows a trend, though in the negative direction, hinting that the effect of complexity on lionfish density decreases with increasing prey biomass (Figure 4). The random effects variance components are 0.015 for Site, 0.013 for Diver, and 0.041 for Date. Again, indicating that temporal variation contributes most to the variability in lionfish density.

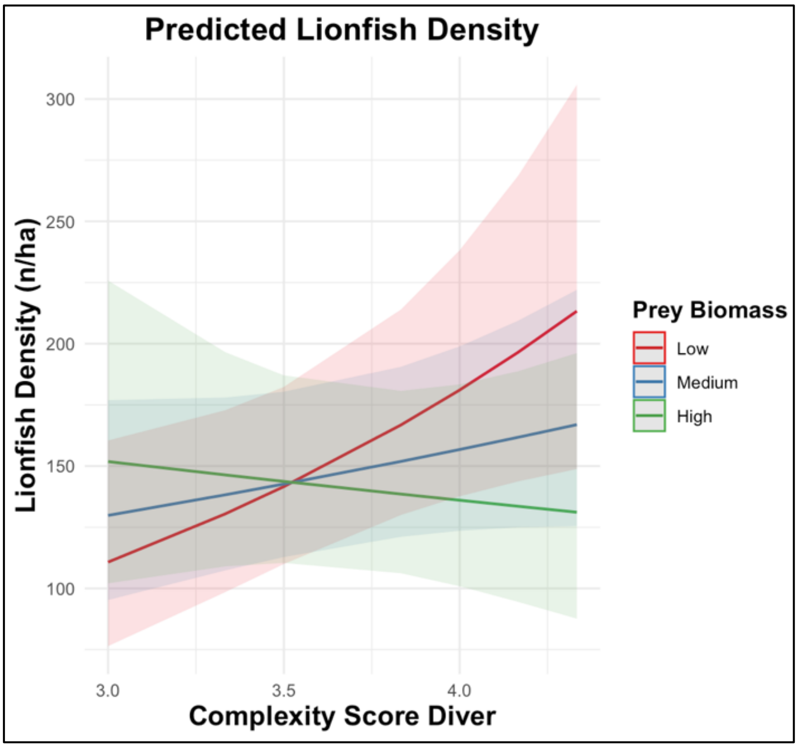

Figure 4. The predicted lionfish density in number per hectare, as a function of habitat complexity (as scored by the divers) and prey biomass, in grams per square meters (low = 0.31, medium = 0.94, high = 1.56).

Table 3. Summary of fixed effects from GLMMs 1 and 2, along with results of the zero-inflation models.

Fixed effect	Estimate	Std. Error	Z value	P value	Significance	Zero-inflation
Model 1: Complexity video						
Intercept	5.21	0.86	6.06	<0.001	***	Estimate = -0.47
Complexity (video)	-0.06	0.28	-0.20	0.84		
Biomass	-0.30	0.51	-0.59	0.56		p-value = <0.01
Complexity:Biomass	0.09	0.18	0.50	0.62		
Model 2: Complexity diver						
Intercept	2.71	1.02	2.66	<0.01	**	Estimate = -0.47
Complexity (diver)	0.64	0.28	2.33	0.02	*	
Biomass	1.70	0.97	1.74	0.08	.	p-value = <0.01
Complexity:Biomass	-0.48	0.27	-1.80	0.07	.	

Discussion

This study shows positive correlations between habitat complexity, prey fish biomass and lionfish abundance, although these results depend on the type of methodology used to assess habitat complexity. When using site complexity scores derived from the video analysis, these correlations are not observed. According to the results of this video-based methodology, lionfish abundance remains consistent across sites of both low and high complexity, contradicting the hypothesized positive relationship. Similarly, prey fish biomass shows a minimal effect on lionfish abundance, which also contradicts the expected positive correlation. This finding is inconsistent with other studies that have found positive correlations between lionfish density and available prey abundance (Cure et al., 2012; Lee et al., 2011). The absence of clear effects on lionfish density may be attributed more to methodological limitations rather than to a genuine lack of correlation between the factors. Contrarily, the results acquired with the second methodology, where divers scored habitat complexity, reveal that lionfish are more abundant at sites where their habitat is more complex. This suggests that lionfish preferentially occupy more complex habitats, possibly due to the enhanced shelter and hunting opportunities such habitats provide. This second finding would be in line with the hypothesized correlation. Though, this positive correlation seems to diminish with increasing availability of prey. Thus, were the effect significant, it would suggest that lionfish seek out more complex areas when food is scarce, but the need for complex habitats becomes less prominent in prey-rich environments. This potentially highlights the interplay between habitat complexity and prey availability in determining lionfish distribution.

Lionfish in their native range have demonstrated to be habitat generalists, showing no particular preference for highly complex habitats (Schultz, 1986). It is important to note that their coral dominated native range is inherently more complex than the rock dominated Mediterranean Sea, since coral reefs show more structural rugosity. Although lionfish in their native range are consistently associated with some form of structure, they even show a preference for low-complexity areas (Cure et al., 2012). This is contradicted by studies done on *P. miles* and *P. volitans* in their invasive range in the Western Atlantic. In these studies, they are consistently found occupying more complex aggregate reef habitats, rather than reef flats, seagrass or patch reefs (Biggs & Olden, 2011), especially preferring deep habitats (Claydon et al., 2012). They are most often present in habitats with hard bottom substrate and show a particular preference for vertical walls (Lee et al., 2011). This difference in habitat preference between native and invasive regions may be attributed to inter-species competition and resource availability (Lee et al., 2011). In their native Indo-Pacific range, lionfish face natural predators, such as moray eels and groupers (Bos et al., 2017). Additionally, they compete with other lionfish species, which may force them to utilize a broader range of habitats to avoid predation and competition. In contrast, in the invaded regions the absence of natural predators and competitors allows lionfish to exploit more complex habitats that offer more abundant resources (Cemal et al., 2017), and possibly enhanced crypsis (Rickel & Genin, 2005). These constraint reliefs may steer lionfish to select more complex habitats in their invasive range. Similar to the studies in the Atlantic and Caribbean, I found support that lionfish are more abundant in complex habitats. This study, therefore, may contribute to the existing body of research on lionfish in invaded regions, demonstrating that their preference for complex habitats in the Mediterranean Sea mirrors the behaviour observed in the Western Atlantic.

Furthermore, larger structural complexity of habitats can support higher fish biomass (Connell & Jones, 1991; Consoli et al., 2018; García-Charton & Pérez-Ruzafa, 2001), possibly making these areas more attractive for lionfish. However, this finding is contradicted by other studies showing no direct relation between habitat complexity and fish biomass or diversity (Giakoumi & Kokkoris, 2013; Pygas et al., 2020). Similarly, I found no support for a direct relationship between habitat complexity and prey fish biomass. Additionally, I hypothesized a positive correlation between prey fish biomass and lionfish density. It is important to consider that, if this correlation was evident, it would not solely be causal. Prey fish abundance does not just attract lionfish, but lionfish affect prey abundance as well, with a non-linear correlation between the two (Benkwitt, 2015). In this study, I found a positive trend indicating that higher prey biomass concurs with higher lionfish density. However, it is noteworthy that this effect is not statistically significant, potentially because we only sampled 12 sites. It is possible that including more sites will reveal such a relationship. Especially since other studies support the connection between lionfish density and prey fish biomass (Cure et al., 2012). The (presumed) interaction between prey biomass and habitat complexity can likewise be attributed to the attraction of fish to complex substrates. The tentative negative effect of this interaction on lionfish density suggests that lionfish prioritize resources over habitat when both are available. These findings indicate that when food availability is low, lionfish may be more drawn to complex habitats, potentially to increase their hunting success through crypsis.

A very important point of this study is that there is a substantial difference in results between the two methodologies for habitat complexity scoring. As previously discussed, the results of my second model fit the hypothesis, but my first model shows no effects at all. Moreover, there is a considerable lack of correlation between the two complexity scores of the sites (Figure 2). This is remarkable, since the two methods should ideally produce similar complexity scores. This highlights the importance of adequate methodology. The complexity scores from the video analysis demonstrated less variability across sites, since the methodology averaged the complexity scores from 48 images per site. Lionfish typically aggregate in small pockets or microhabitats of complex hard substrate, holes or caves (Gavriel et al., 2021). However, the video analysis encompassed the entire site, which often included large areas of sandy substrate. Consequently, even though some patches exhibited high habitat complexity and were favourable for lionfish, the overall complexity scores were likely diminished by the presence of extensive sandy areas. This averaging effect may have led to an underrepresentation of complex habitat characteristics at each site. Additionally, many of the complex habitat features that are particularly important for lionfish, such as vertical walls, caves, and overhangs, were not adequately captured by the horizontally oriented video transects. In contrast, these features were considered by the divers when scoring the sites. However, this second methodology is prone to confirmation bias. Although the scores were given independently and were very similar per site, they were likely influenced by the presence of lionfish to some extent, making the variables not completely uncorrelated. Although both methods show suboptimal characteristics, the scores as assigned by the divers show a more reliable assessment of present complexity characteristics that are relevant for lionfish. This shows that scoring habitat complexity based on expert knowledge is an efficient and cost-effective method, which is more applicable than a time-consuming video analysis.

Additionally, a limitation for both methods is the complexity index itself, which fails to encompass all features important for lionfish. While deep holes, caves, and crevices favour lionfish, the presence of large boulders may not. This index was adopted from existing literature to enhance data comparability, however its applicability has proven to be suboptimal for the use in lionfish specific research. Another measure for complexity could be the use of the chain-transect method, which measures substrate rugosity (Giakoumi & Kokkoris, 2013; Green et al., 2013). This method yields substrate complexity on a very small scale, which is accurate but labour intensive. Moreover, one study in the Atlantic found no correlation between lionfish abundance and habitat complexity using this method (Anton et al., 2014). This suggest that lionfish may prefer larger habitat features, such as caves, over small-scale rugosity of the reef itself, which is better represented by the diver-based methodology. Other options include high-resolution 3D maps (Ferrari et al., 2018), the 'optical intensity' method (Shumway et al., 2007) or a more detailed scoring metric (Pygas et al., 2020). Nevertheless, there is a pressing need for the formulation of a tailored and standardized index dedicated to evaluating habitat complexity. Such an index is crucial for furthering research into lionfish habitat preferences. Moreover, smaller scale research on the exact occurrence of lionfish in relation to the specific habitat features would enhance the understanding of their preferences more, instead of solely looking at site-wide complexity. Another limitation of this study is the limited variation among dive sites. Since site selection was based on lionfish presence, there is an absence of sites representing very low complexity levels, which hinders a comprehensive representation of the complexity spectrum. This resulted from my study being part of a larger research, where diving resources were allocated primarily to sites with lionfish. Thus, to adequately assess the lionfish density as a factor of habitat complexity, greater variation in complexity between sites is essential. Finally, UVC has proven to be an unreliable method for lionfish detection, with a detection rate of less than 30% (Green et al., 2013), primarily because lionfish are hidden during the day. During our research, this was corrected for, since the lionfish per site were individually counted by a dedicated diver, and the lionfish density from the UVC used in the analysis correlated with these separate counts.

Understanding the lionfish's adapted habitat preferences in the Mediterranean Sea is crucial for managing their invasive populations and mitigating their ecological impact. Such knowledge will enable the development of targeted strategies to control the skyrocketing invasion rate. This study highlights the intricate relationship between habitat complexity, prey biomass, and lionfish density, potentially shedding light on their occurrence adaptations in their newly invaded range. Lionfish show to prefer complex substrates, so directing conservation efforts towards such habitats instead of sandy or seagrass covered areas would considerably increase their efficiency. A substantial part of the Mediterranean coastal areas are characterized by this complex, rocky substrate, implicating a large possible extension range for lionfish (Poursanidis et al., 2020). A relevant next step for future research would be the development of more precise and standardized methods for measuring habitat complexity and integrating long-term monitoring to better understand these dynamics. Additionally, the impact of lionfish on the surrounding fish biomass further complicates these dynamics and needs to be addressed by future studies. More insight on specific habitat features attracting lionfish would likewise further enhance the existing knowledgebase. This knowledge can enhance the protection of vulnerable marine ecosystems and promote their resilience against the ongoing invasion.

Beyond the specific case of lionfish, this research may provide valuable insights into the broader dynamics of marine predator invasions. Lionfish serve as an excellent model for testing fundamental invasion ecology hypotheses (Côté & Smith, 2018). These findings may emphasize the critical role of habitat preferences and resource availability in shaping the behavior and distribution of invasive species. The preference for complex habitats when prey is scarce suggests that predators adapt their habitat selection based on resource availability, a behavioral plasticity that could be a key factor in the success of invasive species. Conversely, when prey is abundant, habitat complexity becomes less important, indicating that predators potentially prioritize food availability (Kleitou et al., 2024). These insights can inform conservation strategies for managing invasive species and protecting native predators in marine ecosystems worldwide. Understanding these relationships is crucial for predicting the spread and impact of marine invaders, which are likely to become more prominent due to global climate change. By applying these principles to other marine species and ecosystems, we can potentially better protect biodiversity and maintain ecosystem resilience in the face of a changing climate and increasing human-caused biological invasions.

In conclusion, these findings shed light on the complex interplay of habitat complexity and prey biomass on lionfish density, revealing a prey-dependent preference for complex habitats. By integrating ecological modelling techniques with empirical data, I provide valuable insights into the factors driving lionfish density patterns. This insight can inform targeted conservation strategies to mitigate the impacts of this invasive species on marine ecosystems. Furthermore, I compare two methods for habitat complexity assessment and show that the cost- and time-effective method based on expert knowledge is most reliable.

Acknowledgements

I want to express my gratitude to my supervisors, Davide Bottacini and Alexander Kotrschal, for their guidance during the entire process of my thesis. A special thanks goes to Davide, for teaching me a lot about field work, for helping me develop my ideas and for practical support. Additionally, I want to show my appreciation for fellow students, Carien, Lieke and Elvis, who have helped collect the data and have participated in meaningful discussions. Finally, Greg, Emanuela and Thanos from HCMR have provided a lot of practical, on-site support and expertise, for which I am very thankful.

Disclaimer

I have used ChatGPT to polish my codes and help me solve errors in RStudio. Furthermore, I have used ChatGPT as a grammar and spelling corrector (ChatGPT-4, 2024). Additionally, ResearchRabbit was used to identify relevant literature (ResearchRabbit, 2024).

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Appendix 1 – Supplementary material

Table A. Summary on the dive sites.

Site number	Site name	Latitude	Longitude	Nearest town
Site 1	Pottery	34.969620	25.272430	Tsoutsouros
Site 2	Mediterranean palm	34.962258	25.256928	Tsoutsouros
Site 3	Infinite scootering	34.953583	25.169809	Tris Ekklisies
Site 4	Stingray spot	34.954612	25.164270	Tris Ekklisies
Site 5	Big rock	34.953298	25.157487	Tris Ekklisies
Site 6	Little cave	34.953512	25.155575	Tris Ekklisies
Site 7	Hunting lionfish	34.938274	25.053302	Ag. Ioannis
Site 8	Excellent site	34.939396	25.047690	Ag. Ioannis
Site 9	Fishy spot	34.932847	25.026024	Ag. Ioannis
Site 10	Underwater bay	34.931187	25.019279	Ag. Ioannis
Site 11	Beyond the random fence	35.161867	24.425372	Plakias
Site 12	Turtle rock	35.165423	24.419779	Plakias

Table B. Table of most abundant fish species, as utilized during the UVC fish surveys.

	<1 cm	1-5 cm	6-10 cm		11-15 cm	16-20 cm	21-25 cm	>25 cm
S. rivulatus								
S. luridus								
D. sargus								
D. vulgaris								
O. melanura								
S. mediterraneus								
S. tinca								
B. boops								
C. chromis								
S. cretense								
T. pavo								
C. julis								
M. surmuletus								
P. forsskali								
Atherinidae								
A. imberbis								
S. rubrum								
Gobies								
Blennies								
S. maderensis								
S. scriba								
S. cabrilla								
T. flavimaculosus								
E. marginatus								
E. costae								

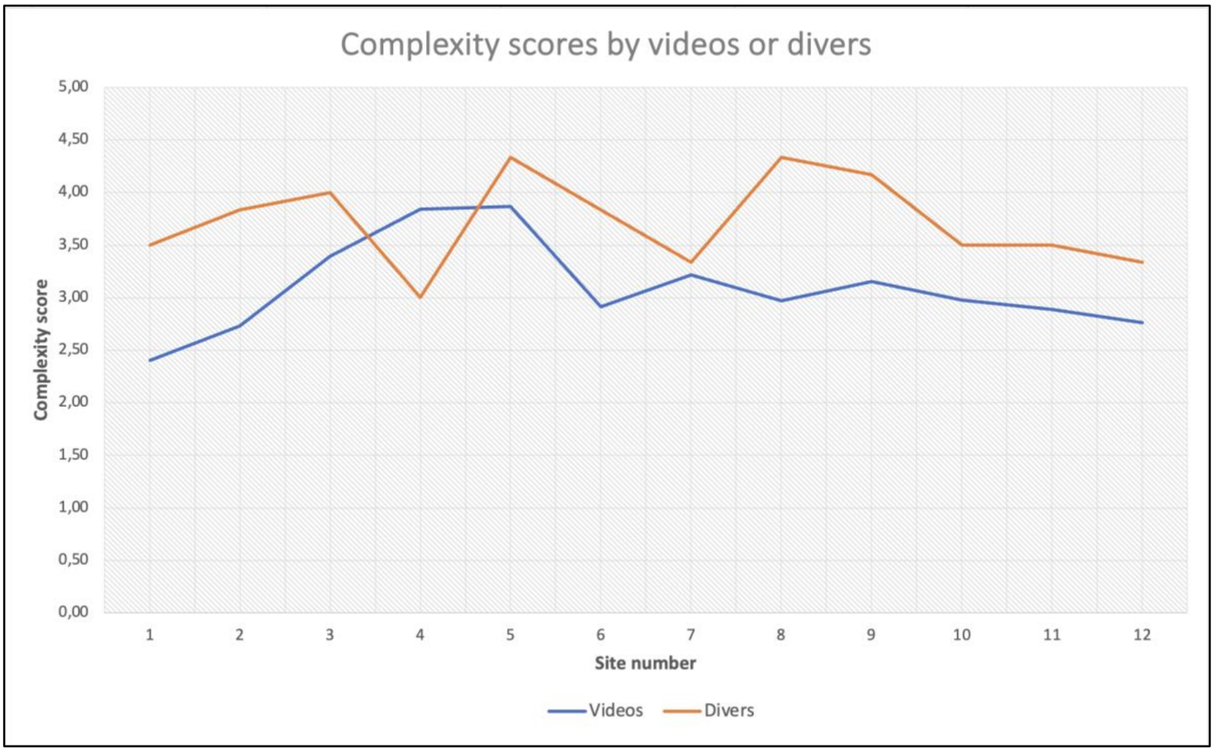

Figure I. Complexity scores of the dives sites, as determined by the video analysis (blue) or determined by the divers (orange).