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Reef fish interactions with soft and hard corals communities in Okinawa (Japan): analysis of potential phase shifts under a climate change scenario

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"Not a man nor a fish, but something betwixt,

Not a man, for his life among fishes he past,

Not a fish, for he perished by water at last."

(*George Shaw's Translation of Anders Celsiul quotation*)

written on Linnaeus copy of Ichthyologia

Riassunto

Le scogliere coralline occupano solo lo 0.1% della superficie terrestre, ma ospitano all'incirca il 35% della biodiversità marina, rendendole l'ecosistema marino più biodiverso al mondo. Nonostante la loro importanza, sono sempre più minacciate dalle attività antropiche, tra cui il riscaldamento globale rappresenta la pressione più rilevante. Tra le principali conseguenze di tali disturbi vi è il phase shift, un cambiamento improvviso e persistente della struttura e del funzionamento della comunità che conduce a un nuovo stato di equilibrio dell'ecosistema. Mentre il passaggio di fase da una comunità dominata da Scleractinia Bourne G.C. a comunità dominate da macroalghe è stato ampiamente studiato, quello che coinvolge gli zoantari è poco conosciuto. In aree con un apporto fluviale e alta concentrazione di nutrienti, in diverse parti del mondo tra cui le Isole Canarie, Spagna, Todos os Santos Bay, Brasile, e la prefettura di Okinawa, Giappone, sono avvenuti eventi di phase shift verso gli Zoantharia Gray, J.E., 1832, in particolare il genere *Palythoa* Lamouroux, 1816. Come conseguenza del phase shift a Zoantharia, studi in Brasile hanno confermato una riduzione della tridimensionalità del substrato e del numero di specie ittiche. Un numero molto ridotto di studi si sono concentrati sulle conseguenze di questo cambio di regime sulla fauna ittica associata al reef, in particolar modo nel Pacifico, dove, questo studio, può essere considerato pionieristico.

Lo scopo di questo studio è stato quello di osservare le differenze di abbondanza e interazione dei pesci di reef, tra patch di coralli duri, incrostanti e massivi, e patch di coralli molli appartenenti all'ordine Zoantharia, *Palythoa tuberculosa* (Esper, 1805) e *Palythoa heliodiscus* (Ryland & Lancaster, 2003) all'interno di quattro siti ad Okinawa, in Giappone, Sosu, Yona, Ginowan e Mizugama, dove, in quest'ultimo è stato confermato un phase shift a *Palythoa tuberculosa*.

La raccolta dati è avvenuta nel periodo da settembre a dicembre 2024, nell'ambito della borsa di studio per tesi in paesi extra UE, dell'Università degli studi di Genova. Sono state svolte diverse immersioni a una profondità massima di 5 metri, utilizzando il metodo del "Unbaited Remote Underwater Video" (RUV). Sono stati registrati video da venti minuti grazie all'utilizzo di 3 GoPro, e un quadrato di riferimento per le dimensioni della patch. Per ciascun video sono stati calcolati: la ricchezza di specie; l'indice di Shannon; e per ciascuna specie e gruppo trofico il massimo numero di individui contemporaneamente a schermo per frame (MaxN), un proxy di abbondanza e il Tempo Totale di Interazione (TTI) dei diversi comportamenti osservati. Le differenze tra trattamenti sono state valutate mediante PERMANOVA con PERMDISP,

Generalized Linear Mixed Models (GLMMs), analisi SIMPER e Community Weighted Means (CWM).

Data la natura esplorativa di questo studio, il basso numero di repliche dovuto al ridotto periodo di tempo, e le condizioni meteo avverse, assieme all'impossibilità di poter confrontare i siti a causa della differenza ecologica, geografica e antropica tra di essi; la maggior parte delle analisi è risultata non significativa. Non sono state trovate differenze significative per quanto riguarda il numero di specie e l'indice di Shannon tra patch di *Palythoa* spp. e quelle di coralli duri in nessun sito. A Sosu l'abbondanza è risultata significativamente maggiore su patch di *Palythoa tuberculosa* rispetto che su quelle di coralli duri, in particolar modo per quanto riguarda gli OTU: *Eviota* spp. Jenkins, 1903, Blenniidae Rafinesque, 1810, *Thalassoma lutescens* (Lay & Bennett, 1839), *T. amblycephalum* (Bleeker, 1856) e *Acanthurus nigrofuscus* (Forsskål, 1775). Questi pattern suggeriscono una maggiore disponibilità di micro-, meio- e macroinvertebrati associati alle colonie di *P. tuberculosa*, probabilmente favorita dalla presenza di spazi tra le colonie, che aumentano la disponibilità di microhabitat per quanto riguarda gli invertivori e una maggiore competizione dei coralli incrostanti con le macroalghe per l'erbivoro *Acanthurus nigrofuscus*. Sempre nel sito Sosu anche il TTI dei morsi è risultato significativo su *P. tuberculosa*, per quanto riguarda gli OTU *Eviota* spp. e *Plectroglyphidodon dickii* (Liénard, 1839), una specie corallivora facoltativa. È stato ipotizzato che la presenza della palitossina non costituisca una deterrenza efficace per i corallivori e che il muco e i polipi di *Palythoa* possano rappresentare una risorsa alimentare maggiormente appetibile di quelli dei coralli incrostanti e massivi. Nel sito di Mizugama, interessato da un evento di bleaching nel 2024, gli erbivori hanno mostrato un maggiore tempo di interazione dei morsi con *Palythoa*. Una possibile interpretazione è quella che vede i coralli massivi e incrostanti maggiormente resistenti allo sbiancamento rispetto a *Palythoa*.

Nel complesso si può ipotizzare che, il phase shift a zoantari non è solo una riduzione del numero di specie e di tridimensionalità del substrato, ma, le conseguenze sulla comunità ittica possono essere molto più complesse. Lo studio dell'interazione e dell'abbondanza di invertivori ed erbivori su *Palythoa*, è un argomento ancora sconosciuto. Futuri studi a breve e lungo termine su eventi di phase shift a zoantari, e la conseguenza sulla comunità ittica, possono essere indispensabili per anticipare uno scenario possibile dove questi cambiamenti di fase potrebbero diventare più comuni.

Abstract

Coral reefs cover only 0.1% of the Earth's surface, but they are home to approximately 35% of marine biodiversity, making them the most biodiverse marine ecosystem in the world. Despite their importance, they are increasingly threatened by human activities, with global warming representing the most significant pressure. Among the main consequences of these disturbances is phase shift, an abrupt and persistent change in the structure and functioning of the community that leads to a new state of equilibrium in the ecosystem. While the phase shift from a community dominated by Scleractinia Bourne G.C., 1900 to one dominated by macroalgae has been extensively studied, the phase shift involving zoanthids is poorly understood. In areas with riverine input and high nutrient concentrations in various parts of the world, including the Canary Islands, Spain; Todos os Santos Bay, Brazil; and Okinawa Prefecture, Japan, phase shifts toward Zoantharia Gray, J.E., 1832, particularly the genus *Palythoa* Lamouroux, 1816, have occurred. As a consequence of the phase shift toward Zoantharia, studies in Brazil have confirmed a reduction in substrate three-dimensionality and a decrease in the number of fish species. Very few studies have focused on the consequences of this regime shift on reef-associated fish fauna, particularly in the Pacific, where this study can be considered pioneering.

The purpose of this study was to examine differences in the abundance and interactions of reef fish among patches of hard, encrusting, and massive corals, and patches of soft corals belonging to the order Zoantharia, *Palythoa tuberculosa* (Esper, 1805) and *Palythoa heliodiscus* (Ryland & Lancaster, 2003) at four sites in Okinawa, Japan, Sosu, Yona, Ginowan, and Mizugama where a phase shift to *Palythoa tuberculosa* was confirmed at the latter site.

Data collection took place from September to December 2024, as part of "borsa di studio per tesi in paesi extra UE" offered by the University of Genoa. Several dives were conducted at a maximum depth of 5 meters, using the "Unbaited Remote Underwater Video" (RUV) method. Twenty-minute videos were recorded using three GoPro cameras, and a reference square was used to determine the patch size. For each video, the following were calculated: species richness; the Shannon index; and, for each species and trophic group, the maximum number of individuals simultaneously on screen per frame (MaxN), a proxy for abundance, and the Total Interaction Time (TTI) of the various observed behaviors. Differences between treatments were assessed using PERMANOVA with PERMDISP, Generalized Linear Mixed Models (GLMMs), SIMPER analysis, and Community Weighted Means (CWM).

Given the exploratory nature of this study, the low number of replicates due to the short time frame, and the adverse weather conditions, along with the inability to compare sites because of the ecological, geographic, and anthropogenic differences among them, most of the analyses were not statistically significant. No significant differences were found in species richness or the Shannon index between patches of *Palythoa* spp. and those of stony corals at any site. At Sosu, abundance was significantly higher on *Palythoa tuberculosa* patches than on hard coral patches, particularly for the following OTUs: *Eviota* spp. Jenkins, 1903, Blenniidae Rafinesque, 1810, *Thalassoma lutescens* (Lay & Bennett, 1839), *T. amblycephalum* (Bleeker, 1856), and *Acanthurus nigrofuscus* (Forsskål, 1775). These patterns suggest a greater availability of micro-, meio-, and macroinvertebrates associated with *P. tuberculosa* colonies, likely facilitated by the presence of spaces between the colonies, which increase the availability of microhabitats for invertebrate-eaters and lead to greater competition between encrusting corals and macroalgae for the herbivore *Acanthurus nigrofuscus*. Also at the Sosu site, the TTI for bites was significant on *P. tuberculosa* with regard to the OTUs *Eviota* spp. and *Plectroglyphidodon dickii* (Liénard, 1839), a facultative coral-eating species. It has been hypothesized that the presence of palytoxin does not constitute an effective deterrent for coral-eaters and that the mucus and polyps of *Palythoa* may represent a more appealing food source than encrusting and massive corals. At the Mizugama site, which was affected by a bleaching event in 2024, herbivores spent more time biting at *Palythoa*. One possible interpretation is that massive and encrusting corals are more resistant to bleaching than the Zoantharia.

Overall, it can be hypothesized that the phase shift in zoanthids is not merely a reduction in the number of species and the three-dimensionality of the substrate; rather, the consequences for the fish community may be much more complex. The study of the interaction and abundance of invertebrate-eaters and herbivores on *Palythoa* remains an unexplored topic. Future short- and long-term studies on zoanthid phase shifts and their impact on the fish community may be essential for anticipating a possible scenario in which these phase shifts could become more common.

Table of Contents

1. Introduction

1.1 Coral reef ecosystem in space and time

Coral reefs are one of the most astonishing, unique and biodiverse ecosystems in the world, despite covering only 0.1% of the Earth's surface and 0.2% of the ocean (M. L. Reaka-Kudla 1997; Marjorie L Reaka-Kudla 2005) Yet, they are home to 5% of the world's known species and 35% of known marine species (M. L. Reaka-Kudla 1997), making them the most biodiverse habitat in the sea. Temperate and tropical coral reefs are found in a band extending from thirty degrees south to thirty degrees north, in warm waters around the globe (Mulhall 2009). All tropical coral reefs are included in four different main regions: Indo-west Pacific, Eastern Pacific, Western Atlantic and Eastern Atlantic (Ravitious and Green 2001). 80% of coral reef are concentrated in Asia and Oceania (Brodie et al. 2019), with the world's most biodiverse place within an area called the Coral Triangle that includes Indonesia, Philippines, Papua New Guinea, Timor-Leste and Solomon Islands (Z. Dubinsky and Stambler 2011). Everyone could try to explain what a coral reef is: "a variety of colors, shapes, and organisms that are most of the time underwater, but sometimes, during the lowest tides, some of them can remain exposed to the sea breeze". But in reality, explaining what a coral reef is, is not so easy. (Ravitious and Green 2001). Wood in 1999 proposed this definition: "discrete carbonate structure formed by in-situ or bound organic components that develops topographic relief upon the sea floor" this explores the process of formation of reefs but also explains the differences between reefs and how they have changed throughout geological time (Wood 1999). The characteristics that differentiate oyster, coral and other biogenic reefs from rock and sand reefs are that biogenic reefs are produced by both geological and biological processes (Hallock 1997).

1.1.1 Reef builders

The extreme biodiversity that characterizes reefs is due to a group of fewer than 1000 stony coral species that literally build the reef (Cairns 1999), the Scleractinia Bourne, 1900, an order belonging to the class Hexacorallia Haeckel, 1896 (WoRMS Editorial Board, 2026). Which secrete calcium carbonate ($CaCO_3$) thanks to the symbiosis with dinoflagellate zooxanthellae (Goreau 1959). Calcifying activities result in a three-dimensional matrix that provides shelter, protection and micro-habitats to an enormous variety of species (Barnes 1983; Mora 2015). The calcification process would be of limited significance if Scleractinia didn't live in colonies, indeed, it is the coral colonies themselves that give rise to the reef structure. These creations are only possible in shallow warm waters, that provide the possibility to obtain enough sun for the

symbiotic algae, and stable temperature (Ravitious and Green 2001). All of this gives Scleractinia the terms of physical ecosystem engineer, that is an organism that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials, increasing habitat heterogeneity and species richness (Jones et al., 1997), which generates a positive feedback loop for themselves (Romero et al. 2015; P. Cheung et al. 2021). Scleractinia corals present various growth forms that reflect both genetics and their capacity to adapt to the environment (Peter A. Todd 2008). Branching morphs: arborescent: has ramified/tree-like branches that gain fast growth and occupation in terms of space (R. N. Hughes et al. 2015); caespitose: bushy shapes with high rates of secondary branches, intermediate between tabular and arborescent (R. N. Hughes et al. 2015); corymbose: bush like form with small branches, diverging first that project upwards (Sadler et al. 2015); digitate: has short, stubby and finger-like branches that project upwards from a common base (S. Muko et al. 2013). Horizontal and plate-like morphs: tabular: wide horizontal plates or "tables" that maximize light capture but highly vurnerable to mechanical damage from storms (Done 1982); foliose: leaf-like or thin plate structure, the flats efficiently collect limited light, so its frequently found deeper (T. Hughes 1987). Robust and solid morphs: columnar: thick, vertical pillars or columns that lack secondary branching (Barnes, 1972); massive: boulder-like forms, extreme resistance to storm damage and slow growth (Done 1982). Other forms: encrusting: they grow as a thin layer following the contours of the rocky substrate, this form is common in areas with high wave energy (T. Hughes 1987); solitary/free-living: single large polyp, and not attached to the seafloor as adults (Pandolfi & Greenstein, 1997).

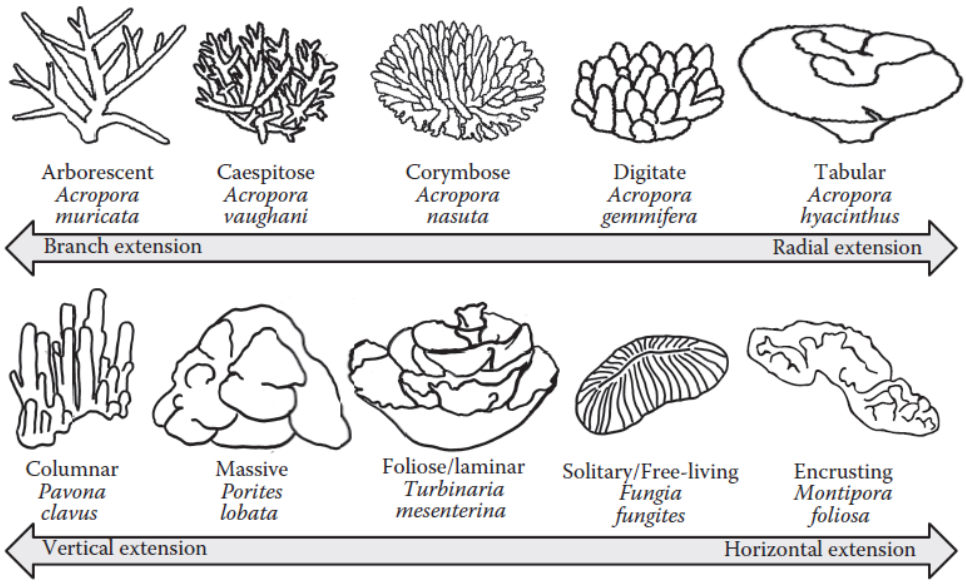

Figure 1(*Hughes et al, 2015. Major growth forms of Scleractinia corals*)

The result of pulses of growth interspersed with erosion periods and dramatically sea level variation during recent ice ages, when reefs have become dry land, or have been flooded (Ravitious and Green 2001) generated “structural coral reef”. Structural coral reefs are differentiated from “nonstructural coral reef” by the production of geomorphologically significant calcium carbonate (limestone), a structure high up to hundreds of meters above the surrounding substrate. Structural coral reefs are present in a variety of forms, common types are fringing, barrier, knoll, pinnacle, platform, ribbon, crescent reefs and atolls. A fringing reef, by definition, is adjacent to a land mass; most of them present a reef crest, where wave action breaks, one or two meters higher than the rest of the reef. From the shore to the crest there is a small space, not navigable, that is called reef flat. The main difference between fringing and barrier reefs is that in barrier reefs this area is navigable. From reef flat, the lagoon differs in terms of depth, where the second is at least two meters deep. Fringing reefs often include lagoons, but the separation of a reef crest and slope from land is more complete in a barrier reef. Reef slope at last is the part of the reef that degrades toward the open sea, beyond the reef edge. The rests of the reef forms are labeled based on their shape (McManus 2001). During geological time reefs were constructed from different taxa, and destroyed several times. Indeed nowadays, coral reefs are the consequences of dramatic extinction, extreme species diversification and natural drivers.

1.1.2 Spatial and temporal patterns of diversity and distribution

Reefs, in many forms, are found in the fossil record, and they represent one of the first bioconstructions in Earth’s history, the first of them were stromatolites, 3.5 billion years ago (Awramik 1992); during the Cambrian explosion gregarious sponges called Archaeocyatha were one of the first reef building organisms (Pruss et al. 2019), In the Ordovician a group of organisms that are present in fossil record could represent very early Scleractinia, the Scleractiniamorph (Stolarski et al. 2011). Also in the Ordovician period another group of Scleractinia-like organisms found in the fossil record, disappeared after the great mass extinction of the Permian, the Anthozoa also called Rugosa that created, together with Tabulata, Paleozoic reefs (Scrutton 1997; Baars et al. 2013). In the mid-Cretaceous, the reefs were composed of both from early Scleractinia and ancient bivalves, called Rudists, that competed for space and reef formation (L. S. Collins 1988; Wood 1999). After the Cretaceous/Tertiary mass extinction, all Rudists and 57% of coral genera became extinct. Nine genera of corals survived and became ancestors of (or closely related to) the Cenozoic coral reef builders (Wood 1999; Rosen 2000). In the Eocene most modern families of Scleractinia appeared and could spread throughout

Tethys. Plio-Pleistocene climatic cooling generated important coral fauna turnover, that created the current composition of coral genera (Wood 1999). In order to understand the factors that nowadays guide the distribution of coral reefs, the most important organisms to observe are the Scleractinia. Although these biodiversity distributions are not only related to hard coral species, but these patterns also reflect most of the species that inhabit tropical coral reefs. After the tectonic movements and closure of the Tethys Sea, Scleractinia evolved during the Triassic with circumpolar distribution, which separated the population into two. One in the Atlantic and one in the Pacific Sea, with development of new distinctive characteristics. During Plio-Pleistocene glaciation, the western part of this division was subjected to massive extinction, removing many of the species which were commonly found before. Nowadays, Atlantic communities share with Indo-Pacific only seven genera, and this has resulted in far lower species diversity in Atlantic reefs, where scleractinian corals have one-tenth of the species of Indo-Pacific. For the Eastern fauna, this period was not as extreme, refuges and locations were able to provide protection from these conditions, and species richness remained high. A specific area of Indo-Pacific, the Coral Triangle, centered in the Philippines, had isolated several times and has maintained good conditions, allowing species to survival and evolve. It has also been considered "center of accumulation" for species originated from outside this area and source for several species during major environmental changes. (McManus 2001; Ravitious and Green 2001). Reefs and Scleractinia are influenced by temperatures, which decrease following increasing latitude from 30°N and 30°S. Most reefs cannot survive at temperatures below 16-18°C for even a few weeks. Also high temperatures can be problematic for corals, if extremely high temperatures occur in a coral reef, these can lead to a bleaching event, where coral extrude symbiotic algae and could cause coral mortality. If temperature determines in an important way reef distribution, currents can disrupt this pattern, warm currents around the globe can give warm-water corals the possibility to grow in places otherwise unlikely. The Leeuwin Current in western Australia, the East Australian Current and the Kuroshio Current in Japan (Fig 2) are some of the most relevant examples. In the other way, cold currents such as upwelling can be critical in preventing coral reefs in areas where conditions would otherwise support their growth. Some examples include the upwelling along the shore of northeastern Somalia and southern Arabia, and western Africa (Ravitious and Green 2001).

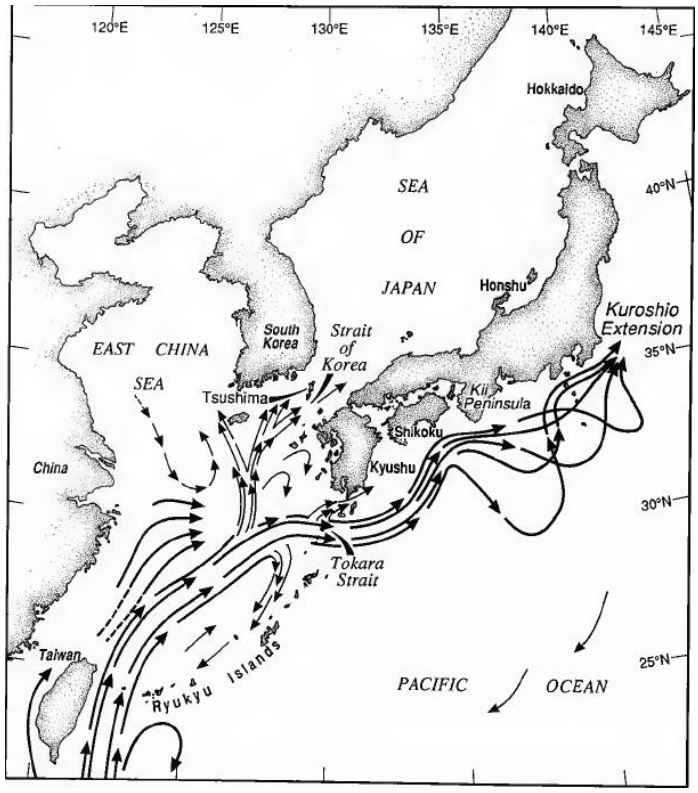

Figure 2(Veron, 1992, representation of the Kuroshio and Tsushima currents)

1.1.3 Importance of reefs

Tropical coral reefs are considered vital for humans and for the entire world. Coral reef gives habitat where species can find a place to spawn, grow and reproduce, including economically valuable species, important to human activities and endemic or rare species, that are difficult if not impossible to find anywhere else (C. Birkeland 1997; Moberg and Folke 1999). Reefs give to millions of people around the world food resources, like fish, and some studies described that 10% of global fish had caught in coralline area (Smith 1978; Moberg and Folke 1999). Jennings and Polunin in 1996 have calculated that 1 km^2 of actively growing reef can support over 300 people if no other protein sources were available (Jennings and Polunin 1996). The restricted link between reef and mangroves and seagrass beds is further supported by the protection of the reef itself that serve as physical buffer for currents and waves, creating, over geologic time, a suitable environment for the rest of the trio (Moberg and Folke 1999; Ulumuddin et al. 2021). In coral reefs the pharmaceutical industry has found several bioactive compounds like anticoagulat properties, anticancer, AIDS inhibiting, antimicrobial, and anti-inflammatory extracts from different organisms (Sorokin 1993; Carté 1996; Moberg and Folke 1999). Coral skeletons are studied for biomimetic purposes and proven to be promising in bone graft operations (Spurgeon 1992; Sun et al. 2025). Ornamental, collection and jewelry trade are also based on coral reefs (Wabnitz et al. 2003). Reefs are also used as building blocks and

construction materials, mostly where other materials are difficult to obtain (Brown and Dunne 1988). Another fundamental resource that geological time and appropriate conditions have generated is fossil fuel. These resources are thought to exist in large quantities below living and ancient reefs, like Siberia, Saudi Arabia, USA, and Canada. Exploitation of these resources conflicts with all the other uses of reefs and can by no means be considered sustainable (Sorokin 1993; C. Birkeland 1997). Without coral reefs protecting the shoreline from currents, waves, and storms there will be loss of land due to erosion; coral reef also builds up land and generate coral sand, that forms coralline islands (Gardiner 1902; C. Birkeland 1985, 1997; Van Zanten et al. 2014). Finally coral reefs have an important cultural, touristic and social service in all the countries where they grow (Jungblut et al. 2020). For the creatures that live inside this ecosystem, reefs provide protection from predators, because of rugosity and three-dimensional structures (Almany 2004), these structures also create an enormous variety of new ecological niches, are fundamental for reproduction, nursery, spawning and feeding area for complex trophic webs if not the food itself for specific organisms (Birkeland 1997; Moberg and Folke 1999; Harborne et al. 2017). The whole ecosystem is maintained by a group of keystone species, like sea urchins, that control algal overgrowth (Moberg and Folke 1999; Marjorie L Reaka-Kudla 2005; Harborne et al. 2017). This intricate trophic web is constantly under pressure and disturb.

1.2 Sign of change

To discuss changes over historical timescales, it is important to distinguish between natural and anthropogenic disturbances that occur on coral reefs. From the first formation to nowadays natural disturbances such as: hurricanes, changes of sea level, and global temperature changes, have reshaped the reefs several times (Scoffin 1993; Barbeitos 2011). But, in the last 150 years, humans have increased the emission of greenhouse gasses, such as CO_2, CH_4 and N_2O, in the atmosphere, which causes the increasing of global temperature (Smith and Buddemeier 1992; Hansen et al. 2006). In addition to human pressure, an important natural disturbance historically and periodically documented, the El Niño-Southern Oscillation (ENSO) can increase local and global warming (Hansen et al. 2006). Global warming is only one of the threats that reef occur, but in recent years, it is considered the worst, because of the great damage that coral suffer, namely bleaching (Hoegh-Guldberg 1999). In addition, this ecosystem, presents high vulnerability to other human impacts that destroy and cause suffering, like Blast fishing (Braulik et al. 2015), all kinds of pollution (Z. Dubinsky and Stambler 2011), land reclamation (Masucci and Reimer 2019), intensive fishing (Braulik et al. 2015) and excessive tourism (Moberg and

Folke 1999). Reef stability is defined by two main components, resistance, the capacity to maintain the status under pressure, and resilience, the capacity to come back to the previous status after a disturbance (Holling 1973; McManus 2001; Harborne et al. 2017). This ecosystem is disturbance driven and it means that the long-term survival relies on a dynamic balance between natural disturbances and the recovery capacity of the reefs (J. H. Connell 1978; McManus and Polsenberg 2004; Harborne et al. 2017). Many catastrophic events on some of the world's reefs, give a certain level of disturbance, considered intermediate disturbances, that increase the number of species, species diversity and evenness (J. H. Connell 1978; Rogers 1993; Ravitious and Green 2001). It is important to specify that the environmental changes that ocean and in particular coral reefs nowadays suffer are unprecedented in recent history. These stresses are not only intense and pulsed but are spread around the globe, take place over a short period of time and become chronic. And the resilience of reefs is now under constant pressure (Nyström et al. 2000). The results of these stresses and changes are reef degradation, bleaching, and phase shifts, and in these cases the loss of the ecosystem services that they normally provide occurs. Most human-induced impacts fall into four broad categories: pollution, sedimentation and improper land use, overfishing and climate change. (Nyström et al. 2000; Ravitious and Green 2001). Natural disturbance normally occurs in pulses, strong immediate events of short duration (Moberg and Folke 1999; Nyström et al. 2000; Done et al. 2007). These events can be divided into four main categories: meteorological events, biological outbreaks, thermal anomalies and geological factors. Meteorological events can be simplified in hurricanes, cyclones and intense storms that immediately destroy part of the reef, in particular fragile corals and reduce three-dimensional structural complexity (Jackson 1991; McManus and Polsenberg 2004; Marjorie L Reaka-Kudla 2005). Biological outbreaks can sometimes be driven by human impact (Nyström et al. 2000; McManus and Polsenberg 2004) like the case of outbreaks of Crown-Of-Thorns-Seastar (COTS) species which can kill 100% of the corals in a vast area (Done 1992; Haszprunar, Vogler, and Wörheide 2017); or an epidemic disease like the one that in 1980s killed 93-99% of a keystone grazer of the reef (Jackson 1991; McManus and Polsenberg 2004; Bruno et al. 2009). Extreme low tide that exposes corals to air, volcanoes with ash and sediment that choke coral and organisms and earthquakes that alter reef topography are some of the geological influences of the reef (Nyström et al. 2000). The lasts natural disturbances are the thermal anomalies: in normal conditions, during the phase La Niña, east to west winds in the Pacific Ocean push equatorial warm waters towards Indo-Pacific, causing an important upwelling of deep nutrient rich waters off the coast of South America. This normal state occasionally can change, when this east to west trade winds slacken, resulting in the warm

water of Indo Pacific flowing back to South America (Smith and Buddemeier 1992; Hansen et al. 2006). This process interrupts the upwelling of deep water causing the increase of water temperature and the creation of the classic El Niño-Southern Oscillation (ENSO) that exacerbates bleaching effects and duration (Glynn 1993; Wilkinson 1998; Moberg and Folke 1999; Nyström et al. 2000). Research indicates that the western equatorial Pacific is warming up faster than eastern equatorial Pacific that may increase the likelihood of strong El Niños (Enfield 2001; Hansen et al. 2006). Bleaching causes massive coral mortality but is not considered only a natural disturbance, but a combination of effects of a natural disturbance increased in duration, and intensity by human global pressure in terms of increased CO_2 emissions that rise global temperature (Williams and Williams 1990; Fujioka 1999). Further than natural disturbances that are considered intermediate disturbance, now, in the Anthropocene, the main damage that coral reef, and most of the global biodiversity occurs is the one conveyed by human. An important threat that reefs suffer is pollution (Zvy Dubinsky and Stambler 1996). Excessive nutrients from sewage, agriculture, livestock excreta or industry pollution, flow from the river or directly on coral reef. Nutrient enrichment can cause eutrophication that triggers algal bloom which can outcompete corals (Bell 1992; Duprey et al. 2016). If the pollution is toxic, like heavy metal or pesticide, it can impair growth and reproduction (Brown and Ogden 1992; Guzmán and Jiménez 1992; D. W. Connell et al. 1998). Fishing practices can damage both ecological balance of reef ecosystems and their physical structure (Pauly 1998). Overfish predators like groupers and snappers or algal-grazing fish can alter the stability of the reef (S. M. Lewis 1986; McManus 2000). Moreover, destructive methods such as blast fishing shatter coral structures, the use of poisons like cyanide or bleach, and bottom trawling are even worse for the reef (Mulhall 2009). These impacts are often intensified by following the Malthusian overfishing hypothesis (Pauly 1990; McManus 2000). Reefs around the world are under constant pressure, due to proximity to human activities, coastal structure and land reclamation. Some of threats that reefs suffer are related to land use, like habitat loss, marine debris, artificial substrate and artificial light (Wilkinson 1998; Carlson et al. 2019). Data reveals that since 1975 global warming has been driven by greenhouse gasses emission. Global surface temperatures have increased by 0.2°C per decades in the last 30 years (Hansen et al. 2006). Several studies suggest that this climate change, is not compared to any described in geological time, in terms of the rate at which it occurs (Smith and Buddemeier 1992; Hansen et al. 2006; Barbeitos 2011). It is demonstrated that human activities increase the normal natural stress and transforms pulse disturbances in chronic damages for reef, that overlook reef capacity to resistance (Smith and Buddemeier 1992; Wilkinson 1998; Moberg and

Folke 1999; McManus 2000; McManus and Polsenberg 2004). About resilience, the question is open; it is demonstrate that reef recovery is poor if affected by natural disturbance, if they have already been exposed to persistent human disturbances (Brown 1997). The loss of buffer capacity "making the coral reef ecosystem more susceptible to natural disturbance that otherwise could have been absorbed" (Holling 1973). Loss of resilience could cause an unpredictable cascade of effects defined system "flip" also called "Phase-shift" where the system find new stability with almost irreversible change (Done 1992; Holling et al. 1995; Davis Reimer et al. 2021).

1.2.1 Phase-shift

After natural or anthropogenic disturbances in different marine ecosystems, such as kelp beds, rocky shores and coral reefs a regime change called phase shift, may occur (Done 1992; Done et al. 2007; Petraitis et al. 2009; Ling et al. 2009; Davis Reimer et al. 2021). According to the definition, a phase shift is an abrupt and persistent change in community structure and function (Giesel 1970). It is reported that both natural e.g. hurricanes (Done et al. 2007), and anthropogenic e.g. ocean acidification (Kroeker et al. 2013), climate change (Wernberg et al. 2016), urbanization (Heery et al. 2018), overfishing (Ling et al. 2009) and decreases of water quality (C. Birkeland 1988), can cause phase shifts. Climate change widely recognized as a global crisis (Cowie et al. 2022) can act as a driver of ecosystem phase shifts. Indeed, mass coral bleaching events are considered the main cause of phase shift in coral reefs, and ENSO events are drivers of rising temperature. After a phase shift, a comeback to the previous regime is rare, and local anthropogenic major disturbances could exacerbate the problem. Phase shift and consequence live coral cover loss result more in changes in reef structural form than trophodynamic situation, due to the different responses that communities could have after regime changes (Done 1992). It cause reduction on rugosity and habitat complexity that influences the associated biodiversity (Mendonça-Neto et al. 2008; Mora 2015; Igor C. S. Cruz et al. 2015; Davis Reimer et al. 2021). Phase shifts in shallow tropical and subtropical coral reefs are well studied due to their high biodiversity, productivity, importance, as well as their susceptibility. According to (Davis Reimer et al. 2021) many tropical and subtropical ecosystem phase shift studies have focused on shifts from zooxanthellate Scleractinia coral to macroalgal dominance (Hatcher 1984; Done 1992; McManus and Polsenberg 2004; Norström et al. 2009; Bruno et al. 2009). These regime changes could be problematic for human if we consider short or long term (Done 1992). An important case study of Phase shift from Scleractinia to macroalgal is that one happened in Caribbean, where, after overfishing from 1960s to present,

hurricane in 1980, disease and mass mortality of grazing Echinoid, an impressive algal bloom happened, and reduced total coral coverage from a mean of 52% to 3% and , algal coverage from 4 % to 92% (Terence P. Hughes 1994; Meltvedt and Jadot 2014). Other studies have focused on phase shift of different groups of organisms, such as cyanobacteria (Paul et al. 2005), sponges (Rutzler and Muzik 1993), sea anemones (Tkachenko et al. 2007), corallimorpharians (Work et al. 2008) and Zoantharia (Davis Reimer et al. 2021). After a phase shift the consequences that the ecosystem presents are various. Species loss (Igor et al. 2016), lower benthic diversity (Woodruff-Madeira et al. 2026), reduce of substrate structural complexity (Igor C. S. Cruz et al. 2015), erosion of carbonate structure (Graham and Nash 2013; Meira et al. 2023), loss of commercial species such as macroalgae (C. López et al. 2020) and inhibition of coral larval settlement (Nyström et al. 2000; McManus and Polsenberg 2004) are only few. An important change that occurs during a phase shift is the associated community. Ecological changes vary depending on the types of shift (Igor C. S. Cruz et al. 2015), if the ecosystem alters from coral dominated to algal dominated, the community of corallivorous fishes and the coral-related species decline, whereas the grazer can increase (Harborne et al. 2017). All phase shifts could potentially be an alternative stable state (Davis Reimer et al. 2021; Meira et al. 2023).

1.2.1.1 Zoantharia phase shift

The order Zoantharia Gray, 1832, is a part of the class Hexacorallia, subphylum Anthozoa Ehrenberg, 1834, and phylum Cnidaria Hatschek, 1888 (WoRMS Editorial Board, 2026). Zoantharia are closely related to Actinaria Hayward 1990, in fact they are commonly called "colonial sea anemones" or "encrusting sea anemones", they are soft-bodied, like anemones,

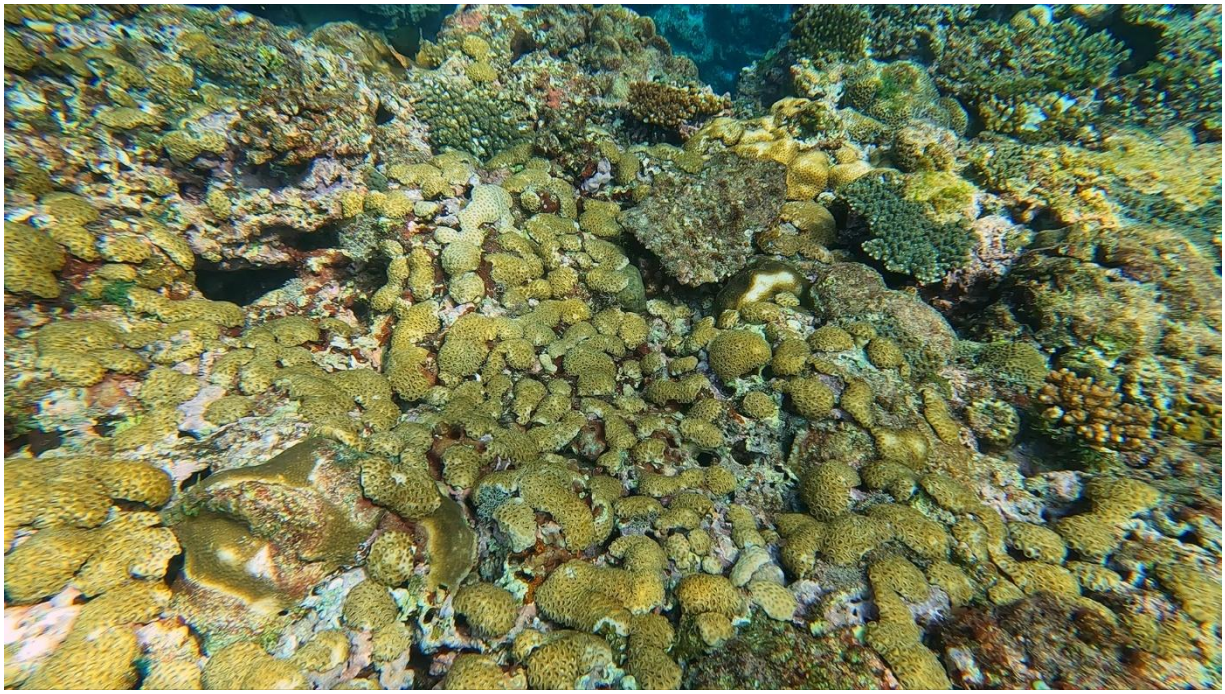

Figure 3 (*The image represents a* Palythoa tuberculosa *phase shifts occurred in Okinawa, Japan, Sosu site where, in some sites, Zoantharia dominates the substrate*).

(with some exceptions), with an oral disk surrounded by two rows of tentacles, retractable when disturbed, or to bring food to the mouth (oral opening). Most Zoantharia grow in colonies, with polyps attached by coenenchyma. Some species have a well-developed coenenchyma and the polyps are almost embedded in (type "Immersae") like *Palythoa tuberculosa* Esper, 1805, (Figure 3).

Other species are included in the type “Lyberae” in this case, the polyps remain individually recognizable with a well-developed erect column or scapus (Ryland and Lancaster 2003) like *Palythoa heliodiscus* Ryland & Lancaster, 2003, (Figure 4).

Figure 4 (Palythoa heliodiscus *found in Maldives (Photo taken by Federico Gualtieri, 2025*)

It is documented that various shallow coral reef in different regions around the world may phase shift from Scleractinia zooxanthellate coral or macroalgal dominance to Zoantharia dominance, called “zoantharian barrens”. It is considered barren when “there was evidence of benthic change, but there had not been enough time to confirm persistence, namely, the maintenance of dominance for five years or more”. It is considered phase shift when it involves “replacement of dominant groups with an increase of zoantharian coverage and a corresponding decrease in the previously dominant group” (Done 1992) and “permanence of Zoantharia dominance for a period of at least five years” (Norström et al. 2009; Davis Reimer et al. 2021). Referring to Norström et al., 2009, to consider a reef a Zoantharia barren or phase shift, it must have more than 25% of coral cover. The areas dominated by Zoantharia usually occur in intertidal or very shallow subtidal waters, often subjected to natural chronic or regular disturbances, like storms, intertidal desiccation or predation, which can limit the growth and expansion of scleractinian corals and macroalgae. Anthropogenic Zoantharia barrens and phase shift instead are deeper, from 1 to 8 meters, and are generated by reduced water quality, with sedimentation, increased turbidity, and wastewater. Despite the lack of a consensus (S.-Y. Yang et al. 2013), Reimer et al in 2021 proposed two possible models to explain how a Zoantharia barren forms: on a stressed

coral reef, after bleaching events scleractinian corals may experience high mortality before zoantharians, leaving free benthic space rapidly colonized by zoantharians thanks to their fast growth rates . Alternatively natural or anthropogenic disturbances may trigger fast Zoantharia growth, allowing them to outcompete Scleractinia and become dominant. In systems originally dominated by macroalgae, outbreaks of sea urchins can remove macroalgae cover leaving space for fast Zoantharian growth (Borges et al. 2019). Based on Reimer et al 2021 review, 13 sites around the world present at least barren conditions, if not phase shift, to *Palythoa*, an important Zoantharia genus located in both Atlantic and Pacific Oceans (Davis Reimer et al. 2021). According to (S.-Y. Yang et al. 2013) the only factor that is statistically correlated with *Palythoa* abundance is the low salinity level, which in marine environments is related to river flows, ground water or precipitation, may therefore be a key factor promoting the presence of *Palythoa*, and may become dominant during phase shifts, in areas influenced by freshwater inputs. Along with low salinity, rivers transport nutrients and sediments, and studies from Brazil have shown a positive correlation between *Palythoa* abundance and nutrient enrichment, particularly nitrate concentrations; and declines in water quality are often mentioned as a mechanisms behind the shift (Costa et al. 2008; Igor C. S. Cruz et al. 2015; Davis Reimer et al. 2021). Consequence of Zoantharia phase shifts includes a reduction in on rugosity and three-dimensionality of the reef, smoothing its structure and generally forming a carpet (Jackson 1991; Cruz et al. 2015). Also a decrease in bio-construction in favor of bio-erosion occurs (Meira et al. 2023), along with the consequences for the environment, such as coastal protection and nursery effects (Meira et al. 2023). The case of the Brazilian phase shift involving *Palythoa* cf. *variabilis* is one of the best studied. Here in Todos os Santos Bay, in Bahia State, the cover of Zoantharia at the sites that suffered a phase shift was calculated as 61-70% and the cover of bioconstructive corals was reduced from 23.3% to less than 1.5% (Igor Cristino Silva Cruz et al. 2016; Davis Reimer et al. 2021; Meira et al. 2023). It was also observed that *P. cf. variabilis* was a better competitor than the main ahermatypic scleractinian corals. The direct contact of coral tissue with *Palythoa* caused necrosis in 78% of the cases, and only 5.5% cover by *Palythoa* was sufficient to affect half of the surrounding coral patches in contact with the zoantharian (Igor Cristino Silva Cruz et al. 2016; Soares et al. 2022). Nutrient enrichment due to sewage outfalls, the proximity to urban areas, and anthropogenic impacts such as port dredging have been positively correlated with the rapid growth of *Palythoa* (Soares et al. 2022; Meira et al. 2023). Despite their success in degraded environments, they also suffer from heat waves. Zooxanthellate dinoflagellates can leave the corals after a thermal stress, causing mortality in the dominated reef, which could allow hard coral recruitment and may represent an opportunity for reversal phase shift (Meira

et al. 2023). Acidification has been shown to reduce the growth rate, weight, and survival of *Palythoa caribaeorum*, a species that overgrowths macroalgae in the Canary Island (Cataixa López et al. 2021; Soares et al. 2022).

1.4 Coral reef fishes, large scale patterns and biodiversity

It is not easy to define what a coral reef fish is, Mora in 2015 discussed the proposal that when someone referred to it the best way to act is identified it as “fishes on coral reef” and not “coral reef fishes”, because of the complexity to define a reef fish. Here, to simplify, we will use both terms equally. Of 36.500 fish species counted (Fishbase, 2026) 5000–8000 are usually cited as reef fishes (Hixon 2011; Mora 2015). However, DNA barcoding and next-generation sequencing expanded this number. Peak of fish biodiversity is concentrated in South-East Asia, within the “Coral Triangle”, with a decline towards edge of Indian and Pacific Ocean. In Atlantic Ocean the peak of biodiversity is concentrated in Cuba and decline towards edge of Caribbean area. Articles proposed different global patterns that explain fishes species richness, temperature has an important role, area, isolation and mid domain effect could be significant too. Basic ecology suggests that the number of species are the result of immigration, emigration, speciation and extinction. It is also essential to consider large scale patterns to better understand coral reef fish distribution. Energy in a coral reef is most of the time linked with temperature and primary productivity. If primary productivity is not strictly correlated with fish biodiversity, data reveal that temperature has varied correlation, from highly to non-significant. Overall, there are three different mechanisms that try to explain how energy drives species richness. “The more individuals hypothesis”, “physiological tolerance hypothesis” and “speciation rate hypothesis”. The first hypothesis could be simplified as productive areas have more individuals and therefore more species, because more genetic diversity of large populations may reduce the risk of extinction. Although it is not strictly correlated with species richness due to the limits of evidence that suggest that food resources are primary driver of fish populations. The second hypothesis postulates that more species can survive in hotter than colder temperatures. However, studies on fish temperature tolerance show that fishes could live in hotter conditions than actually lives, so temperatures are not the only factor, and other mechanism(s) are currently underway. The last hypothesis postulates that “higher temperatures increase metabolic and reproduction rates thus promoting higher rates of speciation”. There are other suggestions that show relationship between temperature and fish diversity, herbivorous fish feeding and digestive processes rate are influenced by temperature and herbivorous feeding rate decreased rapidly as the temperature decreased. Another important correlation whit temperature is the one that links

diversity and coral survival, that can affect habitat availability and consequently species richness. Area and isolation are well studied to test the explanation of diversity of reef fishes; isolation hypothesis is well supported instead of the role of area which is more variable. The area and isolation effect are explained by the principle of island biogeography and the more individual hypothesis's role in speciation. Nevertheless how population patterns translate into higher risk of extinction is unclear. Fish rare species are an amount of total biodiversity, still it is unclear how they manage not to go extinct. There is strong evidence that correlate regional and local diversity that show the contrary of the role of area and isolation "(i. e. local populations are unsaturated and open to the immigration of species from regional pools)". Mid-domain effect postulates that "a gradient in species richness that features a peak of diversity in the center of the domain can arise from the overlap of ranges randomly placed between the bounds of the domain". Mid-domain effect has been tested several times, even for reef fishes, and its effect shows significant effect in regional, interoceanic and at least one global-scale analysis. The logic underlying mid-domain is that it is not related to ecology or biology of the species but only talks about spatial constraints. Indeed this is also his weakness and the reason because scientists consider it controversial. Species areal distributions are of course relate to the presence of environmental gradients or ecological factors, in contrast with the logic of the effect. Following the niche theory which states that: "the spatial distribution of species can be explained as a result of the interactions among species and the species' tolerance to their environment". The limits of the domain are arbitrary, and this could explain why regional studies where the limits are well-defined are well explained by the domain, and where the limits are difficult to trace like global scales the domain is weaker. However, this limitation is due to our incapacity to predict species boundaries and distribution. Rapoport's rule postulates that "gradients in species richness arise indirectly from the tendency for latitudinal range size to increase toward the poles in response to environmental variability", it is not supported by data. Most fish of the reef present their mid-point ranges in tropical areas, in contrast with the rule. And the tendency of the areal dimension following the mid-domain effect, so a simple geometry effect. Environmental stability is strongly related to the intermediate disturbance hypothesis, which shows that species richness is higher when the disturbance is neither too rare nor too frequent (Mora 2015). The last pattern that could explain reef fishes' biodiversity is the complexity of their history and the earth history itself.

1.4.1 Coevolution of reef fishes and their habitat

Based on specimen identified using synapomorphies, it is generally accepted that the earliest record of coral reef fish family was in the Paleocene (66–56 Ma). Reef fish assemblages are the result of at least nine family-level invasions. By combining fossil and molecular analysis, it has been possible to estimate that there were at least six major phases in the evolution of coral reef fishes and in the development of reef fish ecology. The Cretaceous-Paleocene boundary (~66 Ma), represents a key moment, as the mass extinction of dinosaurs and ammonites triggered the evolution of modern coral reef fish families. Subsequently, another mass extinction at the Eocene–Oligocene boundary (34 Ma) occurred, which coincided with significant climate change and shift of marine biodiversity hotspot from the Tethys Sea of Europe to the Indo-Australian Archipelago. Here, molecular evidence suggests that reef fish lineages underwent a period of rapid expansion (Mora 2015). During the Miocene (23–5 Ma), species increasingly resembled modern teleost in terms of specialization, including close fish coral interaction, trophic links, and high-turnover food resources. Moreover, this period corresponds to the highest fish lineage diversification (Mora 2015).Studies shows that there is a strong relationships between coral and fish genera diversification throughout the Cenozoic; however these patterns appear to be closely linked to the expansion of reef rather than to corals themselves (Bellwood et al. 2017). Over the last 5 Ma years, diversification has been characterized by extensive species differentiation, but almost none functional changes (Mora 2015). Notably coral diversification increased markedly during this period, but it occurred later than peak of fish diversity (20-10 Ma). This suggests that coral association is not the main pattern of diversity. In contrast strongly coral-associated fishes presents slower diversification pace to non-coral associated ones, with only exception of coral-dwelling gobies (Duchene et al. 2013; Siqueira et al. 2023).

1.4.2 Ecological niche and functional groups

Ecological niches proposed by Hutchinson can be simplified as “the range of environmental conditions under which a particular individual has an expected lifetime reproductive success of ≥ 1” (Takola and Schielzeth 2022). Ecological niche can be divided into two different categories: the fundamental niche, which includes all environmental (abiotic and biotic) variables, where species could live; and the realized niche, which involve both environmental variables and inter and intraspecies interactions (Polechová and Storch 2018). Reef fishes play different roles in the ecosystem; therefore, one way to classify them and their interactions with the environment is through trophic groups or niches. These are classically divided into: detritivores, planktivores, herbivores and carnivores. (Hiatt and Strasburg 1960; Polechová and Storch 2018; Coker et al.

2023). However this classification is often used due to the limited knowledge on the specific prey they feed on (Coker et al. 2023). Nevertheless, attempts to refine trophic groups allow for greater resolution within these categories. Herbivores, for instance, can be divided into several functional groups: territorial algal turf grazers, organisms that cultivate and crop a small patch of multi-specific algae and defend it (Peter F. Sale 1991; A. Lewis 1997); algal turf grazer, which roam and feed across multiple algal patches (A. Lewis 1997); browsers, which consume established macroalgae (Puk et al. 2016); excavators, which, due to their thought and heavier jaws, can excavate deep bite on corals removing part of the environment, contributing significantly to bioerosion and acting as ecosystem engineers (P. F. Sale 2002; Mora 2015); and scrapers, which, in contrast, scrapes the surface of the same hard surfaces (P. F. Sale 2002). Planktivores fishes, which feed on zooplankton, can be further divided into diurnal and nocturnal, following their daytime activity (W. P. Collins et al. 2022). Detritivores on the other and feed on substrate, ingesting detritus, particulates and/or microbial photoautotrophs, and process this material via mechanical trituration (Choat et al. 2002). Last trophic group, carnivores, includes piscivores, corallivores, and invertivores, which feeding in other invertebrates, such as mollusks and crustacean (A. Lewis 1997). In addition to trophic niches, spatial niches also play a key role. Reef zonation, divided in lagoon, back reef, reef flat, crest, slope and fore reef, creates distinct environmental conditions and therefore different ecological niches (Mora 2015). Moreover. temporal variation contributes to niche differentiation: diurnal fishes are generally more specialized, whereas nocturnal species are often more generalized, particularly in mesocarnivorous strategy. The twilight period is unique in coral reef, here fish often exhibit a “quite period” because large nocturnal piscivores become most active (Peter F. Sale 1991).

1.4.3 Interaction in coral reef fishes

Fishes interact with the reef substrate in multiple ways, using it as refuges, food (e. g. corallivorous and herbivorous), nest, or simply as habitat in which to occupy specific ecological niche (Mora 2015; Moynihan et al. 2022). In order to talk about interaction with the reef, it is necessary to distinguish between reef-associated fishes and coral associated fish (Siqueira et al. 2023). It is estimated that only 5-12% of reef fishes are strictly related to live corals (Mora 2015; Coker et al. 2023; Siqueira et al. 2023). Coevolution is considered another important driver of global scale pattern of diversity (Medeiros et al. 2018); moreover, the intricate network that link fishes of the reef and the reef instead represents the outcome of long-term interdependent evolutionary relationship.(Bellwood et al. 2017; Siqueira et al. 2023). Coral morphology also

could play an important role in the relationship between fishes and corals. The three dimensional substrate offered by branching, tabular, massive and encrusting hard corals differs. (Kerry and Bellwood 2012) suggests that massive hard corals gain less structural benefits for large reef fishes than tabular ones, but provide microhabitats for smaller reef fishes (Precht et al. 2010). Moreover undercut edges of massive corals provide similar benefits to those offered by tabular corals (Kerry and Bellwood 2012). A species of Pomacentridae, *Pomacentrus amboinensis* Bleeker, 1868, lives commonly associated with reef dominated by massive hard corals, and members of Tetraodontidae, like the genus *Arothron* Müller, 1841, feed on the live coral tissue of massive hard coral.(G. P. Jones 1988; Terry P. Hughes et al. 2017). The genus *Elacatinus* Jordan, 1904, a cleaner goby of the Caribbean, uses massive hard coral as cleaning station. If the cover of those corals decreases or a phase shift occurs, these species could change substrate, using encrusting coralline algae, echinoderms or zoanthids as alternative cleaning station base. There is also a positive correlation between massive hard coral density and size and fish species richness (Igor C. S. Cruz et al. 2015). The loss of massive hard coral and their replacement by zoanthids may reduce rugosity and tree-dimensional structure. Is has also been observed that fish communities changed, with an increase of benthic invertivores that found refuges between softer tentacles of the new rulers (Igor C. S. Cruz et al. 2015; Meira et al. 2023). Biting on massive hard coral is more difficult than other branching forms, and this morphology could be important to understand fish behavior (Cole et al. 2008), biting branching morphs could become a complete branch removal by a singlefish bite, whereas, on massive morphs could results in a smaller bites (Cameron and Edmunds 2014). Encrusting hard corals, on the other hand, grow in less turbid water, with higher hydrodynamics, and reinforce, cement and bind reef structures (Stoddart 1969; Hallock 1997; Peter A. Todd 2008; Hennige et al. 2008; Wild et al. 2011; Lough and Cantin 2014; Cresswell et al. 2020). Their morphology, like that of massive corals, reduces biomass and abundance compared to branching or tabular ones (Kerry and Bellwood 2012). *Porites rus*, an encrusting or submassive hard coral, shows a positive correlation between live surface area, number of holes and amount of interior empty space and fish abundance (S. J. Holbrook et al. 2002). Despite their differences in morphology, the mere presence of living tissue is a critical factor for fish species richness (S. Holbrook et al. 2008). Reef slope, where massive and encrusting hard coral are dominant due to the strong current and high wave energy, are characterized by the prevalence of carnivorous and planktivorous species (Terry P. Hughes et al. 2017). Despite all of these, some obligate corallivores Chaetodontidae, like *Chaetodon lunulatus*; and facultative corallivores, like *C. citrinellus* and *C. kleinii* showed significant positive use of encrusting and massive hard coral rather than other forms likes corymbose or

tabular. And Nanami, 2020 suggested that butterflyfishes feed more easily on polyps of less complex corals than on corals with greater morphological complexity. Encrusting and massive forms could be an important habitat and food for obligate and facultative corallivores, and habitats dominated by them could be an important foraging sites (Nanami 2020).

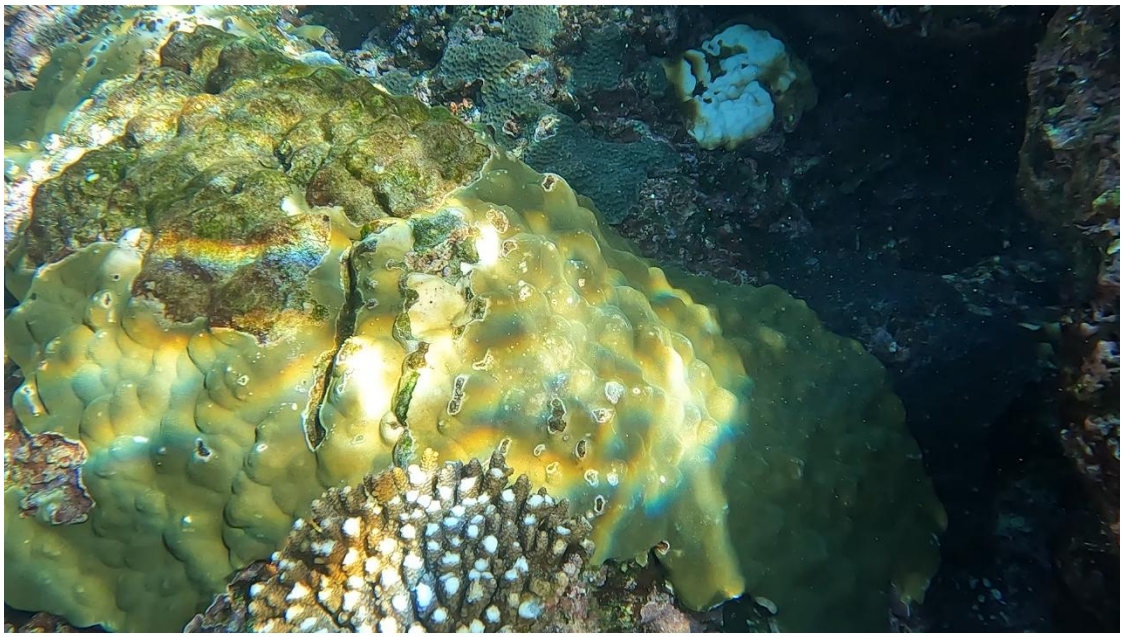

Figure 5 this image shows different encrusting hard corals that inhabit Mizugama site

Broadly, interaction include competition, predation and symbiosis (Hixon 2011; Karplus 2014; Mora 2015). Competition occurs when individuals affect another one by consuming common, limited resources. Consequently, it may reduce individual fitness, population growth rate, and long-term abundance. Competition can be divided into interspecific and intraspecific, occurring between different and the same species, respectively (Mora 2015). Competition also involves both food and space. Food resources in coral reefs are highly diverse and often not the primary limitation; in contrast, space is more frequently limited, because it is importance for mate/nest, for shelter or simply for territorial species, access to food resources. Last competition is competitive interaction, where fishes could exploit resources and consume it enough to reduce their availability to others. This competition could occur without interaction between the actors, like organisms that feed on the same resources but in different daytime (competition by exploitation). On the other hand, interference competition involves direct interactions between individuals, such as aggression for territory, resource theft, or behaviors that increase energetic costs or cause injury (Mora 2015). Predation is defined as the consumption of one organism (the prey) by another (the predator) (Nikinmaa 2014). It is often considered primary interaction among species; capturing prey and escaping from predation (piscivorous) are historically but

not robustly considered the major role to drive populations dynamics and structuring communities of fishes on coral reef. Large top predators such as sharks and big bone fish like grouper (Epinephelidae Bleeker, 1874), jack (Carangidae Rafinesque, 1815), barracuda (Sphyraenidae Rafinesque, 1815) and snapper (Lutjanidae Gill, 1861) are globally overfished. However, fishes settle on the reef as tiny post-larvae, during that period a large group of organisms prey upon them, thereby influencing community composition. As a result, the overfishing of large predators may allow piscivorous mesopredators that feed on post-larvae to proliferate, generating a phenomenon known as “mesopredator release”, which can trigger a trophic cascade, increasing mesopredator abundance while reducing the survival of recruits and small fishes. The importance that these groups and other organisms have on new recruits can be substantial and except in case of Malthusian overfishing most of the mesopredator piscivorous fishes are not targeted by most fisheries (Mora 2015). In order to feed on corals, corallivores had to envelop a particular type of feeding, the manipulation, in which the jaws are directly applied to the prey and used to remove it from the substratum (P. F. Sale 2002). Coral-feeding species are most numerous within Chaetodontidae Rafinesque, 1815, but also in: Labridae Cuvier, 1816, Tetraodontidae Bonaparte, 1831, Monacanthidae Nardo, 1843, Pomacentridae Bonaparte, 1831, subfamily Scarinae (Westneat and Alfaro 2005) (family Labridae), Rafinesque, 1810, Balistidae Rafinesque, 1810, Gobiidae Cuvier, 1816, Blenniidae Rafinesque, 1810, Ostraciidae Rafinesque, 1810, live corals can be part of the diet. within these families, some species are obligate corallivores (more than 80% of their diet is based on corals) whereas others are only facultative live coral feeders. The proportion of species within a family that feed on coral is low, typically <10%, except Chaetodontidae, where it exceeds 60% (Mora 2015). Corallivores may feed on different part of the corals, some of them are polyps feeder, like the pickers (Chaetodontidae) that bite directly the coral, tearing of it (P. F. Sale 2002, 2002); other feed on mucus product by the corals (P. F. Sale 2002, 2002; Karplus 2014). Studies reveal that one-third of corallivores fishes are obligate (Cole et al. 2008b).

Coral feeder primarily focus on Scleractinia; however some species, of Chaetodontidae often feed on soft corals (alcyonarian) (Cole et al. 2008b) and facultative association occur when fishes use soft corals as a food source or refuge (Lim et al. 2026), although no species are obligate soft coral corallivores (Cole et al. 2008b). Soft coral has seems to have positive correlation between fish species richness and soft coral cover (Epstein and Kingsford 2019). Within corallivores only two families, Chaetodontidae and Pomacanthidae Jordan & Evermann, 1898, are considered Zoantharia feeders (P. F. Sale 2002), Notably, eDNA analysis of Chaetodontidae stomach content have confirmed that Zoantharia is part of the diet (Coker et al.

2023). A specific genus of Zoantharia, *Palythoa* contains Palytoxin (PTX), one of the non-proteinaceous and structural complexities strongest marine biotoxin (Walsh and Bowers 1971). Different studies shows that different organisms feed on *Palythoa* (Fukui et al. 1987; Bonaldo et al. 2005; Mendonça-Neto et al. 2008) and mucus and polyps are considered palatable for a variety of species (Gleibs and Mebs 1999; Mendonça-Neto et al. 2008; Biré et al. 2013) also palytoxin has been detected in different fish species (Fukui et al. 1987; Kodama et al. 1989) despite the dangerous of the toxin (Gleibs and Mebs 1999). Coral hormone and chemical molecules may also play a role in larval settlement, as chemical signals can guide larvae toward suitable habitats (Mora 2015). In addition 320 species from 39 families are reported to use live coral as habitat. Both juveniles and adults may use live corals as shelter. Structural complexity and three-dimensionality provides refuge from predators, and enhances post-settlement survival (Mora 2015). When these bond, during geological times, became closer, it may develop into symbiotic relationships (Roughgarden 1975). For example, Fish that inhabiting coral branches, can fertilize the coral, excreting ammonium from the gills, or defecating, thereby benefiting the host (Meyer and Schultz 1985; Karplus 2014). Some nocturnal Pomacentridae behavior increases oxygen availability to corals through movement, while also scatter detritus that can choke polyps. Finally some small fishes has found inside coral an optimum habitat, referred to as coral dwellers (Karplus 2014).

1.4.3.1 How to study fish-coral interactions

In order to study fish-coral interactions without removing organisms, several methods have been used, from SCUBA at the surface to ROV in the deep (Edgington et al. 2006; Lindfield et al. 2014). Underwater Visual Census (UVC) method is commonly used to study fish biodiversity, abundance/density and body length. There are three main types of UVC: visual transect, point counts and rapid visual techniques. All of these involves the operator remaining in the water, and counting fishes; they produce quantitative data and have minimal post-survey processing. Like all others sampling methods, it presents limitations. The presence of the operator in field most of the time using SCUBA, generates bubbles and sound which may reduce fish abundance and species richness. And it can take several hours for the community to recover after the disturbance. Moreover, divers conducting UVC surveys must also be experts in fish identification; differences in experience between operators may induce errors in fish counting or in determining body length or distance. Data collected cannot be validated or controlled after being collected. Diver Operated Videos, (DOVs) are videos recorded along transects; they

provide the possibility to estimate length and identify species with more precision. However, fish behaviors are still altered by the presence of the diver. Baited Remote Underwater Videos (BRUVs) are commonly used to study fish behavior; attracted by animal or algal baits, results can change depending on different baits or environmental condition. Unbaited Remote Underwater Videos (RUVs) can capture natural behavior without interference or attraction. Fish activities are normally quantified using focal sampling, like the number of bites, or counting the frequency of each behavior within the camera range (Hsu et al. 2025; Lim et al. 2026). All these methods cannot provide estimates of abundance and density, because of the high probability of overestimating the community due to double counting of the same individual. There are two common methods to estimate the relative abundance: one is MaxN, the maximum number of individuals recorded at any timepoint across the video; the second is "MeanCount", the average number of individuals over a given number of time points or frames sampled from the video. Analyzing videos is time-consuming and Artificial Intelligence and deep learning algorithms can identify species, tracking them and counting behavior faster and with more efficient (L. Yang et al. 2021; Hsu et al. 2025).

1.4.4 Phase shifts and coral reef fishes

Almost all studies which focused on the relationship between phase shifts and coral-associated fishes are based on a shift from Scleractinia-dominated habitats to macroalgal dominated-habitats. Several studies have assessed that herbivorous fishes are fundamental in mitigating phase shifts from coral reef to macroalgal dominance. Only a few families are considered capable of feeding on mature macroalgae and thus reversing macroalgal phase shifts; they are: Siganidae Richardson, 1837, Kyphosidae Jordan, 1887 and some *Naso* species Lacepède, 1801 of Acanthuridae Bonaparte, 1835. When a phase shift occurs and the benthic community dramatically changes, major shifts in fish assemblages are likely to unfold. A shift from coral cover to macroalgal cover will also typically result in a reduction in reef structural complexity, which is known to have major impacts on the abundance, composition, diversity, and size structure of reef fish assemblages. The fish community associated with coral and the fish community associated with macroalgae are different. Coral feeder fishes include Chaetodontidae, Labridae, and Tetraodontidae, completely different from macroalgal feeders: Acanthuridae, Scarinae, Siganidae, Ephippidae Bleeker, 1859, Kyphosidae, and Pomacanthidae. Even regarding the usage of macroalgal beds as habitat, the community is strongly different; therefore, major benthic phase shift should result in a parallel shift in the assemblage of fishes inhabiting that reef (Mora 2015). Fish responses to different phase shifts are not well

documented; if a phase shift occurs from hard coral to sponges, it is supposed that these organisms might have the capacity to provide an alternative, structurally complex habitat (Seemann et al. 2018; Coppock et al. 2022), with the major problem of larval settlement, which relies on coral scent (Mora 2015; Coppock et al. 2022). The limited role of soft coral-dominated substrates for reef fishes has been well documented, with very low α-diversity; however, a low β-differences from patch reefs with rock alone has also been reported (Syms and Jones 2001; Mora 2015). As demonstrated by Lim et al. (2026), certain soft coral species support a diverse array of reef fishes, with structural complexity positively influencing fish abundance and chemical defenses potentially shaping species-specific associations. The Zoantharia phase shift is not well documented; only a few studies are interested in fish assemblages after such changes (Igor C. S. Cruz et al. 2015). In the Canary Islands it has been noted that the reefs dominated by *Palythoa* show less fish abundance and species richness than macroalgal-dominated beds (Moreno-Borges et al. 2022). On the Brazilian coast, a phase shift to a species of *Palythoa*, *Palythoa* cf. *variabilis* Duerden, 1898, has been studied, in order to assess whether fish communities differ between normal reefs and *Palythoa*-dominated reefs. The shifted reefs present 20% fewer species than normal reefs, show different trophic fish assemblages, and a higher proportion of mobile invertivores. Furthermore, Zoantharian-dominated reefs had a higher density of *Chaetodon striatus* Linnaeus, 1758, in contrast with previous literature, but no difference in fish abundance (Igor C. S. Cruz et al. 2015). Bleaching events can also cause drastic changes in specialized fish communities, leading to more species of habitat- and feeding-generalist fishes, such as in the case of Orpheus Island (Bellwood et al. 2006), where even after coral recovery the fish community remained unchanged (Bellwood et al. 2012).

2. Aim of the Thesis

On shallow tropical coral reef many studies have focused on phase shift from zooxanthellate scleractinian coral dominance to macroalgal dominance, but only a limited number have focused on phase shifts from Scleractinia and algal dominance to Zoantharia dominance. Moreover, even less studies focused on phase shift to Zoantharia dominance in the Pacific, examined the consequences of such shifts on fish communities and coral-associated fishes. Since *Palythoa* spp. and other Zoantharia are known to reduce structural complexity and habitat heterogeneity, a shift toward their dominance may significantly alter the composition and behavior of reef fish assemblages. To gain a better understanding of the future of coral reef if Zoantharia barren spread and substitute hard coral, it is important to understand how coral-feeding and coral-associated fishes interact with toxic corals compared to hard corals. Encrusting and massive

Scleractinia were selected as the reference group through their morphological similarity with *Palythoa* spp. patches. Therefore, this study aims to assess whether coral-associated fishes differ in abundance and interaction between patches of two species belonging to the genus *Palythoa*, *Palythoa tuberculosa* and *Palythoa heliodiscus,* and massive or encrusting hard corals within different sites in Okinawa, Japan, where *Palythoa* patches are notably abundant and one where phase shift already happened.

3. Materials and methods

3.1 Geographical region and study sites

The Ryukyus is a subtropical archipelago located in southwestern Japan, they including approximately 160 islands. Okinawa island (Okinawa-jima in Japanese) is the largest (1208 km^2) and most populated island in the archipelago (Veron 1992; Masucci and Reimer 2019), (Japan Statistics Bureau. 2017). Ryukyus archipelago presents important coral reef cover, 90% of the Japan's Scleractinia species (~360 species out of ~415) (Veron 1992) and Okinawa island in particular present at least 68 of the 83 known genera of Scleractinia found in Japan (Hisata et al., 2025). Japan also presents significant zoantharian biodiversity, with 14 of all 27 presently recognized genera. However, the designation as a global hotspot for Zoantharia diversity should be an inaccuracy, due to lack of information from surrounding countries and regions (Reimer and Fujii 2017). This high diversity of coral species and well-developed coral reefs in higher latitude is maintained by the warm currents of Kuroshio and Tsushima (Hongo and Yamano 2013; Iguchi and Hongo 2018). The reef structure around Okinawa Island is divided in bathymetric and geomorphology zone (Irei et al. 2011). The moats are shallow lagoons few meters deep, with low water exchange, the substrate is sand and gravel with coral rubble. Thanks to the low water exchange and low currents the moats are affected by runoff of freshwater from terrestrial ecosystem that lowers the salinity (Irei et al. 2011; Iguchi and Hongo 2018; Soyoka Muko et al. 2019; Nishitsuji et al. 2023). Fringing reefs are the main type of coral reef ecosystem along the Ryukyu Archipelago and Okinawa island (Hongo and Yamano 2013; Masucci and Reimer 2019) and all the sites in this study are of this types of reef. The genus *Palythoa* is well distributed around Okinawa, and the sites that are chosen for this study, were chosen to provide sufficient coverage of *Palythoa* spp. and massive or encrusting hard coral and one site for the presence of a uniqueness reef, with *Palythoa heliodiscus*. Mizugama (Fig 6) (26°21′35.17″N, 127°44′18.88″E), located in center west of the island, is a well-studied site in Okinawa. Several

papers have already taken place here and the great Zoantharia cover makes it a good site (S.-Y. Yang et al. 2013; Davis Reimer et al. 2021). According to the literature, the presence of the Hija River, located 390 meters from the site, may have played a crucial role, as Reimer et al. (2021) reported, for the phase shift from Scleractinian corals to *Palythoa tuberculosa* in the same area. Here the patches of *Palythoa* and hard coral are on the flat, and during low tide corals remain only one meter below the sea surface. Ginowan (Fig 6) (26°17'20.01"N 127°44'38.77"E) is also positioned in the center west of the island and distant 580 meters from an unnamed Urban runoff channel, the unique feature of this reef is the dominant presence of *Palythoa heliodiscus* that growth only in the first meters of the reef slope. Yona (Fig 6) (26°46'02.07"N 128°11'40.99"E) lies northwest of the island, also near Yona River's mouth. Here patches are distributed on the flat, this site is located in the least developed part of the island. Sosu (Fig 6) (26°47'31.7"N 128°19'13.2"E), the most exposed site, is found in the northeast of the island, in the Kunigami district, in a region called Yanbaru. Is one of the most protected and best conservated area in the island, 10 km of natural coastline are part of the UNESCO World Heritage Site of Yanbaru. Watercourse flows too and big patch of

Palythoa tuberculosa growth on reef flat here. Is defined as an important coralline community, but no study has ever been carried out here before.

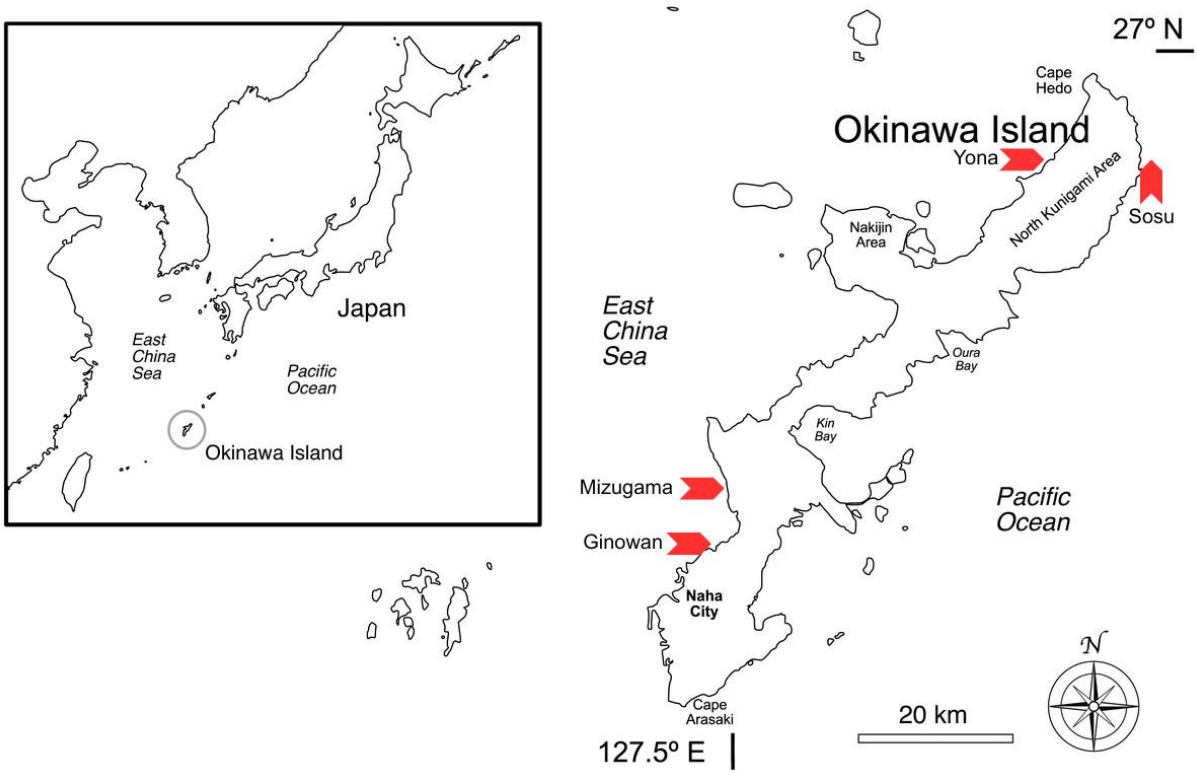

Figure 6(*Masucci & Reimer, 2019, Okinawa Island and surrounding areas in southern Japan, northwestern Pacific Ocean and the four location discusses in this research*).

All the sites, using literature information, have been tabulated as follows:

	Sites	Mizugama	Yona	Sosu	Ginowan
1	**Turf coverage%**	~41.8	~48.7	ND	~64.5
1	**Hard coral coverage%**	~15.3	~47.1	ND	~10.9
1	**Soft coral coverage%**	~32.5	~0.1	ND	~20
1	**Of which *Palythoa* %**	~9	<0.1	ND	<1
1	**Other %**	~10.4	~4.1	ND	~4.6
2	**exposure**	SW	NW	NE	SW
	***Palythoa* species considered**	*P. tuberculosa*	*P. tuberculosa*	*P. tuberculosa*	*P. heliodiscus*
3	**Currents**	Kuroshio	Kuroshio	Ryukyu's current	Kuroshio
3	**Currents direction**	NE	NE	NE	NE
4	**Anthropogenic Pressure Score**	2	8.5	6.5/7	2
2	**River by 600m**	Yes	Yes	Yes	Yes
2	**River's Name**	Hija river	Yona river	Sosu river	Unnamed channel
5	**River's quality**	B	ND	ND	ND
5	**COD* mg/L**	1.1	ND	ND	ND
5	**BOD* mg/L**	0.8	ND	ND	ND
6	**Land reclamation**	High	Low	Low	High
7	**SPSS**	5a	ND	6	ND

*Table 1: **1** % coverage (S.-Y. Yang et al. 2013; Lalas et al. 2024); **2** River by 600m, exposure, River's name (using Google Earth Pro (7.3.7.1155));**3** Currents (Cruz Salmeron et al. 2022); **4** Anthropogenic Pressure Score (DiBattista et al. 2020); **5** River's quality, BOD (Biochemical Oxygen Demand), COD (Chemical oxygen demand) (Water Quality Measurement Results, 2025); **6** Land reclamation (Masucci and Reimer 2019; Nakajima et al. 2025); **7** SPSS (Content of Suspended Particulates matter in Settled Sediment) (Okinawa Prefectural Government, 2021)*

Due to the extreme differences of the sites, related to the exposure, lack of previous data, distances, human pressure, coral coverage; and due the arbitrary decision of the sites because of the presence of enough *Palythoa* spp. coverage and the arbitrary chosen of *Palythoa* spp. and hard coral patches; Mizugama, Sosu, Yona and Ginowan sites, were considered separated.

3.2 Data Collection

During the period from September to December of 2024 the research fellowship in Okinawa was conducted, there, due to the MISE (Molecular Invertebrate Systematics and Ecology) lab, sites were selected for the strong presence of both *Palythoa tuberculosa* and *Palythoa heliodiscus* and massive or encrusting hard coral patches. Deployments took place on SCUBA during daylight hours (8.00 – 17.00), at maximum 5 meters depth, to make the most of the light and at high tide, to reduce the risk of damaging and be damaged from the corals. A PVC pipe

frame was used as a camera stand; it consisted of a square frame (50cm x 50cm) and a vertical pipe (50cm high) in which, through the holes, a GoPro accessory and a bolt kept the camera blocked (Fig 6). To keep the frame for the entire duration of the video on the seafloor, SCUBA weights were attached using zip ties (Fig 6). Two GoPro Hero 10 cameras and one GoPro Hero 9 camera were used, each enclosed in a waterproof housing and set to record at 1080p resolution with a wide field of view at 60 frames per second. Cameras were positioned at a straight angle to restrict the field of view to the reference frame (1 m × 1 m) and reduce wide-angle distortion. Reference frames were important to set a scale of the patch and to ensure a standard patch dimension. Each frame was first positioned over corals that filled at least 50% of the quadrat. The three cameras were deployed simultaneously on different focal colonies, at least 1 meter far from each other and oriented differently to avoid field-of-view overlap. After a first short recording of the entire frame, which was subsequently been used as a scale reference video, the frame was removed and with the GoPro in the same position, the ~25/30 minute videos were started. The corals were chosen from four different groups, *Palythoa tuberculosa*, *Palythoa heliodiscus*, massive hard coral, and encrusting hard coral, where *Palythoa tuberculosa* and hard coral, occurred in Mizugama, Sosu and Yona, while *Palythoa heliodiscus* and hard coral were found in Ginowan. Encrusting and massive Scleractinia corals were selected for their similar growth form and were considered together as hard corals without branching or three-dimensional morphs, in order to make the best possible comparison with *Palythoa*. The limited number of plots (replicates) (Table 1) has already been considered due to adverse weather conditions during the rainy season, time constraints, and the preliminary nature of the study.

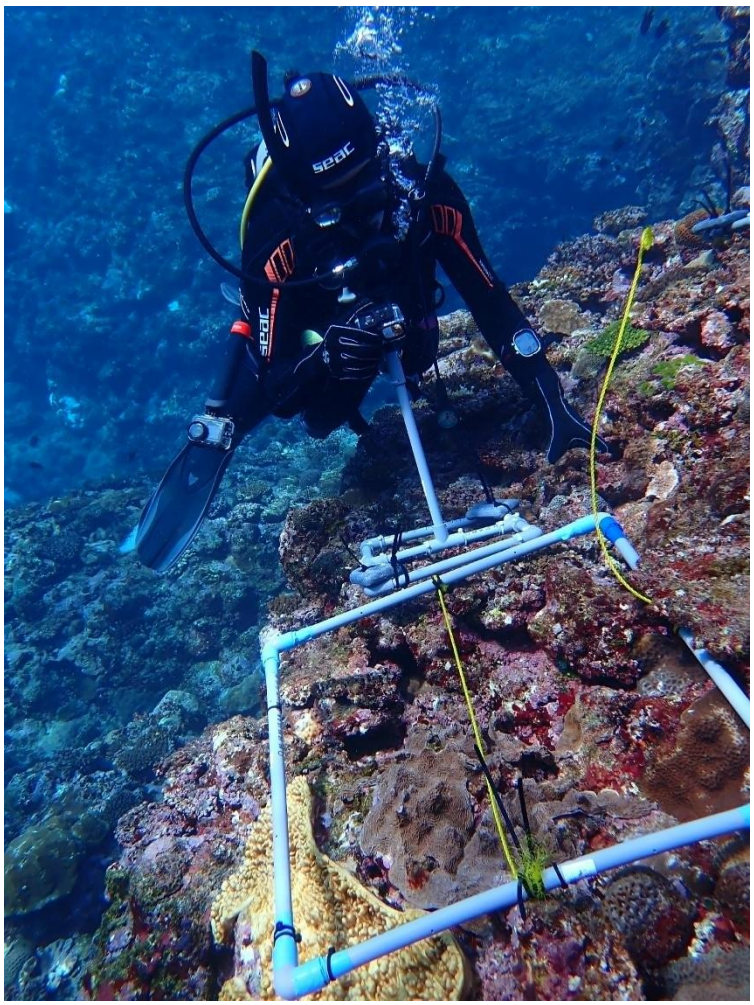

Figure 7 (*Positioning the camera frame at correct distance to see the entire reference frame*).

3.3 Data Analysis

Each video (approximately 25–30 minutes in duration) was analyzed using Media Player Classic.Ink (2.3.6). To minimize human interference caused by the positioning and removal of the plot, analysis was standardized and restricted to the central 20 minutes of each recording, excluding the opening and closing segments. All data were compiled in Microsoft Excel (2604). To standardize the sampling frame, the reference video for each plot was used as a dimensional reference, with black tape attached to the screen to exclude the external area. Each time a fish entered or exited the frame area entirely, a timestamp was captured and the specific behavior was recorded. Fish were identified at the lowest taxonomic level possible, with the help of a fish expert. To better visualize all the data, and due to the difficulty to identify all the organisms at species level, we decided to use the Operational taxonomic unit (OTU) definition. Juveniles were not considered, and trophic groups, vulnerability, habitat, substrate and diets were determined from the literature. The maximum number of individuals of a given species

simultaneously present inside the frame was used as a proxy of abundance and referred to as MaxN. The starting and ending times of each behavior performed by a species were recorded as timestamps and later used to calculate the Total Time Interaction (TTI), using the formula: =IF(A1=0;1;-(B1-A1)+1), TTI includes every type of behavior, Behaviors were classified into two categories: interaction and no interaction. Interaction included only biting, whereas no interaction comprised hiding, scratching, static, swimming above, and territorial behavior. Statistical analyses were carried out in Rstudio software (2025.05.0+496). For each species, Time Interaction was quantified as the duration spent performing a given behavior, rather than the number of events. Shannon diversity and species richness were calculated, Wilcoxon-Mann-Whitney test were used.

Box plot were created with Mean, SD and median, Outlier were visualized using a standard criterion:

lower <- Q1 - 1.5 * IQR_val
upper <- Q3 + 1.5 * IQR_val

Outliers were retained in the dataset as they represent biological variability rather than measurement errors, and the possibility to bias introduction, after the removal. Only one plot, the 12th were removed from MaxN analysis, due to a school of *Acanthurus nigrofuscus* Forsskål, 1775. Boxplot, of mean MaxN, Total Time Interaction (TTI), Total Time Interaction of Biting, Static and Hiding (TTI Biting, Static, Hiding), Proportion of TTI Biting / TTI per site and treatment were carried out; and a Wilcoxon-Mann-Whitney Test were used to test the statistical differences of treatments between proportions. Pie charts were constructed to visualize the Trophic group distribution for each site, between hard coral and *Palythoa* spp. To further investigate the relationship interactions, we performed multivariate analysis to evaluate statistical differences of MaxN, TTI, TTI biting, trophic group, between treatment across sites. After Shapiro-wilk test and Levene's test normality of the data and homogeneity of the variance were not satisfied, so, Permutational Multivariate Analysis of Variance PERMANOVA, and Permutational Analysis of Multivariate Dispersions PERMDISP were carried out. MaxN, TTI, TTI biting and trophic group were also examined using GLMMs, Generalized Linear Mixed Models, using Plot and Species, or only plot as Random Effect; and Treatment, Species and Trophic group as fixed effect. Considering n_plot >= 2 the threshold of minimum number of times a species is presents in at least one hard coral and one *Palythoa* patches. To gain a better understanding of the community composition and trying to gain a different overview of the data, vulnerability, substrate and habitat trait were obtained from Fishbase (Fishbase, 2026). Also

SIMPER analysis were carried out, along with GLMMs to identify significant OTU. Community Weighted Means (CWM) is used to test if treatments are influenced by a trait, in particular it consists in a weighted means of each species for his abundance or Total Time Interaction for a specific trait. Vulnerability was obtained from fuzzy expert methods that estimate the intrinsic vulnerability to fishing of each species and Fishbase database (W. W. L. Cheung et al. 2005; Fishbase, 2026). Habitat and Substrate information were obtained from Ecological information, on Fishbase database (Fishbase 2026).

4. Results

Site	Treatment	N° Plot	Species	Genera	Families
Ginowan	Hard_coral	7	17	1	2
Ginowan	*Palythoa_heliodiscus*	9	8	0	2
Mizugama	Hard_coral	6	34	2	4
Mizugama	*Palythoa_tuberculosa*	5	36	3	5
Sosu	Hard_coral	8	22	4	6
Sosu	*Palythoa_tuberculosa*	7	24	3	4
Yona	Hard_coral	4	17	3	3
Yona	*Palythoa_tuberculosa*	5	20	0	4

Table 2 (this table presents the four different sites, the treatment for each site, the number of replicates, and the number of organisms identified at the highest taxonomic level possible).

In Table 2 is possible to see the lack of replicates, and the maximum level of taxonomic identification for each site and treatment

Mizugama is the most widely studied and documented of our sites in scientific literature among those included in this study. According to Reimer et al. (2021), following more than five years of zoantharian barren, this site represents a fully established *Palythoa* spp. phase shift, as no such transition has been documented at the remaining sites. To investigate this site, Species richness and Shannon diversity along with Wilcoxon-Mann-Whitney Test were carried out, and no statistical differences were observed.

PERMANOVA analysis also did not show statistically significant differences in MaxN, TTI, TTI biting, of species and trophic group between hard coral and *Palythoa tuberculosa* treatments in Mizugama. These treatments explained only 3-5% of the observed variation, this means that 93-97% of the differences occurred within groups rather than between them. Furthermore the non-significant PERMDISP results support the reliability of the test, indicating homogeneous multivariate dispersion between treatments. Abundance, and total time spent in the proximity of

encrusting and massive hard coral or *Palythoa tuberculosa*, did not differ significantly. Similarly, TTI biting indicated that, encrusting and massive hard coral, that were considered as the same as *Palythoa tuberculosa* as substrate for fish species and trophic groups, did not present statistically significant differences. Generalized Linear Mixed Models (GLMMs) were used to test whether species MaxN, Total Time of Interaction (TTI), TTI biting, and trophic group TTI and TTI biting differed between treatments. A threshold of ≥ 2 plots was applied, meaning that each species had to be present in at least one plot per treatment to be included in the analysis. This relatively permissive criterion was adopted because of the limited amount of data and the low number of replicates. Results indicated that variation within treatments exceeded variation between treatments across most metrics. Specifically, species MaxN, species TTI, trophic group TTI, species TTI biting, species TTI hiding and species TTI static, showed no statistically significant differences between treatments. In contrast, the analysis revealed a significant effect of trophic group between treatment on TTI biting. Mean biting time was significantly higher in plots dominated by *Palythoa tuberculosa* than in hard coral plots, (z-ratio = 2.015, p.value = 0.044). With herbivorous fishes showing substantially greater biting times than the other trophic category. At last, CWM of vulnerability, substrate and habitat were calculated, no statistical differences were found.

To better visualize these results, different boxplots and pie charts were carried out.

Figure 8 illustrates that species richness at Mizugama did not differ significantly between treatments. Although plots dominated by *Palythoa tuberculosa* exhibited slightly higher richness values than hard-coral plots, this difference was not statistically significant.

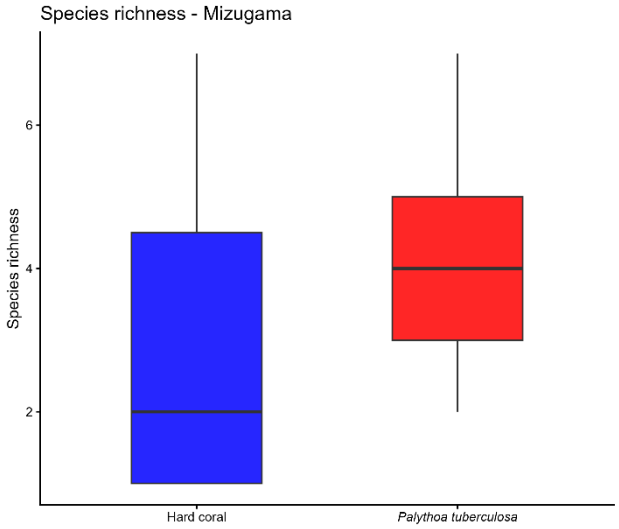

Figure 8 Species richness boxplot of both treatment in Mizugama

Figure 9 shows the Shannon diversity index, although no statistically significant differences were detected, slightly higher diversity values are present in plots dominated by *Palythoa tuberculosa* treatment than hard coral plots.

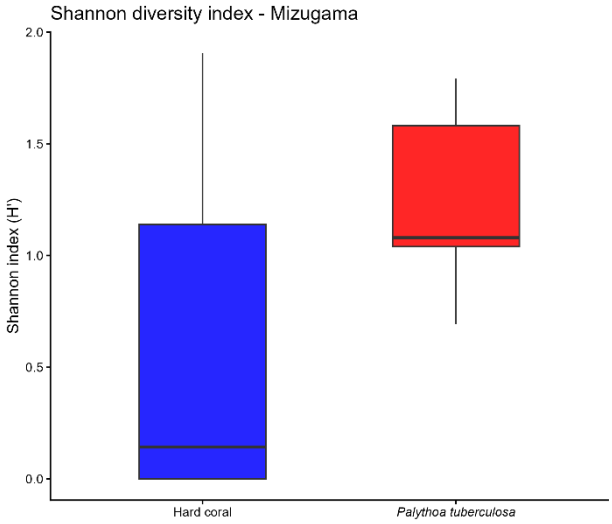

Figure 9 Shannon diversity boxplot of both treatment in Mizugama site

To improve the visualization of MaxN boxplots at Mizugama, Figure 10 and 13, excludes Plot 12 because its extreme value reduced the readability of the remaining data. The other outliers were retained, as they do not substantially affect figure interpretation and reflect biological variation. The figure displays distribution of Maximum Number of individuals (MaxN) per treatment at Mizugama, showing the median, interquartile range and outliers.

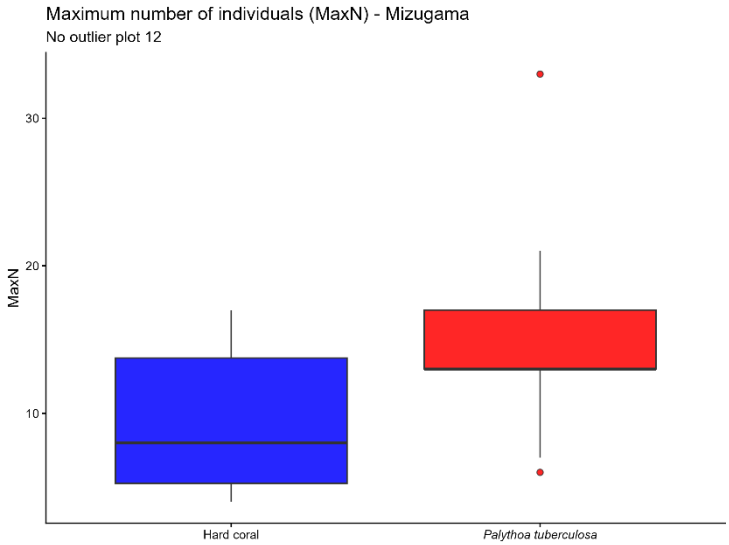

Figure 10 boxplot of mean MaxN of both treatment in Mizugama site

Figure 11 presents the total Time of Interaction (TTI) per plot for both treatments at Mizugama. Hard coral plots showed slightly higher TTI values than *Palythoa tuberculosa* plots; however, this difference was not statistically significant.

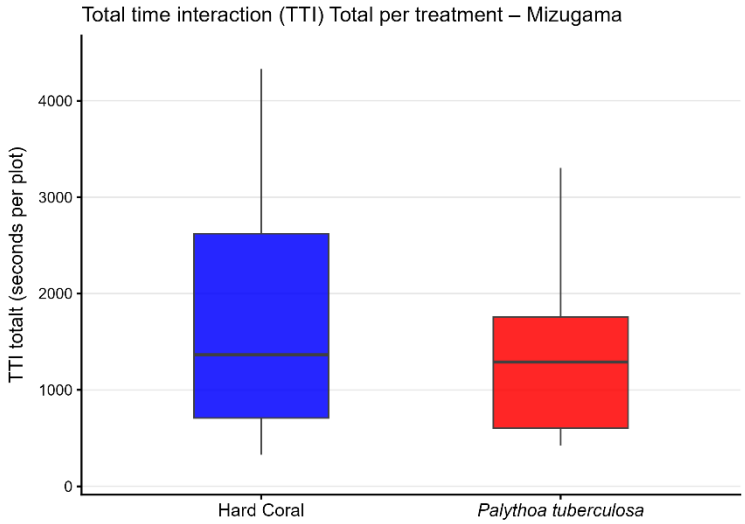

Figure 11 Boxplot of TTI total per both treatment in Mizugama site

Figure 12 highlights the Total Time of biting recorded for fishes on both treatments. A Mann-Whitney U test was performed to compare the proportion of biting interaction time between Hard coral and *Palythoa tuberculosa* treatments at Mizugama. Although *Palythoa tuberculosa* plots showing a higher mean proportion of biting (20.48%) compared to Hard coral (8.89%), the difference was not statistically significant (W = 22, p = 0.341).

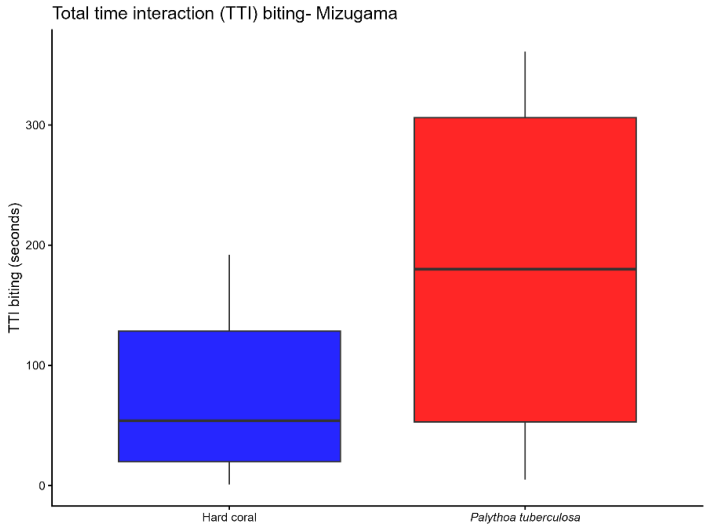

Figure 12 shows boxplot of both treatment of Total Time Interaction Biting in Mizugama site

Figure 13 provides an overview of the trophic groups composition of both hard coral and *Palythoa tuberculosa* treatments. Herbivore in both treatments were dominant, whereas omnivores were also well represented in *Palythoa tuberculosa* plots.

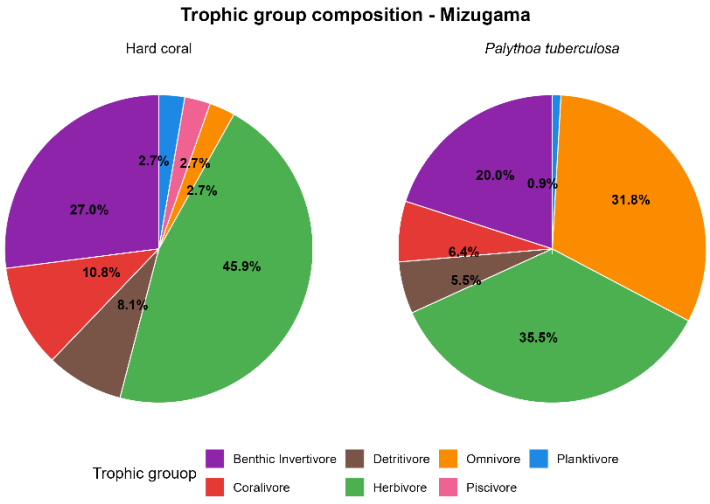

Figure 13 Pie chart of trophic group composition of both hard coral and Palythoa tuberculosa *treatment in Mizugama site*

Figure 14 shows MaxN values for the main trophic groups which were recorded at least twice per treatment. Benthic invertivore and corallivore abundance was comparable between treatments, whereas herbivores showed higher abundance on *Palythoa tuberculosa*, although this difference was not statistically significant.

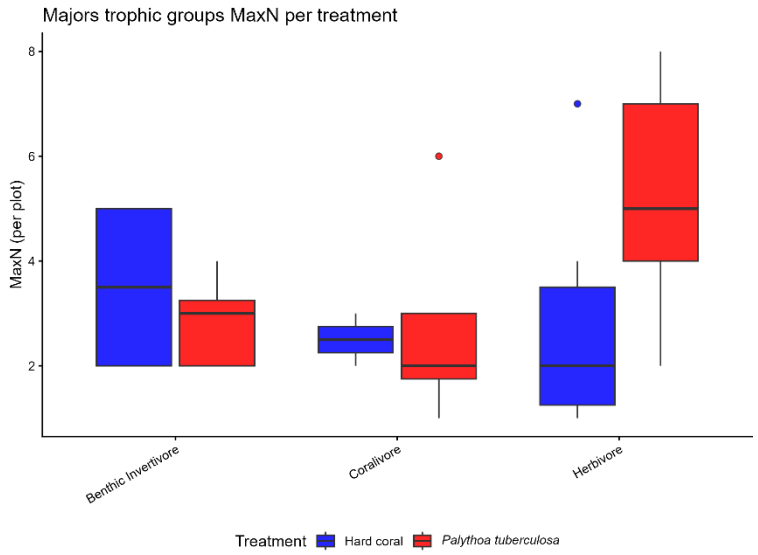

Figure 14 Boxplots of the main trophic groups per treatment, Plot 12 is eliminated, whereas other outlier are considered. Mizugama site

Figure 16 shows the TTI biting across trophic groups for each treatment. Herbivores recorded the highest biting activity overall. Corallivores, detritivores, and benthic invertivores also showed higher biting on *Palythoa tuberculosa* than on hard coral, although none of these differences reached statistical significance. Outliers are frequently observed in these plots due to the mathematical definition used to identify them (Q1 − 1.5×IQR; Q3 + 1.5×IQR). When most observations within a group are zero, the IQR collapses to zero, and any value greater than zero is automatically classified as an outlier, regardless of its biological significance.

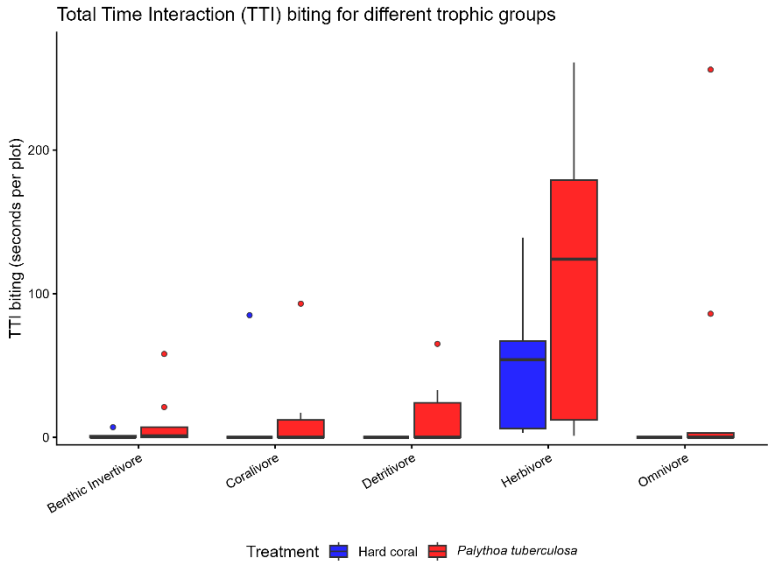

Figure 15 shows TTI biting of the main trophic group, for each treatment per Mizugama site

Sosu was selected for this study because of anecdotical observation of extensive coral cover of *Palythoa tuberculosa*. Although this site received little scientific attention, it is located within the World Heritage Site area and is exposed to the Pacific Sea. To investigate this site, species richness and Shannon diversity along with Wilcoxon-Mann-Whitney Test were carried out, and no statistically significant differences were observed. The same Statistical analysis were then performed for community composition. PERMANOVA showed no statistical differences in species MaxN or trophic-group MaxN between treatments. However PERMANOVA detected a significant difference in TTI biting between the two substrates (p.value = 0.047). The non-significative PERMDISP result supports validity of the test. Following the Analysis of Variance, GLMMs analyses were performed on species TTI, TTI biting, TTI hiding, TTI static, and TTI biting per trophic group, no statistically significant differences were detected between substrates. In contrast MaxN per species differed significantly between treatment (z = 0.6505; p=0.021), with higher fish abundance recorded on *Palythoa* spp. than on massive or encrusting hard coral. To identify the species contributing most to this difference, a SIMPER analysis was performed. finally, CWM indices of of vulnerability, substrate, and habitat were calculated, no statistical differences were found.

To better visualize the community composition, different boxplots and pie charts were generated.

Figure 17 shows that species richness was slightly higher in shows the Total Time of Interaction (TTI) per plot at Sosu for each treatment. No statistically significant differences were detected between Hard coral and Palythoa tuberculosa. Although TTI values on Palythoa tuberculosa tended to be higher, this difference did not reach statistical significance plots than in hard-coral plots. However, the Mann–Whitney test indicated that this difference was not statistically significant.

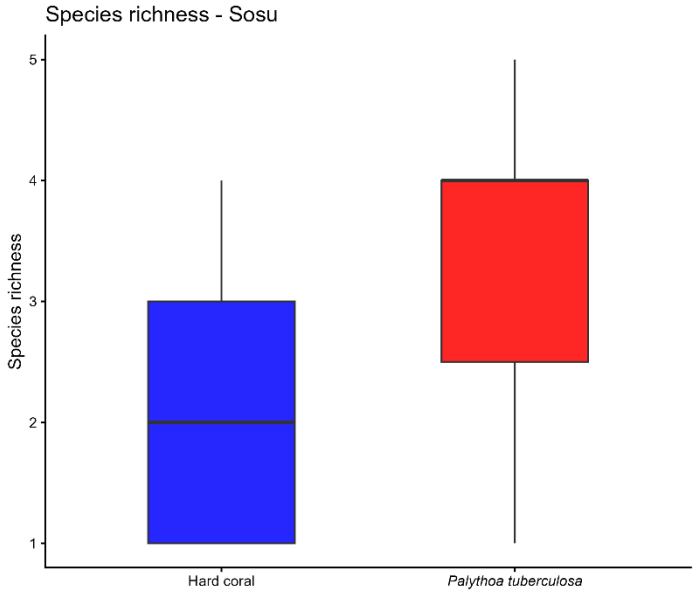

Figure 16 Boxplot shows the species richness in both treatment in the site of Sosu

Figure 18 also shows slightly higher Shannon diversity values in *Palythoa tuberculosa* plots. Nevertheless, no statistically significant difference between treatments was detected.

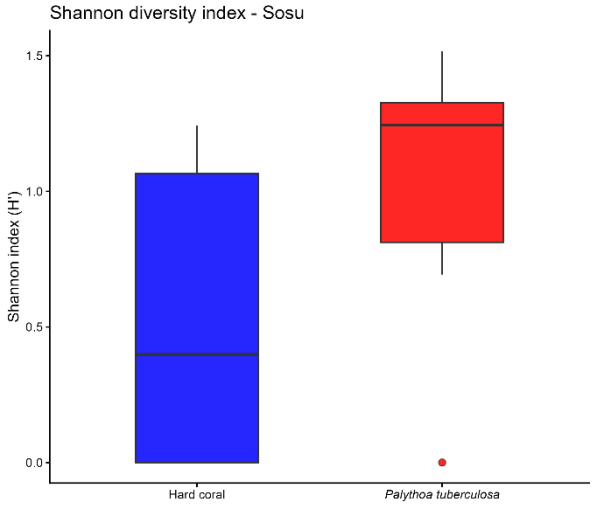

Figure 17 This boxplots shows hard coral and Palythoa *Shannon diversity in Sosu site.*

Figure 19 shows the Maximum Number of individuals (MaxN) per species per plot at Sosu for each treatment. A significant difference was detected between treatments (p = 0.031), with *Palythoa tuberculosa* plots supporting significantly higher fish abundance than Hard coral plots. Outliers are present but likely reflect natural biological variation.

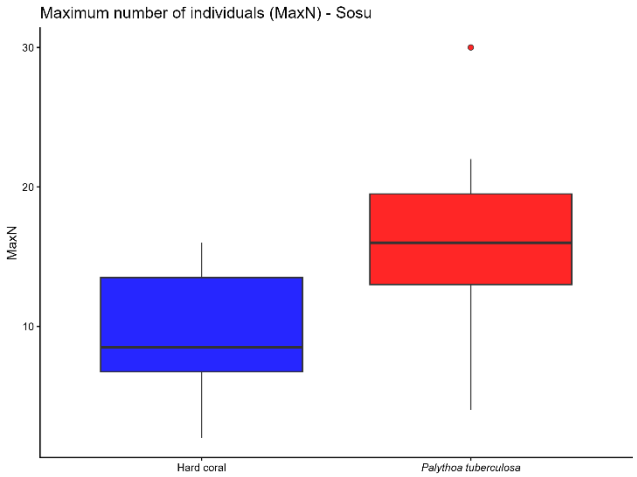

Figure 18 This boxplot highlights sum of the Total Time Interaction per treatment per site

Figure 20 shows the Total Time of Interaction (TTI) per plot at Sosu for each treatment. No statistically significant differences were detected between Hard coral and Palythoa tuberculosa. Although TTI values on *Palythoa tuberculosa* were slightly higher, this difference did not reach statistical significance.

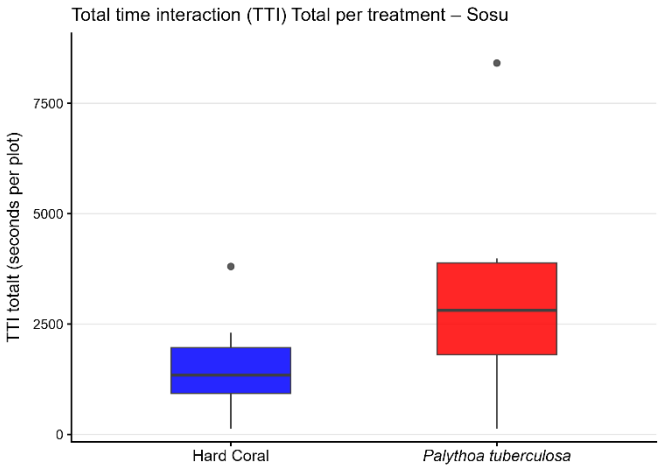

Figure 19 This boxplot highlights mean MaxN per treatment, in the site Sosu

In Figure 21 Total Time of Interaction (TTI) biting at the Sosu site revealed a significant difference between treatments in the PERMANOVA analysis ($R^2 = 0.10$, $p = 0.047$), supporting the pattern observed

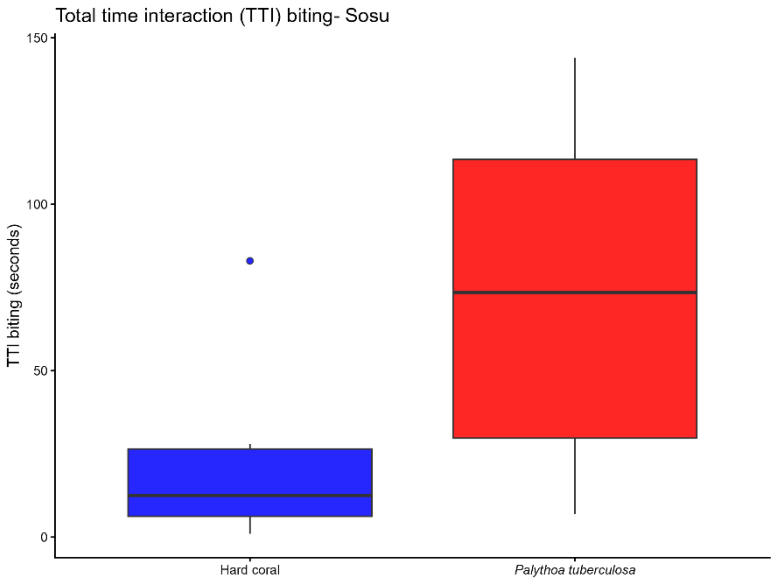

Figure 20 TTI Boxplot of TTI in seconds in both treatment in Sosu

Figure 22 illustrates the trophic-group composition of the fish community. Benthic invertivores were dominant in both treatment, and herbivore the second most dominant.

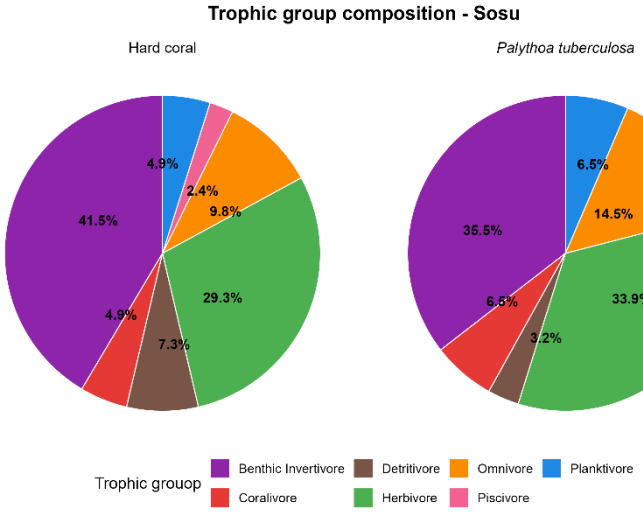

Figure 21 Pie charts visualize the trophic group composition, considering MaxN, in both treatments, at Sosu site

Figure 23 represents the abundance of the major trophic groups (those recorded in at least two plots per treatment) for each substrate. Benthic invertivore abundance was similar between treatments, whereas herbivores and omnivores showed a slight dominance on *Palythoa* plots. Corallivores were almost exclusively found on *Palythoa tuberculosa* patches.

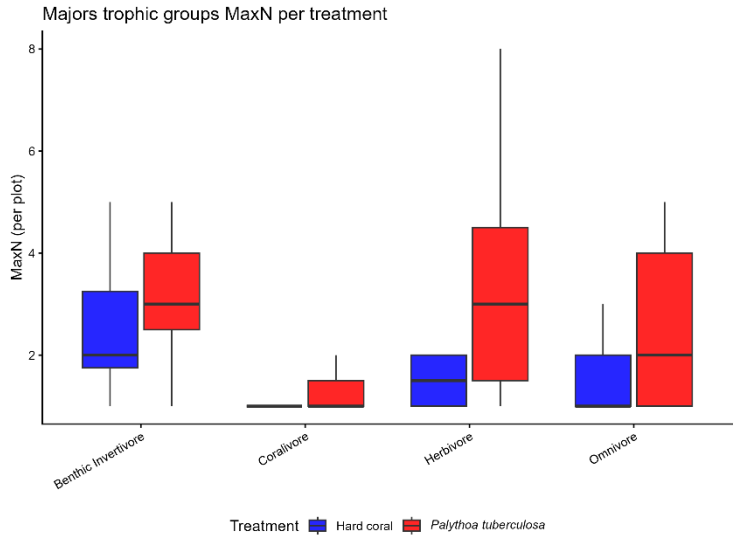

Figure 22 Boxplot that shows the distribution of main trophic groups, Omnivores, Benthic invertivores and herbivore, and their proportion in each treatment

At the Sosu site, herbivores and corallivores exhibited the highest biting activity among all trophic groups, with both showing higher values on *Palythoa tuberculosa* than on hard coral, as illustrated in Figure 24. As discussed above, outliers occur frequently, and the low number of replicates contributes to the high variance observed between plots. Benthic invertivores, despite the lack of statistical significance, exhibited higher biting activity on hard coral than on *P. tuberculosa*.

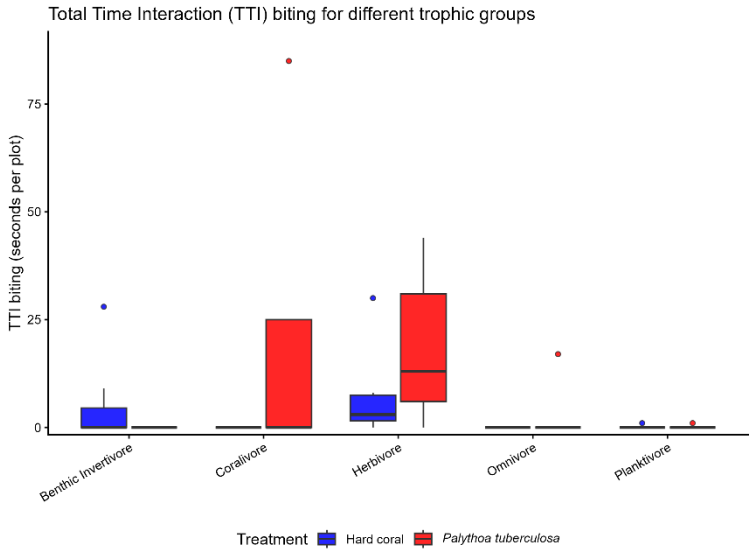

Figure 23 TTI biting described by boxplots, of main trophic groups and both treatments, in the site of Sosu

Yona is an almost pristine site located in the northwestern coast of Okinawa Island. Coral cover was previously evaluated, and the dominance of hard coral distinguishes this site from Mizugama. To investigate this site, species richness and Shannon diversity along with Wilcoxon-Mann-Whitney Test were carried out, and no statistically significant differences were observed. Statistical analyses were also carried out, and PERMANOVA results showed no statistically significant differences in species MaxN, TTI, TTI biting, or trophic group MaxN. The non-significant PERMDISP result confirmed the homogeneity of dispersion assumption underlying the analysis. GLMM analyses were also carried out, and species MaxN, TTI, TTI biting, and trophic group TTI biting showed no significant differences between treatments. Corallivores exhibited biting behaviour exclusively on *Palythoa tuberculosa* patches (being recorded in two of the four plots) and were never observed biting hard coral, although this difference did not reach statistical significance (Mann-Whitney, p=0.069). At last, CWM of vulnerability, substrate and habitat were calculated, no statistically differences were found.

To better visualize the community composition, different boxplots and pie charts were generated:

Species richness, in figure 25 despite the non-statistical differences, shows slightly higher value in hard coral patches towards *Palythoa* ones.

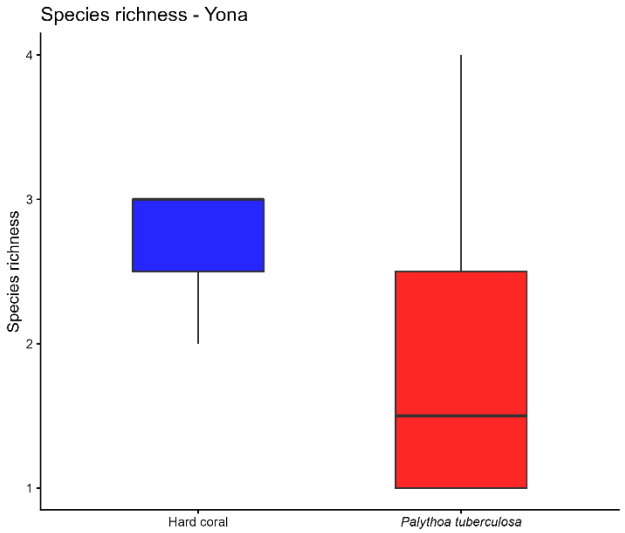

Figure 24 Boxplot of both treatments considering mean species richness, at the site Yona

Figure 26 also shows boxplots reveal higher value of Shannon diversity in Hard coral treatment, bearing in mind that the results were not statistically significantly.

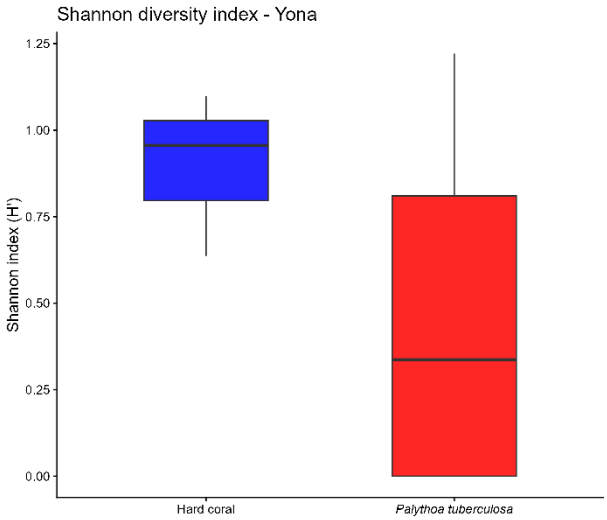

Figure 25 Boxplot at the site Yona that shows Shannon-Diversity in both Hard coral an Palythoa tuberculosa *treatments*

The community composition in terms of abundance at the Yona site was similar for both substrate types, as Figure 27 shows, with a slightly higher abundance in hard coral plots.

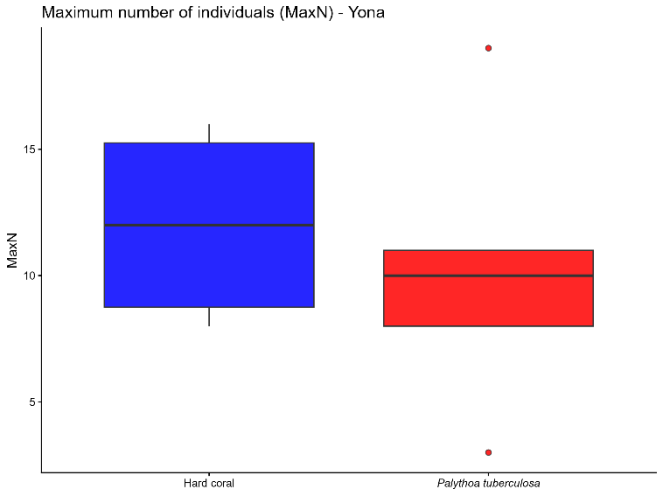

Figure 26 This figure shows boxplot of treatments MaxN, at the site of Yona, with two outliers

Total Time Interaction, for the site of Yona, are well explained on the Figure 28, that shows two boxplots, each one for the treatment.

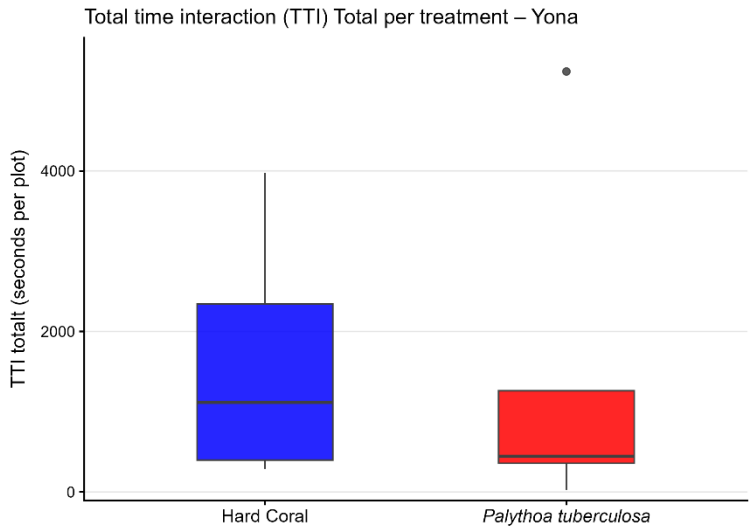

Figure 27 Boxplot of total Total Time Interaction at the site of Yona, both treatments are represented

Total Time Interaction biting as Figure 29 shows, on the other hand presents higher variance on Palythoa patches, respectively hard coral.

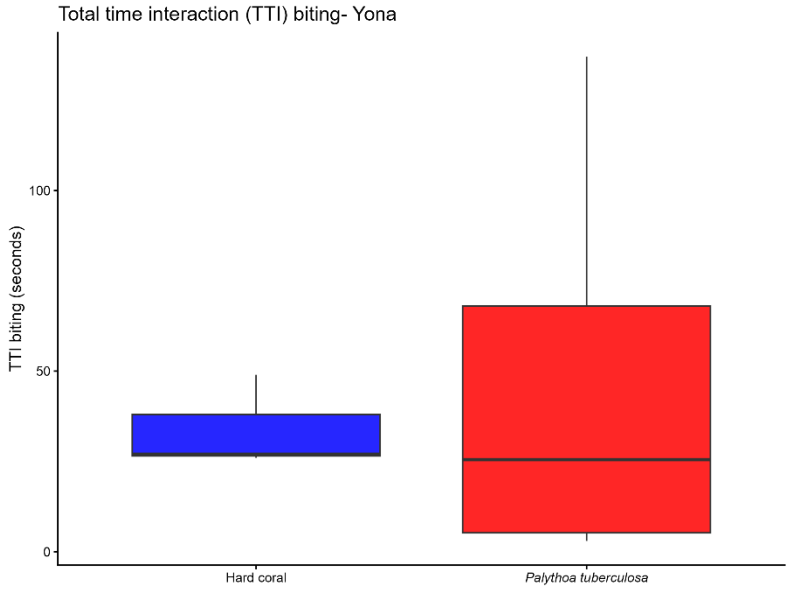

Figure 28 Total Time Interaction of biting for both Treatments are represented, in this boxplot at Yona's site

Pie chars as illustrates in Figure 30, represent the MaxN trophic group composition,corallivores are more important on *Palythoa* treatment, whereas almost disappear on hard corals.

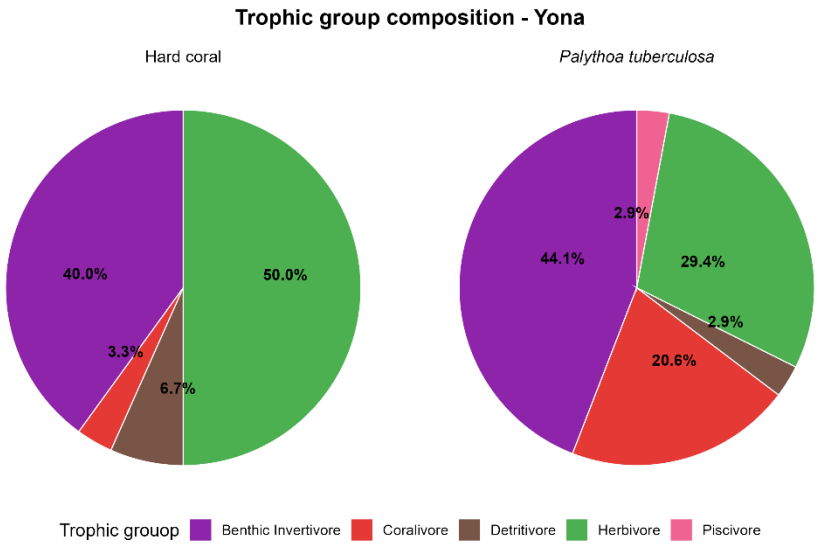

Figure 29 this Pie chart shows trophic group composition, at the site of Yona, for both treatments.

The trophic group composition are illustrated in Figure 31, where MaxN values show the abundance of the main groups. Omnivores were exclusively recorded on Palythoa tuberculosa patches, whereas herbivores and benthic invertivores were well represented across both treatments.

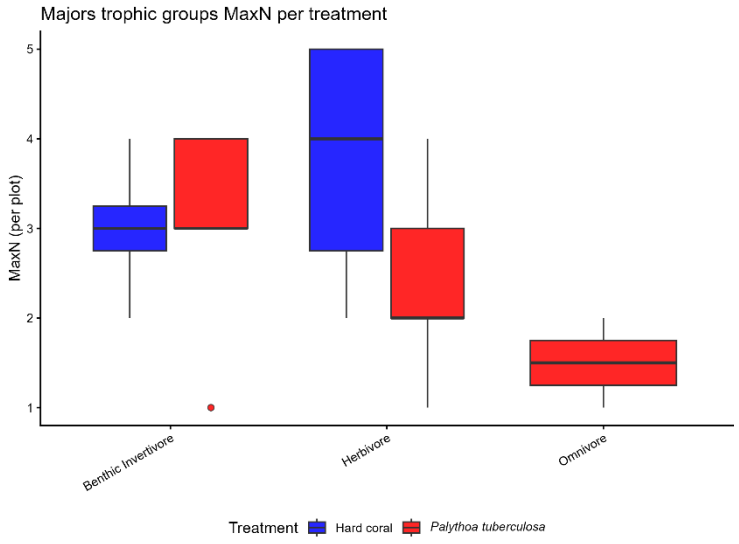

Figure 30 boxplots Shows the main trophic groups and their abundance considering both hard coral and Palythoa *treatments, at the site of Yona*

In Yona, Benthic invertivores bites only hard coral substrate. On the other hard corallivores bites only *Palythoa*, whereas herbivores are equally distributed. Figure 32 explains this distribution.

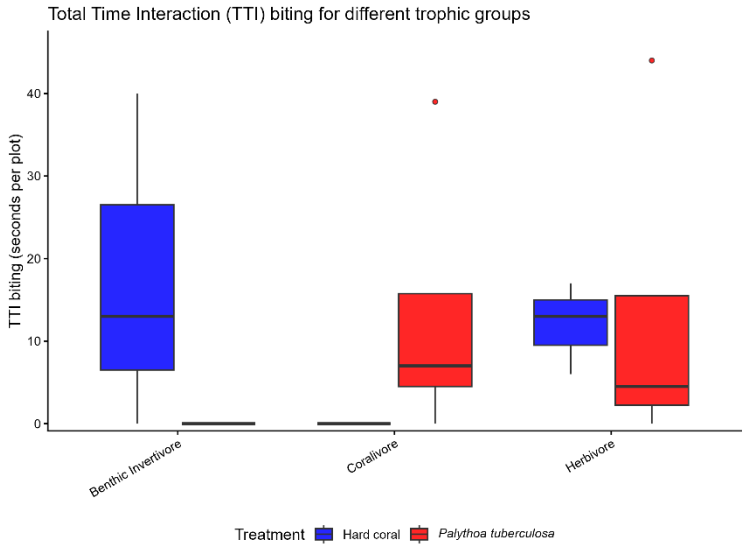

Figure 31 Shows TTI biting of the main trophic groups, and the distribution between both treatments, in the site of Yona

Ginowan site is located near Mizugama, in a human-developed area close to a port on the southwestern coast of Okinawa Island. Low coral cover (10% hard coral and 20% soft coral) is offset by extensive coverage of turf algae (64%). At this site, the zoantharian species *Palythoa heliodiscus*, a lyberae forms of Zoantharia, was compared with massive and encrusting hard coral to investigate possible differences in fish abundance and interaction patterns. Species richness, Shannon diversity along with Wilcoxon-Mann-Whitney Test were carried out, and no statistically differences were observed. Permutational Multivariate Analysis of Variance (PERMANOVA) and Generalized Linear Mixed Models (GLMMs) were performed on MaxN, Total Time Interaction (TTI) total, TTI biting and trophic group TTI and TTI biting. None of these analyses detected statistically significant differences between treatments. At last, CWM of vulnerability, substrate and habitat were calculated, no statistical differences were found.

To better visualize the community composition different boxplot and pie chart were generated:

Species richness was calculated and no statistical significance were detected, *Palythoa heliodiscus* present slightly lower species richness than hard coral, as it possible to see in Figure 33.

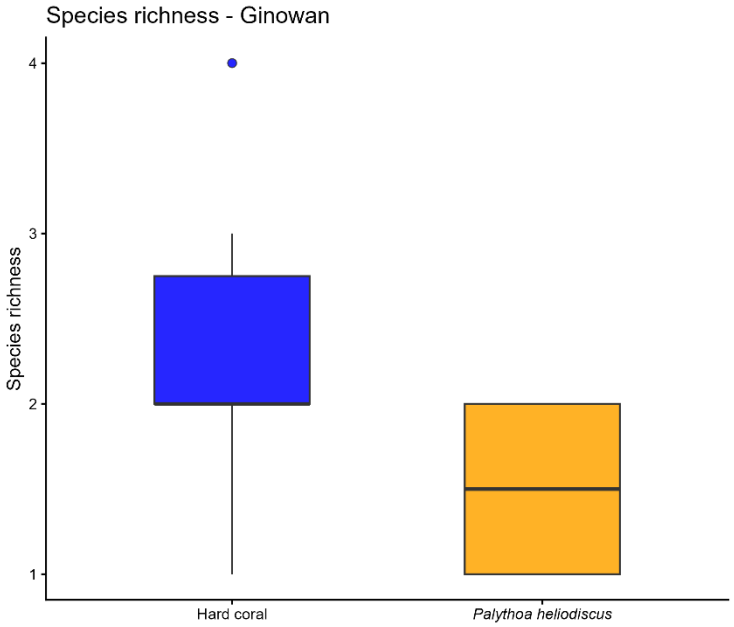

Figure 32 Species richness boxplot at the site of Ginowan, of both treatment

In figure 34 is possible to observe the graphical representation, using boxplot, of Shannon diversity; hard coral exhibited slightly higher but not significantly Shannon diversity than *Palythoa heliodiscus* plots. Two outliers are present, reflecting natural biological variation.

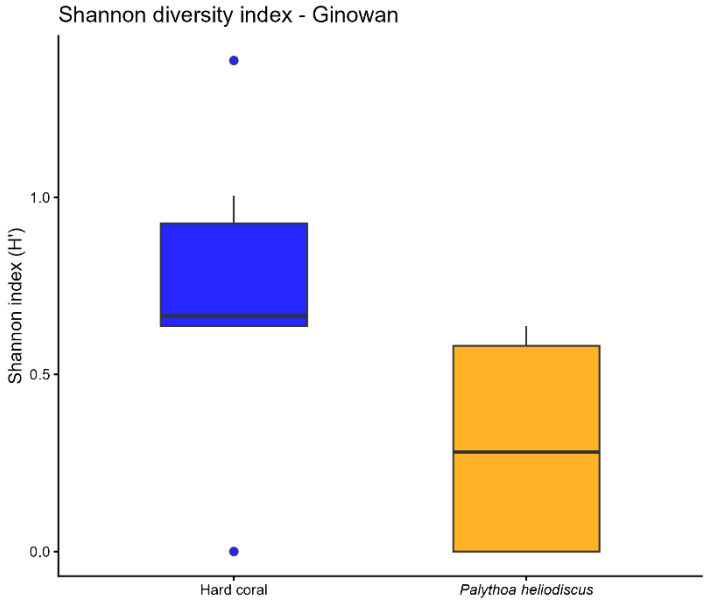

Figure 33 shows boxplot of Shannon diversity considering both treatment at the Ginowan site

Figure 35 illustrates the Maximum number of individuals (MaxN), used here as a proxy for fish abundance, at the Ginowan site. *Palythoa heliodiscus* plots showed lower fish abundance than hard-coral plots; however, this difference was not statistically significant.

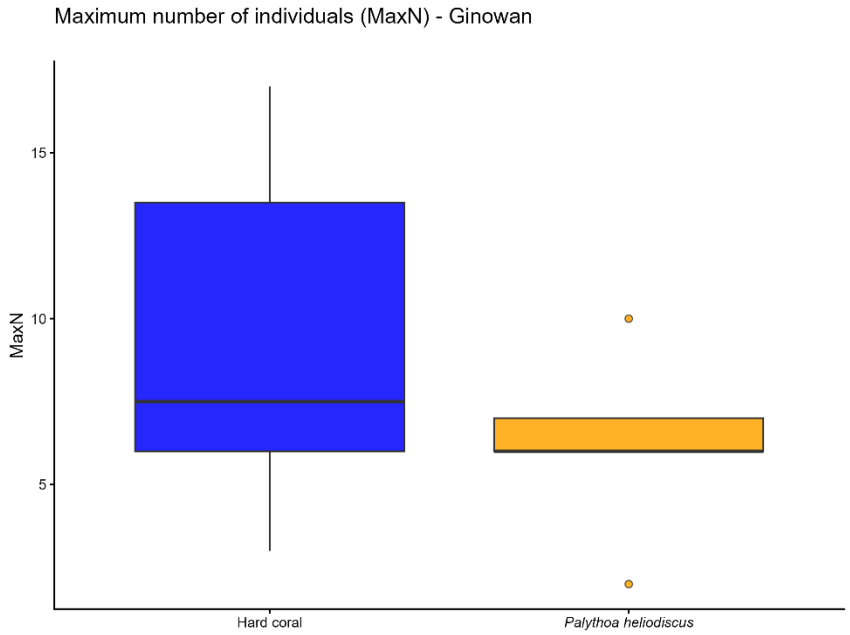

Figure 34 shows the MaxN of both treatment in the site Ginowan

Figure 36 illustrates the Total Time of Interaction (TTI) per plot at the Ginowan site. TTI values were similar between *Palythoa heliodiscus* and hard-coral plots.

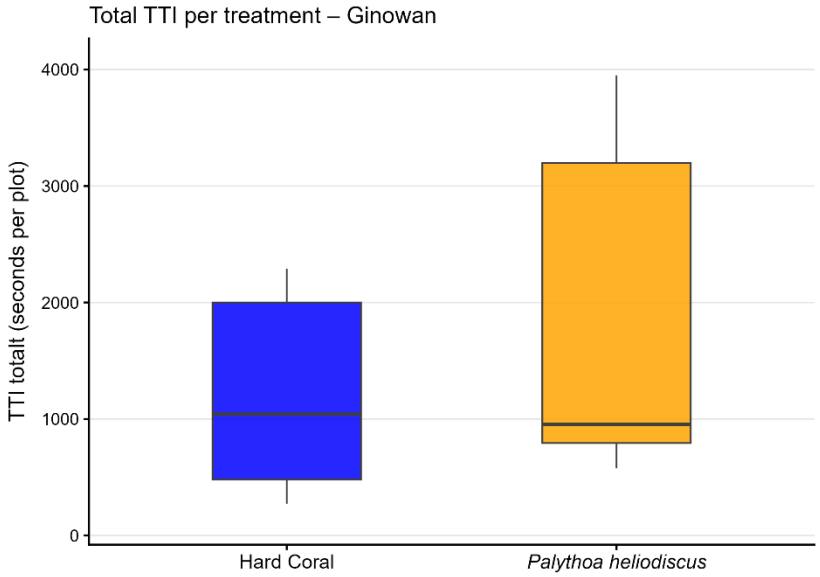

Figure 35 shows Total Time Interaction total per treatment at the Ginowan site

Figure 37 summarizes the Total Time Interaction biting at the Ginowan site. Summarizes the multivariate results, which consist in a no statistically significant differences in biting time between *Palythoa heliodiscus* and hard coral.

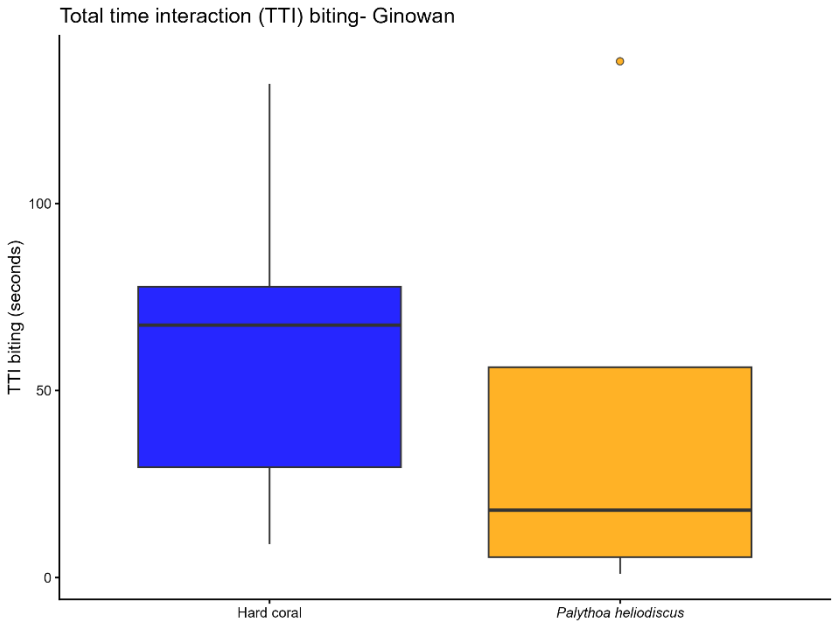

Figure 36 display TTI biting in seconds of both treatment at Ginowan site

At Ginowan, herbivores represented the dominant trophic group, accounting for more than 50% of the total fish abundance, they were followed by benthic invertivores on hard coral and piscivores on *Palythoa* patches as it possible to observe in figure 38

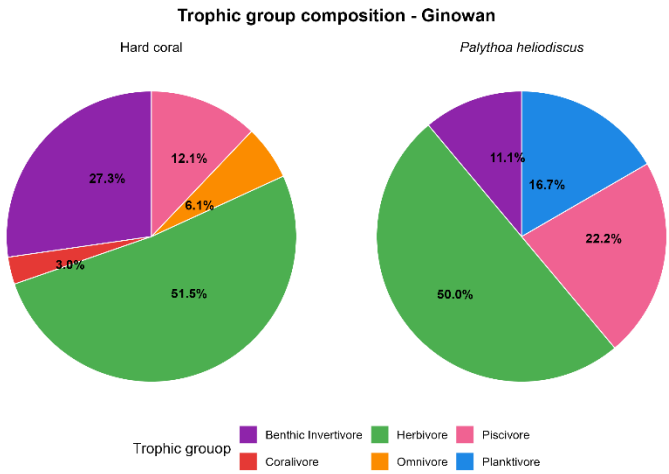

Figure 37 Trophic group composition is well explained in this pie chart, that shows both treatment at Ginowan site

Figure 39 displays the MaxN of the most abundant trophic groups. Benthic invertivores and corallivores were more abundant in hard-coral plots and were not recorded on *Palythoa heliodiscus*. However, none of these differences reached statistical significance. Conversely, planktivores were recorded only on *Palythoa heliodiscus* although this pattern was also not statistically significant.

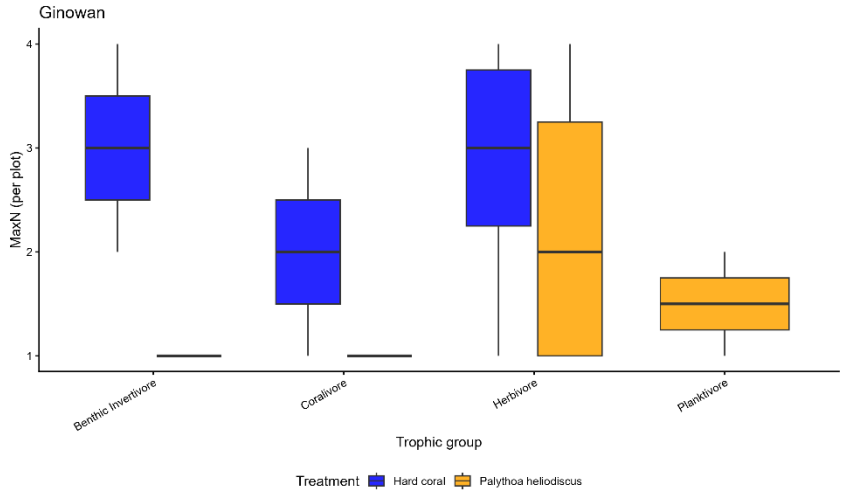

Figure 38 shows MaxN of the main trophic group, considering both treatment for the site Ginowan

Figure 40 illustrates biting interaction of the main trophic groups on both treatments, is it possible to observe that herbivores showed similar biting activity on *P. heliodiscus* and hard coral, whereas benthic invertivores displayed no apparent preference for either substrate and rarely engaged in biting behavior.

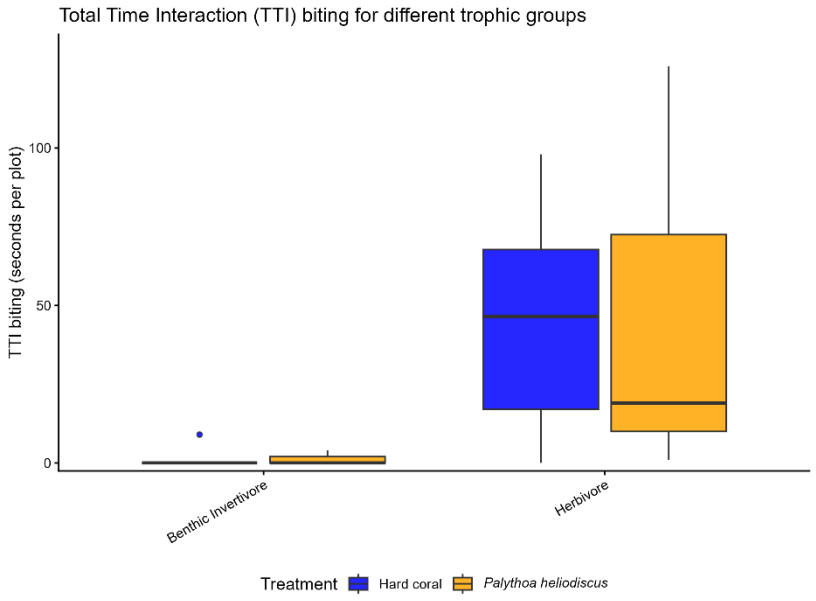

Figure 39 explain TTI biting of the main trophic group on Palythoa heliodiscus *and on hard coral, at the site of Ginowan*

5. Discussion

The sites were considered separate due to the differences between them, Mizugama is located at the southwest of the island, along with Ginowan which present a different *Palythoa* species. Yona is located at the northwest, they are influenced by the Kuroshio current, and face west, toward the East China Sea. Sosu is located at the northeast of the Island, faces open sea, toward the Pacific Sea, with the input of the North Pacific Sea, and the Ryukyus current (Cruz Salmeron et al. 2022). Mizugama and Ginowan are located in the developed part of the island, on the other hand Sosu and Yona, are far away from the city, and Sosu is located inside the UNESCO World Heritage Site of Yanbaru, but has a human breakwater barrier, behind the reef. The only common characteristic of all sites, in according with literature, that shows negative correlation with the salinity level and the presence of *Palythoa* patches, is the presence of a river mouth (S.-Y. Yang et al. 2013).

5.1 Multivariate analysis

Statistical multivariate analyses were carried out despite the low number of replicates, which resulted in high variance and increased random errors. This was due to the limited duration of the internship, adverse weather conditions, and biological variability, which prevented any further increase in sampling effort an increase that would otherwise have decreased the error.

5.1.1 MaxN

Generalized Linear Mixed Models GLMM in Sosu, studying MaxN expressed a statistical difference, where fishes seems to prefer *Palythoa* patches compared to hard coral; GLMM join all the species together and gives this outcome, SIMPER analysis expose which species explain most of the diversity: the OTU that belongs to the genus *Eviota* sp. Jenkins, 1903, the OTU of the family Blenniidae, and the OTU of the species *Thalassoma lutescens* Lay & Bennett, 1839, *Thalassoma amblycephalum* Bleeker, 1856 and *Acanthurus nigrofuscus* are the only taxa that were resulted differently. *Eviota* is a Gobiidae genus commonly named dwarfgoby, (Jenkins 1903) which feed primarily on small invertebrates; like other Gobiidae, some species are benthonic, and rest and wait on the substrate, such as corals for preys (Greenfield 2017; Vaz et al. 2025), waiting on *P. tuberculosa* patches does not appear to be deterred by the toxin, though this was not directly tested here (Hirata and Uemura 1985; Mendonça-Neto et al. 2008; Aratake et al. 2016; Greenfield 2017). *Eviota* spp. feeds on small invertebrates like copepods, tanaids or amphipods, and studying on encrusting hard corals showed lower species diversity of copepods on them (Cheng et al. 2016), another interesting observation is the abstract of Borges et al. 2019,

that tried to explain the majority of abundance of Micro invertebrates on macroalgal patches due to the limited space between *Palythoa caribaeorum* Duchassaing & Michelotti, 1860 patches that limits microhabitat for small invertebrates. *Thalassoma lutescens* is a benthopelagic Labridae that feed primarily on shelled benthic invertebrates. No studies focused on the macrobenthic invertebrate associated with *P. tuberculosa*, or other Zoantharia, so is not possible to assess relationship of *Eviota* spp. or *T. lutescens* with *Palythoa*, but it is plausible to think that if benthic invertivores are more abundant in proximity, if not on the substrate, the presence of prey is as likely as possible. Some studies reported a limited use of massive and encrusting hard corals by non-coralline invertebrate feeders, probably because these substrates provide relatively few refuges for small invertebrates (S. J. Holbrook et al. 2002; S. Holbrook et al. 2008; Kerry and Bellwood 2012; Cheng et al. 2016; Nanami 2020). Considering these findings, together with the relationship between microhabitat complexity, three-dimensional structure, and the availability of shelters for small invertebrates, it is plausible that the structural differences between *Palythoa tuberculosa* patches, and massive or encrusting hard corals contribute to the higher abundance of these two species preys. In situ, and non-quantitative observation have shown that the coral carpet observed in Canary Island, in Borges et al 2019 study, were not repeated in Sosu (Fig 3), instead the larger number of crevices, holes and spaces between *P. tuberculosa* patches may provide more suitable habitat for small benthic invertebrates, rather than Scleractinia encrusting and massive forms (Fig 5). *Thalassoma amblycephalum* on the other hand is a zooplanktonic feeder of shrimp and crab larvae, copepods, and mysids (Myers 1991; Sandin 2010); as explained before there are no information of the associated fauna of or above *P. tuberculosa* or other Zoantharia, but is assessed that encrusting forms presents lower copepods species richness than other morphs (Cheng et al. 2016), and the lack of crevice and space on these two types of Scleractinia coral, therefore may results in lesser attraction for invertivores. *Acanthurus nigrofuscus* family Acanthuridae at last, is a herbivore that feeds on filamentous algae. There are no studies regarding relationship of algal growth and Zoantharia, but Scleractinia coral and the competition with algae is well studied, filamentous and turf algae could overgrowth and compete with corals for space (Jompa and McCook 2002) also Zoantharia could compete with macroalgal for space, like the case study of Canary Island, where phase shift from macroalgae to Zoantharia happened, and trophic group were different among Zoantharia and macroalgal habitats. Also for herbivore a greater abundance of them on *Palythoa* patches could be the results of the distance between colonies that may provide a free area for filamentous algae to grow (Fig 3, 32). Moreover Swierts and Vermeij 2016 seen that encrusting and massive corals are the most commonly engaged in competitive interactions with

turf algae, and the first won in 35% of the cases and the second on 13%, corroborating the previous hypothesis of a difficulty of algae to grow near encrusting and massive Scleractinia patches (Swierts and Vermeij 2016; Borges et al. 2019). This results are also possible to observe in (Fig 18).

5.1.2 Total Time Interaction biting

In Mizugama Generalized Linear Mixed Modules GLMMs analysis show statistical differences considering Total Time Interaction Biting of trophic group, where herbivores fish seems to prefer bites *Palythoa* rather than hard coral. During the research period, an intense events of bleaching occurred, confirmed by the preprint (Gösser et al. 2026). An unconfirmed result, but an in-situ observation showed that most of the corals of Mizugama site bleached (Fig 32), Following Reimer et al. 2021 hypothesis, which suggested that: although the capacity of Zoantharia to better resist to bleaching event; given that the capacity of encrusting and massive hard coral to tolerance bleaching (Nanami 2020); may have exceeded the threshold for *Palythoa tuberculosa*, of limiting algal formation, leading to the formation of an algal film on top of it, which in turn probably resulted in a higher number of bites from herbivores fish on Zoantharia.

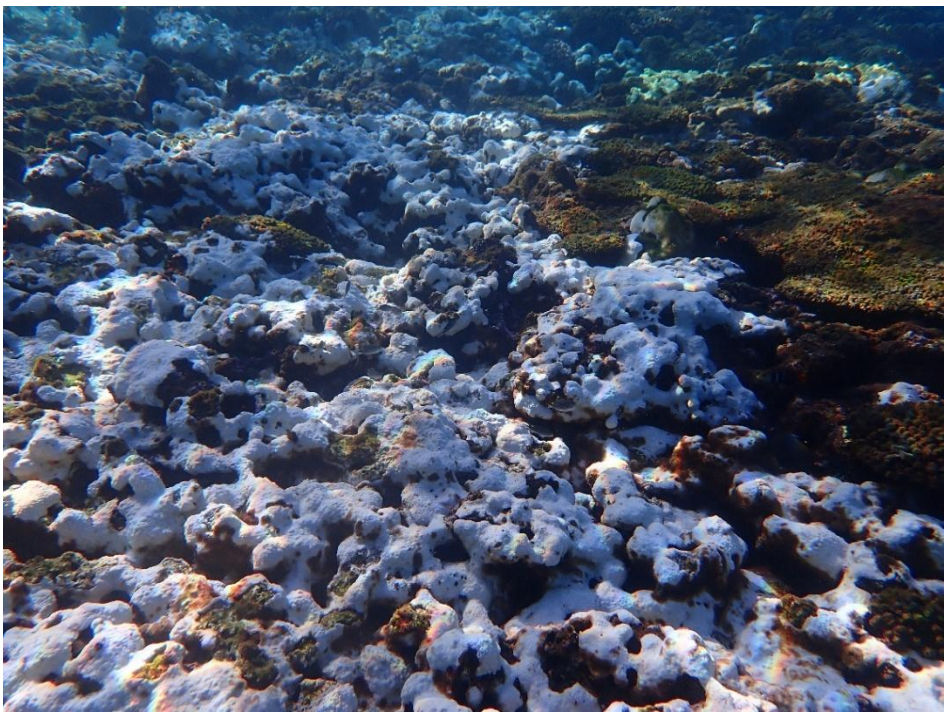

Figure 40, Bleaching at Mizugama Site

In Sosu PERMANOVA analysis shows statistical differences of TTI biting, even though it explains only 10% of the differences (Fig 20). This difference is primarily guided by a bunch of taxa, with only two that describe 30% of the differences: the OTU corresponding to *Eviota* spp

Eviota sp. Jenkins, 1903, and that one corresponding to *Plectroglyphidodon dickii* Liénard, 1839. Both taxa seem to prefer bite *Palythoa* rather than encrusting and massive hard corals. *Eviota* species characteristic were already explained, and the hypothesis discussed before, about abundance, could be also here a possible explanation of majority timing in bites of *Eviota* spp. Regarding *P. dickii* it is a species of Pomacentridae commonly associated with *Acropora* Oken, 1815 and *Pocillopora* Lamarck, 1816 corals, considered a facultative corallivore, that feeds on filamentous algae, small benthic invertebrates, including coral polyps, and occasionally small fishes (Myers 1989; Ho et al. 2009). Despite the known toxicity of *P. tuberculosa* due to the presence of palytoxin (Walsh and Bowers 1971; Wiles et al. 1974; Kodama et al. 1989), mucus from *Palythoa* is reported to be palatable by a great variety of fishes and some species are reported to bite it (Fukui et al. 1987; Kodama et al. 1989; Gleibs and Mebs 1999; Mendonça-Neto et al. 2008; Biré et al. 2013). Studies have shown that encrusting hard coral present a positive correlation between live coral area and tissue, and number of holes with fish abundance and fish species richness (S. J. Holbrook et al. 2002; S. Holbrook et al. 2008), while other studies suggest that, biting interaction could follow the hypothesis that feeding efficiency is related to coral morphology (Cole et al. 2008b; Hannigan 2022). For *P. dickii* encrusting and massive hard coral, given their competitive interaction with algae (Swierts and Vermeij 2016), that limits the omnivores possibilities of the Pomacentridae, and the preference of corallivores fishes to feed on branching corals over all other forms (Hannigan 2022), could therefore be considered a substrate of lesser interest than *P. tuberculosa*. (S. J. Holbrook et al. 2002; S. Holbrook et al. 2008; Kerry and Bellwood 2012; Fraser et al. 2020; Nanami 2020; Vaz et al. 2025).

5.1.3 non-significant results

The other results of PERMANOVA analysis of MaxN and Total Time Interaction of each behavior, Wilcoxon test of species richness and Shannon diversity, GLMM of MaxN and TTI of each behavior, and CWM of vulnerability, substrate and habitat, shows no statistical differences at all, for Mizugama, Sosu, Yona and Ginowan. In Ginowan *Palythoa heliodiscus* is almost never bite and the interaction with it is almost only did by herbivore that equally interact on hard corals. This is probably due to the presence of macroalgal growth in proximity of the Zoantharia. The exploratory nature of the study and the limited number of replicates could be the reason of all of these results.

6. Conclusions

In such a changing scenario, characterized by increasing sea surface temperatures (SSTs), more intense and frequent marine heatwaves (Mercator Ocean International, 2025; Smith and Buddemeier 1992; Hansen et al. 2006), and more frequent extreme climatic events (Holland 2012) and biological outbreaks (Done 1992; Haszprunar et al. 2017), coral reefs are undergoing unprecedented ecological changes that have escalated the prevalence and extent of mass coral bleaching events (Spady et al. 2026). All of these could cause one of the most important ecological changes affecting coral reefs, the phase shift (Giesel 1970; Done 1992). Globally, the most studied phase shift is the one which consists of a change in dominance of scleractinian corals to macroalgae (Norström et al. 2009). In this case, the reduction of rugosity and habitat complexity (Done 1992) causes a change in community composition (Norström et al. 2009; Bruno et al. 2009; Igor C. S. Cruz et al. 2015). Fishes could also suffer from this change; a decline of corallivores fishes and coral-related species, and an increase of algal grazing species could be the possible stable state (Harborne et al. 2017). If these events occur near a freshwater stream, with low salinity and high nutrient levels, they could become the condition under which a unique phase shift happens, the Zoantharia phase shift. Around the world several zoantharian phase shifts have been reported; genus *Zoanthus* Lamarck, 1801 and *Palythoa* are the taxa that overgrowth Scleractinia and, in some cases, macroalgae too. The Canary Islands, Spain; Todos os Santos Bay, Brazil; and Okinawa, Japan, are only some of the areas where this particular phase shift has occurred (S.-Y. Yang et al. 2013; Davis Reimer et al. 2021). Along with the dominance of these organisms, the three-dimensionality of the reef was reduced, the associated community changed, and fish species diversity decreased (Igor C. S. Cruz et al. 2015; Igor Cristino Silva Cruz et al. 2016). This study aimed to investigate how, coral-related fishes interact with the species *Palythoa tuberculosa* and *Palythoa heliodiscus* by comparing them with encrusting and massive hard corals in a phase-shifted site, Mizugama, while in the other three sites, in Okinawa, these zoantharian species were sufficiently abundant to conduct the observation. All the sites were considered separately because of their differences in exposure, anthropogenic pressure, and limits in ecologi Butcal data, and all of these were reflected in the heterogeneity of the results. Overall community-level metrics, species richness, and Shannon diversity did not differ significantly between *Palythoa* and hard coral treatments at any site. Abundance was significant at the Sosu site, where fishes seemed to prefer *P. tuberculosa* rather than encrusting or massive hard coral. In Mizugama, herbivores fishes showed higher Total Time Interaction while biting on *Palythoa tuberculosa* patches. In Mizugama, as confirmed by a

preprint of Gösser et al. 2026, a bleaching event happened before the study started, and this event may have influenced the results. In Sosu, fishes were more abundant and spent more time biting on *Palythoa tuberculosa* patches. The differences were primarily driven by a limited number of OTUs: Blenniidae, *Eviota* spp., *Thalassoma lutescens*, *T. amblycephalum*, and *Acanthurus nigrofuscus* for MaxN; and *Eviota* spp. and *Plectroglyphidodon dickii* for biting, whose ecology follows the presence of small invertebrates that seem to prefer the *P. tuberculosa* microhabitat and reduced algal competition rather than the toxicity of the coral. The results of this study should be considered exploratory, but could suggest that the consequences of a *Palythoa* phase shift for coral-associated fishes may be more complicated than a simple reduction in species richness (Igor C. S. Cruz et al. 2015); conversely, fish do not appear to avoid *Palythoa* patches and, in some cases, may even preferentially bite them rather than encrusting and massive hard corals. Bleaching events, which in a future scenario may occur more frequently due to the rising temperature, remain an open question. The more time spent by herbivores biting on *Palythoa* patches, as observed in Mizugama, seems to go in the opposite direction to the literature that reports the substitution of Zoantharia over Scleractinia after a bleaching event. However, encrusting and massive hard corals are considered highly resistant to higher temperature, whereas *Palythoa* has been seen to suffer from ocean acidification and rising temperature, which cause bleaching events. Rising temperature also reduces river flow, with the possible future scenario of streamflow reductions and the consequences of less freshwater on the coast and the implication for *Palythoa* growth and ecology (Carroll et al. 2024). The results of this study present several limitations, due to the low number of plots per site and treatment, driven by seasonal weather constraints and the limited duration of the fieldwork period. Future studies would be more effective with larger replication, perhaps before, during and after a phase shift event in order to visualize the differences in the associated community. Also, choosing well-studied sites could help with the analysis and would make it possible to compare them. Another possible study would be to observe the micro-, meio-, and macroinvertebrates fauna associated with *Palythoa* and maybe compare them with that associated with encrusting and massive hard corals, in order to better understand the fish community, and the reason for the higher abundance and biting time on *Palythoa*. Overall, the *Palythoa* and zoantharian phase shift and the associated community remain poorly understood. This study suggests that the response of coral-associated fish communities to increasing *Palythoa* dominance may be more complex than previously assumed. highlighting the need for further investigation to anticipating and better understanding the consequence of future phase shift scenario that the rising world temperature could exacerbate.

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