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Mid-trophic generalists dominate reef fish community impacted by overfishing

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Abstract

Overfishing is one of the most severe threats to oceans globally and predates all other human impacts on the marine environment. A common tool to manage fisheries sustainably are marine protected areas (MPAs). However, to achieve the desired results effective management plans integrating continuous monitoring need to be in place. This study assessed the MPA effect of nine sites within the Santa Luzia marine reserve, by employing diver-operated stereo- video transects along with an assessment of the benthic composition to account for natural variability. Specifically, differences to a previous assessment in 2009 were evaluated in terms of reef fish relative biomass by trophic group, relative densities and frequency of species using multivariate analyses and change of community descriptors (species richness, diversity, and evenness). In 2022, the community was dominated in terms of biomass and density by two pomacentrids of the genus Chromis and three omnivorous sparid species of the genus Diplodus. A pronounced shift from a more specialized community in 2009 with high proportions of the biomass at the lower and upper end of the trophic spectrum, to a more homogenous community dominated by mid-trophic generalists was observed. There was no significant difference between the benthic cover composition and fishing intensity is the only environmental predictor that was weakly related to community composition. In the virtual absence of natural variation accompanied with over 20% loss of species richness and significantly higher evenness, the reef fish community of Santa Luzia exhibits signs that previously have been related to high fishing pressure. The functional redundancy of reef fishes was heavily impacted, and the implementation of more effective management measures is necessary to restore the reef fish community and ensure ecosystem functioning.

Keywords:

Conservation MPA Trophic groups Reef fish Overfishing

Resumo

A sobrepesca é uma das ameaças mais graves para os oceanos a nível mundial e antecede todos os outros impactos humanos no ambiente marinho, como a poluição, a degradação da qualidade da água, as alterações climáticas de origem antropogénica e outras causas de extinção ecológica. Um instrumento comum para gerir a pesca de forma sustentável são as zonas marinhas protegidas (AMPs), que são consideradas benéficas para a conservação da biodiversidade, mitigação e a resiliência às alterações climáticas, redução do risco de catástrofes naturais e melhoria da pesca devido a um aumento da biomassa e da abundância das espécies visadas dentro e fora dos seus limites. No entanto, para produzirem os resultados desejados, as AMPs têm de ser geridas de forma adaptativa, integrando as comunidades locais e recorrendo a ciclos de gestão adaptativa usando monitorização contínua e experimental. A gestão adaptativa permite governar em função do estatuto da reserva, melhorando assim a tomada de decisões perante a incerteza. Deste modo, a escolha dos indicadores para a conceção do inquérito deve ser adequada ao respetivo objetivo da AMP. A biomassa é um indicador mais forte do que a abundância, especialmente no que se refere à pesca, já que os peixes maiores são seleccionados devido ao seu maior valor de mercado. A biodiversidade é geralmente avaliada, mas muitas vezes não reflecte a redundância funcional, que é um indicador importante para estudar a resiliência ecológica de um ecossistema e a manutenção de funções e processos fundamentais.

Assim, este estudo avaliou o efeito da AMP em nove locais diferentes da reserva marinha de Santa Luzia, através de um método estéreo-vídeo em Cabo Verde, onde foram utilizados transectos operados por mergulhadores juntamente com uma avaliação foto-quadrante da composição bentónica para ter em conta a variabilidade natural. O desing inquérito foi mantido semelhante à avaliação anterior da AMP, que empregou o censo visual subaquático. Santa Luzia é a ilha mais pequena do arquipélago isolado de Cabo Verde e é uma ilha deserta. A sua importância para a biodiversidade e as comunidades naturais foi reconhecida pelos pescadores artesanais e pelo governo, tendo sido aprovada uma lei para a sua conservação em 2003.

Posteriormente, os vídeos foram analisados no VidSync, os peixes do recife foram medidos e o peso foi calculado utilizando relações comprimento-peso específicas para cada espécie. A biomassa relativa dos grupos tróficos mais importantes foi comparada com a única avaliação anterior da AMP, efectuada em 2009. As densidades de todas as espécies e as frequências das espécies dominantes foram avaliadas utilizando escalonamento multidimensional não métrico e agrupamento hierárquico ou PERMANOVA, respetivamente. Depois, ambas foram relacionadas com descritores ambientais, tais como a intensidade da pesca, a complexidade do

habitat, a sobretensão da água e a cobertura relativa de corais, algas, zoantídeos e algas crustosas coralinas. Os descritores da comunidade (riqueza de espécies, diversidade e regularidade) foram determinados e testados quanto a diferenças entre os anos.

Em 2022, a comunidade foi dominada em termos de biomassa e abundância por dois pomacentrídeos do género *Chromis* e três espécies de esparídeos do género *Diplodu*s. O efeito e os enviesamentos do cardume *Chromis* foram observados na avaliação anterior, e a dominância do omnívoro *Diplodus* fez com que os omnívoros fossem o grupo trófico mais importante em termos de biomassa. Em comparação com 2009, verificou-se uma mudança para os omnívoros de nível trófico médio, o que pode ser atribuído à importância das espécies *Diplodus* em 2022. Simultaneamente, registou-se uma perda de biomassa em ambos os extremos do espetro trófico, com destaque para a diminuição dos herbívoros nos níveis tróficos 2,0 e um declínio numa vasta gama de grupos funcionais de predadores com um nível trófico superior a 3,3. A composição das espécies foi muito diferente entre os anos, o que pode ser atribuído às espécies altamente abundantes anteriormente referidas, bem como a quatro espécies de elevado valor comercial. Os descritores da comunidade reflectem as diferenças entre os anos. Verificou-se uma perda significativa de riqueza de espécies superior a 20%, enquanto a regularidade aumentou de forma estatisticamente significativa, não tendo sido detectada qualquer diferença estatisticamente significativa na biodiversidade. A composição relativa da cobertura bentónica com base em oito categorias (algas, corais, zoantídeos, algas crustosas coralinas, invertebrados e substrato) não apresentou diferenças estatisticamente significativas entre os anos. O ajuste de preditores ambientais não mostrou alta correlação com a comunidade de peixes do recife.

A falta de correlação com os preditores bióticos ocorre frequentemente em comunidades dominadas por generalistas, que são mais independentes do seu habitat e podem procurar alimento numa vasta gama de condições. Uma vez que as comunidades bentónicas de ambos os anos eram virtualmente semelhantes, é pouco provável que quaisquer mudanças na comunidade sejam atribuíveis a variações naturais. No entanto, a mudança de uma comunidade dominada por espécies especializadas com uma vasta gama de grupos funcionais para uma proporção homogénea e elevada de biomassa trófica média não só reflecte os objectivos da pesca artesanal local, como também se assemelha muito às estruturas de biomassa trófica de comunidades fortemente pescadas noutros oceanos. Ao contrário do paradigma "fishing down the food web", que descreve um declínio do nível trófico médio, outros estudos encontraram um aumento da biomassa proporcional dos níveis tróficos médios, semelhante à mudança observada na reserva marinha de Santa Luzia. Com a dominância de espécies generalistas, a

redundância funcional dos peixes recifais foi fortemente afetada. Estudos anteriores sugeriram limiares para a manutenção de pescarias de piscívoros em recifes de coral, sendo necessária mais investigação para determinar esse limiar para as comunidades de peixes de recife em Cabo Verde. Quer este limiar tenha sido ultrapassado ou não, os resultados deste estudo mostram que a comunidade de peixes de recife da reserva marinha de Santa Luzia está sujeita a uma pressão de pesca insustentavelmente elevada e precisa de ser restaurada e conservada para garantir o funcionamento do ecossistema.

Este estudo sublinha a necessidade de uma monitorização estreita e contínua das AMPs para permitir uma gestão eficaz. Mostra também que uma conceção de monitorização baseada em diferentes métodos de inquérito produzirá resultados valiosos no que respeita ao efeito da AMP. Mais importante ainda, os resultados sublinham a urgência da implementação de medidas de gestão mais eficazes para a reserva marinha de Santa Luzia.

Palavras-chave:

Conservação AMP Grupos tróficos Peixes de recife Sobrepesca

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AGADO. *Água Doce*

AGARU. *Água Ruim*

ANOVA. *Analysis of variance*

BRUV. *Baited remote underwater video*

C. *commercial species*

CCA. *Crustose coralline algae*

CEPF. *Critical Ecosystem Partnership Fund*

CO. *Complexity*

CPCe. *Coral Point Count with Excel extensions*

CREOL. *Ponta Creolo*

CURAL. *Curral*

df. *degrees of freedom*

DOV. *Diver-operated video*

EEZ. *Exclusive Economic Zone*

ENORT. *Enseadinha Norte*

ESPQI. *Espequinho*

EU. *European Union*

F. *F value*

FI. *Fishing intensity*

FL. *Fork length*

FOC. *Flags of Convenience*

g. *gramm*

H'. *Shannon-Wiener diversity index*

ILHEU. *Ilhéuzinho*

ind. *individuals*

IUU. *Illegal, unreported, and unregulated [fishing]*

L. *low commercial value*

N. *species richness*

NA. *not applicable*

NC. *Non-commercial species*

NMDS. *Non-metric multidimensional scaling*

m. *meter*

MCS. *Monitoring, Control and Surveillance* m.Invert. *mobile invertebrate feeder*

MPA. *Marine Protected Area*

p. *p-value*

PBRAC. *Ponta Branca*

PC. *Principal Component*

PCA. *Principal Component Analysis*

PCHIC. *Ponta Chica*

PERMANOVA. *Permutational multivariate analysis of variance*

PPRAI. *Ponta Praia*

PPNOR. *Ponta Preta Norte*

R^2. *R quared. Coefficient of determination*

rov.Herbi. *roving herbivore*

SCUBA. *Self-Contained Underwater Breathing Apparatus*

SD. *Standard deviation*

SE. *Standard error*

SFPA. *Sustainable Fisheries Partnership Agreement*

s.Invert. *sessile invertebrate feeder*

t. *t value*

terr.Herbi. *territorial herbivore*

TL. *Total length*

UPGMA. *Unweighted pair group method with arithmetic mean*

UVC. *Underwater visual census*

W. *W value*

WS. *Water surge*

IV. General introduction

A. Coral reefs

Coral reefs are the most diverse ecosystem within the marine realm and are often referred to as the “rainforests of the sea”. The name giving taxon functions as ecosystem engineer and accumulates calcium carbonate structures through its colonial polyps, creating complex structures which are the foundation for a highly productive environment. Coral reefs are home to a vast array of marine life, such as fish, invertebrates, and algae. Even though they only cover a small area in relation to the total ocean floor, about a quarter of ocean’s fish rely on healthy coral reefs for shelter, food or as a nursery for their young.

Even so, over half a billion people rely on coral reefs and its ecosystem services. Not only do they provide essential protein to coastal communities, but because of their high structural complexity, they also create a physical barrier that protects coastal areas and communities from storms and swells and mitigate erosion risks that will result from rising sea levels (Harris et al., 2018; Ferrario et al., 2013). They play an important role in the cycling of nutrients and attract tourists which increase revenue and can support the local economy. Additionally, as a biodiversity hotspot, they potentially harbour undiscovered components that could advance medical science, for instance in the development of a cure for cancer.

i. Threats

Worldwide reefs’ health is declining drastically, which means that affected reefs are lacking the resilience for natural processes of recovery. Causes for degradation of reef health are the overharvesting of herbivores, low coral cover, high macroalgae cover, high sedimentation, and eutrophication (Mumby & Steneck, 2008).

Since the 1980’s, a decline of coral cover has been observed throughout the world. Ultimate drivers are related to climate change (global warming, ocean acidification, and storms), trophic shifts resulting in dysfunction of the system, and other factors related to anthropogenic activity. Global warming causes coral bleaching and sea level rise, resulting in widespread mortality events. Ocean acidification is driven by an increase of atmospheric carbon dioxide and negatively affecting the durability of the coral skeleton as well as coral growth rates. Climate change causes an increase in the frequency of severe tropical cyclones. Reefs worldwide are overexploited by fisheries, adding additional pressure to the ecosystem (Newton et al., 2007). Additionally, anthropogenic pressures on local scales are often inorganic and organic pollution, and an increased discharge of sediment loads, which can cause eutrophication (Mumby & Steneck, 2008). The direct causes, or proximate drivers for coral decline are numerous, some of the most crucial are coral disease, bleaching and algal competition (Mumby & Steneck, 2008).

It is important to understand the complex interactions of coral reef organisms and their environment to develop effective conservation strategies and protect this ecosystem with all its services for future generations.

B. Functional groups

i. Changes in reef fish assemblage

The diversity of habitat types within a seascape can contribute to their ability to serve as a refuge during disturbances. By providing a larger range of ecological and physical features, heterogeneous seascapes are more likely to support species that are more resilient to impacts and stresses.

Coral is essential for the survival of many reef fish species as it provides a refuge from predators, suitable substrate for settlement and prey is highly abundant for a wide range of trophic levels. Almost two thirds of species have been found to be affected by coral loss, highlighting the importance of topographic complexity and live coral cover for the reef fish community (Wilson et al., 2006).

Associated with a decrease in coral cover are shifts in the reef fish community. Especially coral-dependent species suffer from drastic changes in the reef habitat caused by coral bleaching, crown-of-thorns starfish outbreaks, or diseases (Pratchett et al., 2006). The recruitment of fish larvae will be limited, as less suitable habitat is available for recruits to settle. With a decrease of corals, the habitat will no longer support the original diversity of the fish assemblage; specialist species relying on corals for recruitment, food or shelter will be lost and replaced by a few species that prefer algal or rubble substrata (Jones et al., 2004; Munday, 2004; Graham et al., 2006).

A shift from trophic and habitat specialists to dietary generalists, such as omnivores can also be expected. These patterns of change have been observed in cryptobenthic fish, in which they can be detected much earlier than in larger reef fish, as crypto-benthic fish have a much shorter longevity, and their generation periods are shorter than those of their larger counterparts. However, the patterns detected here might translate to more mobile and larger reef fish, but could take decades to manifest (Bellwood et al., 2006; Pratchett et al., 2006). This post-impacting event generalist dominated assemblage might be more resilient withstand or adapt to future impacts as they can utilize different feeding modes (Bellwood et al., 2006).

A loss of coral cover will eventually negatively affect the structural complexity of the reef system. Graham (2006) found a decline of species richness and a shift in the size population of reef fish species. With the degradation of the reef matrix and the loss of varying habitat characteristics, smaller fish species, such as pomacentrids, that rely on those niches face increasing competition for food and shelter and are highly affected by predation (Graham et al., 2006; Wilson et al., 2006). Larger fish species only decline in abundance with a higher loss of structure.

The survival of a species in response to a degrading habitat will depend on the resource limitation, namely the availability of suitable (micro-) habitats for living and recruitment, its ecological versatility or its ability to utilize alternate resources, and on its sublethal response or its ability to compete for remaining resources (Wilson et al., 2006).

ii. Herbivory

The benthic community structure on coral reefs can experience phase shifts, which commonly occur after major coral mortality events. Subsequently macroalgae grow in abundance, shifting from coral to algae dominated state. Three herbivorous groups – bioeroders, scrapers and grazers – play a critical role in controlling these phase shifts and the health of the reef system. Bioeroding fish remove dead corals, creating space and suitable habitat for coral larvae to settle. Scrapers remove algae and sediment; this further promotes settlement of coral larvae and supports growth and survival of corals. Grazers remove seaweed and are directly reducing coral overgrowth and shading by macroalgae, therefore lowering competition with space-monopolizing algae (Bellwood et al., 2004).

The relationship between coral cover and herbivore biomass creates well-established ecological feedback loops. These can either lead to a resilient reef system (positive feedback) or to an unhealthy reef system that is dominated by macroalgae (negative feedback) (Mumby & Steneck, 2008).

In a healthy reef system, the herbivores grazing impact reduces macroalgae cover, which increases the availability of suitable habitat for coral larvae to settle. A higher coral recruitment expands the coral cover which then increases grazing activity and structural complexity. A higher structural complexity has been found to enhance the recruitment of fish and which then again results in increased grazing activity (Mumby & Steneck, 2008). Additionally, it has been shown that large herbivores will have a disproportionately larger impact on grazing of macroalgae (Mumby et al., 2006), and a higher reproductive output which will stabilize this state long-term.

On the other hand, in macroalgae-dominated alternative states the high macroalgae cover overgrows suitable space for coral recruits (Hughes et al., 2007). Reduced recruitment leads to reduced coral cover, and decreases in grazing activity and structural complexity. Less fishes are recruited, and therefore the grazing intensity by herbivores is reduced, which in turn promotes macroalgae growth (Mumby & Steneck, 2008). This negative feedback can be enhanced further as some seaweeds produce metabolites that can cause coral bleaching or deter herbivores (Rasher & Hay, 2010) or through trophic cascades and top-down control resulting in changes of the food web structure and ecosystem function (Hughes et al., 2007; Dulvy et al., 2004).

Once established, large macroalgae can be difficult to remove because of herbivore behaviour and food preferences, which can stabilize a macroalgae- dominant reef community. It has been shown that herbivorous fish were discouraged from entering a reef system with high density of macroalgae, likely because the large upright stands of macroalgae are a barrier for predator detection, but not for predator movement (Hoey & Bellwood, 2011). Opposed to a coral reefs high structural complexity that provides spatial refuges from predators, the high structural complexity created by dense macroalgae patches might be perceived as a hazardous environment and reduce herbivore activity and consequently promote macroalgae growth (Hoey & Bellwood, 2011). In addition, there are few herbivores that graze on large macroalgae, often propagules and early stages of algae are preferred, whereas a single herbivore species may be solely responsible for almost all the consumption of adult seaweed (Hoey & Bellwood, 2009; Rasher & Hay, 2010). This implies that the harvesting of key species in critical functional groups can have tremendous consequences for coral health.

The number and diversity of herbivores generally are powerful indicators when assessing the health of the reef system and its resilience. Reef communities with high species richness have a higher potential for functional redundancy across different key functions and consequently may have a better chance of recovery if one species is lost from a functional group (Bellwood et al., 2004). But previous studies highlight the need to assess the specific functional role of individual species for the maintenance of the ecosystem (Hoey & Bellwood, 2009; Rasher & Hay, 2010). The identification of key species in functional groups and their critical role in dynamic ecological processes should be taken into consideration when developing effective resilience-based management strategies.

iii. Predatory fish

As they are on top of the food chain, predatory fish often display large sizes and are therefore in the focus of fisheries. Landings shifted from large piscivorous fish to smaller invertebrate-feeding and planktivorous fish, causing a decline of mean trophic level in all oceans, generally termed as ‘fishing down the food web’ (Pauly et al., 1998). Myers & Worm (2003) estimated that we lost 90% of large predatory fish globally. This depletion of fish stocks has increased in the beginning of the second half of the 20th century remaining beyond sustainable levels ever since (Christensen et al., 2002), with drastic implications for ecosystem functioning. The removal of predatory fish lowers the abundance of large fish, reducing the predation mortality on the size range below the fished range. A substantial increase of these individuals follows, not only increasing the predation pressure on the next lower size class, but also increasing the competition for food within the size class, thus negatively affecting the growth rates of these individuals, further enhancing the increase of abundance within a certain size class (Andersen & Pedersen, 2010). These trophic cascades originating from the harvesting of predatory exceed the fish community and can facilitate starfish outbreaks which in return prey on coral, causing a shift in the whole reef system from carbonate-accreting reef builders to a macroalgae-dominated state (Dulvy et al., 2004).

iv. Atlantic islands reef fish community structure

The reef fish communities of volcanic Atlantic islands are typically dominated by high densities of planktivores, namely in Fernando de Noronha Archipelago (Krajewski & Floeter, 2008), St Peter & St Paul’s Archipelago (Luiz et al., 2015), São Tomé Island (Maia et al., 2018), and Trindade Island (Pinheiro et al., 2011). In terms of biomass, the results are variable; in Fernando de Noronha Archipelago roving herbivores dominate by 40 % (Krajewski & Floeter, 2008), in St Peter & St Paul’s Archipelago over two thirds of the total biomass is attributed to omnivores (Luiz et al., 2015), in São Tomé Island planktivores are also the most important trophic group in regard to biomass (Maia et al., 2018), and in Trindade Island the distribution of biomass is more equal between carnivores, omnivores and roving herbivores (Pinheiro et al., 2011).

These differences have previously been related to latitudinal differences of the locations. Towards the tropics, species that utilize low-quality food sources such as herbivorous fish dominate in terms of density as well as species richness, whereas in colder sites food of intermediate quality is seasonally more abundant and promotes the abundance of diversity of more versatile species, especially those of omnivorous sparids with shifting diets depending on food availability (Floeter et al., 2004). However, even fish communities of Atlantic Islands close to the equator are characterised by low species diversity and richness and appear homogeneous as a result of dominance of generalists (Krajewski & Floeter, 2011; Luiz et al., 2015).

Generalists can tolerate a wide range of environmental conditions and are not limited by key factors. Consequently, reef fish communities of Atlantic islands have been found to be weakly related to environmental variables (Krajewski & Floeter, 2011) or biotic variables such as benthos composition (Luiz et al., 2015; Maia et al., 2018). However, depth can be an important driver of community structure as it can promote density of planktivores, omnivores, macrocarnivores, and sessile invertebrate feeders, but may negatively affect territorial herbivores, herbivores-detritivores, macroalgae feeders and mobile invertebrate feeders (Luiz et al., 2015; Maia et al., 2018). Differences in the effect of depth in between localities could potentially be attributed to variations in fishing pressure, as deeper areas in some cases may be less accessible and more undisturbed resulting in lower fishing pressure (Maia et al., 2018).

C. Overfishing

Marine resources provide 4,3 billion people with 15% of their protein needs and supply an income for more than a tenth of the world's population (Costa-Pierce, 2016). A rising demand for protein to feed growing human populations globally puts an increasing pressure on fish stocks, other marine resources and on marine ecosystems, with an unproportionally high pressure in fast-growing, poor coastal communities of developing countries. Simultaneously, the commercial exploitation of global fisheries depletes marine resources globally (D et al., 2002; Myers & Worms, 2003). Different sources estimate a depletion of the world's fish stocks anywhere from a third to three quarters of all global stocks (Liddick, 2014). Reliable numbers for fish stocks are largely missing, lack in interpretability or are subject to the 'shifting baseline syndrome' (Pauly, 1995). This paradigm describes a shift in the evaluation of fish stocks and species composition over generations of fisheries scientists and highlights the importance of developing frameworks that incorporate earlier knowledge to paint a more accurate picture of trends in fisheries.

Historically, overfishing predates pollution, degradation of habitats and water quality, and anthropogenic climate change and is often a necessary precondition for eutrophication, outbreaks of disease and introduction of invasive species. It is the most severe human disturbance to marine ecosystems, causing ecological extinction that is worse than any other human impact on marine ecosystems. Especially in coastal regions that are under greater fishing pressure, overfishing causes structural and functional changes in fish communities, in all ecosystems a loss of biomass and decline in the abundance of large individuals is apparent. There is a delay between an altered ecosystem response and the onset of fishing, due to functional redundancy; meaning a different species can fill in the same function and therefore compensate the loss of another. However, the ecological extinction of entire trophic levels can be devastating, making an entire ecosystem more vulnerable and less resilient to other natural and human disturbances (Jackson et al., 2001).

The effects of overfishing are most severe in coastal communities of developing countries. Their livelihoods highly depend on small-scale fisheries, but they cannot compete with industrial fleets. The competition over marine resources highly drives overfishing, the harvesting of fish stocks beyond a sustainable limit, meaning a population will not be able to recover to its original population size. Marine resources are openly accessible, so opposed to terrestrial farmers with privatized produce, no fisherman solely carries the full effect of stock declines. The catch-per-effort decreases equally as every single fisherman is contributing to the overharvesting. Along with this high drive of competition also comes a typically short-term perspective, that adds socio-economic challenges to the sustainable management of fish stocks. Already a challenge on national basis, a substantial part of marine resources can be found in the high seas and their management does not fall under the jurisdiction of a single country, thus requiring international agreements to incentivize sustainable management.

Even if fisheries of a single species or stock that is prone to collapse or already largely depleted is regulated, this population can be further threatened as unintended bycatch in multi-species fisheries. Due to its small size, a population suffers severe effects on its genetic variability and as a result population persistence, the societal and managerial responses and their speed of action is critical as it determines the size and age structure of the population and largely affects its recovery process (Hutchings & Reynolds, 2004).

Illegal, unreported and unregulated (IUU) fishing significantly contributes to the depletion of fish stocks worldwide, affecting both coastal zones and the high seas and is widespread among all types and sizes of fishing vessels. IUU fishing refers to a wide array of activities that typically are more lucrative than licit fisheries activities as they operate on lower costs and score higher revenues, such as the use of banned fishing gear, the harvest of prohibited species, fishing without a license or out of season, and disguising illicit catches. But also, the dumping of smaller, low-quality fish, known as ‘high grading’, falsifying catch weights or the use of ‘Flags of Convenience’ (FOC), which is a perfectly legal practice, creating a loophole for vessels to circumvent management and conservation measures. About a tenth of the global fishing fleet flies FOC and are often linked to complex ownership, decreasing traceability and complicating enforcement of regulations and prosecution (Liddick, 2014). IUU fishing is not only linked to poor governance and gaps in international law, but also to other institutional factors such as corruption and often simply the lack of Monitoring, Control, and Surveillance (MCS) capacities. Economic causes are the overcapacity, describing the imbalance between fishing capacities and fishing possibilities, ineffective management, and subsidies (Gallic & Cox, 2005).

In the prevalence of poor economic conditions and prospects, as the case in developing countries IUU is more likely to occur, a previous study identified the greatest IUU activities in the Eastern Central Atlantic (Agnew et al., 2009). As long as the benefits outweigh the costs, IUU fishing stays lucrative and disrupts the local economy of the affected country, the costs for global economies sums up to as much as $10 to $23.5 billion annually (Agnew et al., 2009). IUU activities further contribute to hunger and poverty, harms target species and disturbs ecosystems (Liddick, 2014).

Besides IUU fishing, apparently regulated fishing with the intentions to promote sustainable fisheries, often lacks efficiency in its implementation. Affluent nations or unions often ratify agreements with poorer, developing countries that have jurisdiction over valuable marine resources. In the case of Cabo Verde, the country controls with 740 000 km^2 a large exclusive economic zone (EEZ) relative to its land area. While the domestic fishing sector consists mostly of traditional, small-scale artisanal fisheries, the country grants fishing permits for numerous foreign vessels within its EEZ. In 2020, over half of the industrial fishing licenses were issued for foreign vessels, of which the European Union (EU) fleet is the largest. Licenses for EU vessels (mostly Spain, Portugal, and France) are issued based on a bilateral agreement, the Sustainable Fisheries Partnership Agreement (SFPA). Besides a financial compensation, this agreement also includes development of the partner countries' administrative, technical, and scientific capacities to promote sustainable fisheries. In more detail, the EU agreed to assist the surveillance of fisheries activities, strengthen scientific knowledge about fisheries resources, support local communities, aid international cooperation, and develop 'blue economy' and aquaculture (European commission, 2019). In contrast, the EU has been shown to historically overexploit fish stocks within the EEZ of Cabo Verde and the activities of the EU fleet negatively affect artisanal fisheries (Mundt, 2012). The efficiency of this bilateral agreement is limited as the EU fails to follow through on several of the set objectives and lacks transparency from Brussels, using the agreement to prioritise EU interests in Cabo Verde (Aquino, 2022).

Aquaculture is often considered to take pressure off wild stocks but comes bearing more problems as it harms wild fish, its stocks are prone to disease and in developing countries coastal wetlands are commonly destroyed to build aquaculture facilities (Shakouri & Yazdi, 2010). The most efficient strategy to reduce overfishing is therefore to stop subsidies for fisheries which only promote fishing and decrease the capital costs of IUU vessels, and to tackle financial benefits associated with IUU fishing such as increasing the gap between the market value of illicit and legally caught fish and increasing costs regarding the risk and operating of IUU activities (Gallic & Cox, 2005; Shakouri & Yazdi, 2010). International cooperation will be needed to close gaps in international law and come to agreements that provide the legal framework for a more sustainable management of marine resources in international waters, the latest glimmer of hope emerges through the adaptation of the High Seas Treaty by the United Nations in June 2023 (United Nations, 2023).

D. MPA

Marine Protected Areas (MPAs) are widely established as a tool for fisheries management and conservation, as they limit (partially or fully) the extraction of resources within a certain area. Some common benefits include the conservation of biodiversity, climate mitigation and resilience, disaster risk reduction and improved fisheries due to an increase in fish biomass and density not only within the MPA (Halpern, 2003; Côté et al., 2001), but also beyond MPA boundaries, as larvae and adults are exported due to the spillover effect (Di Lorenzo et al., 2020). The effect of the MPA depends on the time after establishment and is species-dependent, the commercial value and the life-history traits of a species are good indicators for the effect on a given species. The earliest effect after establishment is the increase in size of commercially targeted species, especially in large-bodied species, and therefore an increase in biomass (Claudet et al., 2006). This effect is stronger for species under higher commercial pressure and responses increase with time since protection (Claudet et al., 2006; Claudet & Guidetti, 2010). Then follows an increase in abundance of targeted fish species, as fish live to grow larger. Larger females have a disproportionally higher reproductive value. Non-targeted species show varying responses to reserves, in some cases declines of biomass and abundance can be explained by higher predator pressure on the species. However, these benefits vary depending on the protection level(s) within the MPA, the level of enforcement, and along these lines the engagement of local communities can be a critical factor (Zupan et al., 2018; Di Lorenzo et al., 2020, Côté et al., 2001).

i. MPA effectiveness

Over the last two decades, the area of MPAs increased rapidly, from around 1% protection of total ocean area in 2000 to over 8% in 2023 (Worm, 2017; MPAtlas.org, August 2023). Nations worldwide are propelled to meet conservation targets, such as the Sustainable Development

Goal 14 and Aichi Target 11. This rapid establishment might be deceiving, as they might meet targets based on area coverage, but fail to sufficiently integrate additional biodiversity targets and show shortfalls in conservation outcomes (Tittensor et al., 2014; Worm, 2017). Only strongly or fully protected areas that are appropriately managed show the desired benefits of international targets (Sala & Giakoumi, 2018), their effect is improved when partially protected areas are adjacent (Zupan et al., 2018). The principles of an MPA should be in line with those set by international targets and meet all clauses of the targets, i.e. "effectively and equitably managed" in Aichi Target 11, as otherwise the MPA can be considered a 'paper park' and consequently desired MPA effects fail to appear (Gill et al., 2017).

During the MPA design, goals need to be explicitly stated according to objectives (Halpern, 2003). Objectives should be specific, measurable, attainable, relevant and time bound. To increase and ensure the effectiveness of an MPA, it should be designed and managed appropriately with realistic conservation targets that are based on scientific advice. Scientific justification such as ecological criteria and information on the area present a valuable base in the design of MPAs and facilitate the assessment towards its effectiveness and therefore its ability to provide desired benefits.

The success of MPAs increases when local communities are integrated in the conservation strategies, ideally from the initiation of the reserve. If the strategies are not adhered to, for instance if local fishermen do not comply, the MPA objectives are not achieved which can cause mistrust in the success of MPAs. Not only does the level of compliance of stakeholders affect the MPA's success, the MPA's success affects the attitude of the stakeholders towards the protection measures and can show contrasting effects for stakeholders, often negatively affecting some groups or subgroups of stakeholders (Mascia et al., 2010).

Further reasons for the ineffectiveness of MPAs can be attributed to small management staff size, insufficient financial, logistical, and technical support, lack of scientific information, and insufficient institutional, decision-making, and political support (Di Franco et al., 2016; Gill et al., 2017). Furthermore, MPAs can be highly affected by terrestrial and coastal management, such as coastal vegetation destruction and anthropogenic development, that is not under the control of the MPA management authorities. All these factors should be considered throughout the different stages of the MPA design process: Planning, implementation, and active and adaptive management. The last stage involves continuous monitoring of the MPA to routinely evaluate its effectiveness and when needed, adapt management approaches and strategies to fulfill or reassess the conservation targets.

ii. Adaptive management

Adaptive management reduces uncertainty by enabling managers to evaluate and adjust objectives and strategies to improve effectiveness over time (Chambers et al. 2019). It is system-based, proactive, flexible, iterative, and responsive, and participatory. Adaptive management strategies recognize MPA objectives and identify a clear target with limit, which should be considered in the planning and design of the MPA (1), first step of the adaptive management cycle. After its implementation (2), continuous monitoring (3) is carried out to allow for learning and adjusting (4). Then the adaptive management cycle starts again, leaving room for adaptive experiments (step 2-3) and adaptive governance (step 4-1). The assessment of MPA effectiveness needs to be based on appropriate and target-related criteria and compared to a control.

Every MPA survey design should be based on scientific predictions of expected effects and MPA goals. To differentiate between natural variability and MPA effect, the design ideally includes multiple control areas, long-term variability, and data from before the MPA establishment (Fraschetti et al., 2002). Ideally, MPA effects are measured through a before-after-control-impact (BACI) approach, which is often not possible (Claudet & Guidetti, 2010). The most applied approach is inside the MPA versus outside (control) with a similar habitat and fish assemblage to the protected area. Before and after establishment is another possibility, but often fails to integrate long-term variability and a before assessment is often not available. It is crucial that sampling and analytical designs are adapted and appropriate to the individual MPA context (Claudet & Guidetti, 2010).

The MPA targets need to be defined on the level of the effectiveness indicator and set with confidence limits. Effectiveness measures should be selected to account for uncertainty of 1) biological processes based on the knowledge of the system; 2) measurements of appropriate indicators (confidence intervals or standard deviation of the mean) improved by increasing replication and reduction of bias; and 3) the model, which should consider alternative hypothesis (Syms & Carr, 2001; Pomeroy et al., 2004). Additionally, when assessing MPA effectiveness, the socio-cultural context should be considered to adequately evaluate ecological responses (Claudet & Guidetti, 2010, Batista et al., 2015). Specifically, the assessment of fisheries dynamics, such as fishing intensity, as well as the level of enforcement must be considered as they strongly affect the MPA's success. Adaptive management approaches then can improve long- term impacts on natural resources and communities depending on them, through learning (failures and success), the diagnosis of specific issues and adaptation.

iii. Indicators

The evaluation of MPAs should consider a set of indicators that accurately assess the outcome of set conservation targets (Di Marco et al., 2016, Claudet & Guidetti, 2010). Several indicators have been employed to assess fish assemblages, their ability to detect changes within the community however are disputed. Commonly species richness, diversity, evenness, abundance, and biomass are determined to describe communities and determine the effect of their protection.

However, the community structure can experience pronounced shifts, whereas parameters like abundance, diversity, and species richness do not differ significantly (Bellwood et al., 2006; Soykan & Lewison, 2015). Biomass is an important indicator regarding fisheries and much more sensitive than abundance measures as larger and heavier fish are predominantly targeted, thus strongly impacting the size population structure of populations under fishing pressure (Wilson et al., 2010). Therefore, the biomass of commercial fish and herbivorous fish is considered in the reef health index, along with other indicators such as fleshy macroalgae and living coral cover. The selection of indicators can vary depending on the MPA context, but they should always be appropriate for the associated conservation target that is being assessed.

After the selection of indicators, the planning and conduct of evaluation, the last step in the evaluation process is the communication of the results and the adaptation of the management (Pomeroy et al., 2004). Targets should be evaluated in regard to time, as biological processes are not instantaneous and the MPA effects can lag over varying time scales. MPA management is often facing constraints on evaluation such as time restrictions, seasonal activities, and weather conditions, as well as lack of expertise to perform evaluation with indicators and appropriate measurement methods (Pomeroy et al., 2004).

iv. Survey methods

MPAs are generally sampled through non-invasive, non-extractive methods, such as underwater visual census (UVC) conducted by divers, or video and stereo-video methods (Table 1).

Diver-operated video (DOV) surveys are a cost-effective alternative to UVC and deliver representative results in species identification, and abundance (Pelletier et al., 2010). The use of DOV reduces the time spent in the field, and therefore costs or can generate more data at the same cost compared to UVC. It also decreases (inter-) observer bias, and bias due to misidentification, and presents opportunities in standardization over long time series. Additionally, , it provides a permanent video record, which can be used and reanalysed in future

Table 1: Advantages and disadvantages of three non-invasive, non-extractive methods (UVC, stereo-DOV, and BRUV).

Method	Advantages	Disadvantages
Underwater Visual Census (UVC)	• Comparatively inexpensive • Detection of crypto-benthic species	• Requires skilled observers • Inter-observer variation • Fish avoidance/ attraction to divers • SCUBA limitations in depth and bottom time
Diver-operated video (stereo- DOV)	• High accuracy and precision in fish length estimates → robust assessment of biomass and size structure • Overcomes observer biases • Standardization over long time-series • Delivers a permanent record • Transect based: accurate density estimates in defined boundaries	• Fish avoidance/ attraction to divers • SCUBA limitations in depth and bottom time • Crypto – benthic species are often undetected
Baited remote underwater stereo-video (stereo-BRUV)	• High accuracy and precision in fish length estimates → allows for a robust assessment of biomass and size structure • Overcomes diver presence and observer biases • Standardization over long time-series • Delivers a permanent record	• Unknown and varying area of attraction (bait plume) • Primarily targets carnivorous species

studies that might also consider other aspects or variables previously not investigated, such as fish behaviour.

When assessing an MPA which has an objective to conserve or restore fisheries stocks, biomass is a better indicator than abundance, and is therefore a better parameter to assess MPA effectiveness. Biomass can be overestimated in UVC compared to stereo-DOV but is comparable when unmeasured fish are integrated in the analysis over a size median (Wilson et al., 2018). Stereo-DOV delivers more accurate and precise length estimates and therefore more precise biomass estimates than those of experienced diver scientists (Harvey et al., 2002). In stereo-DOV the estimation of the total study area is also more precise (Cappo et al., 2003). Taken together, this gives greater statistical power, and makes it a more suitable non-invasive method for detecting changes in fish populations (Goetze et al., 2015). With new software and technology arising, stereo-DOV approaches provide a valuable database; the methods and software employed could be developed further and modified in the future to allow sampling by less experienced personnel, and allow for surveying and monitoring at lower cost, and could lead to more effective management of MPAs.

This study uses the free, open-source software VidSync (Neuswanger et al., 2016), for its application in stereo-DOV a calibration object (Figure I) and a camera mount (Figure II) are required. The technical details, such as the angle of the cameras and the separation of the cameras on the mount or the separation distance of the screens, can vary depending on the application and habitat surveyed.

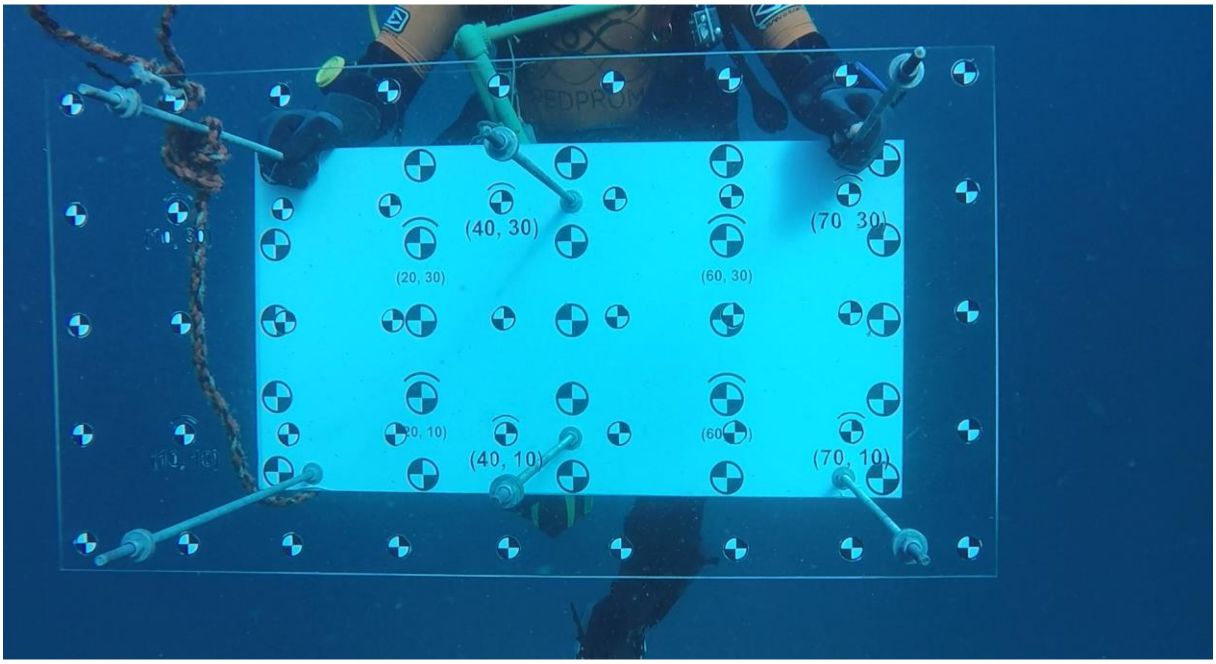

Figure 1. *Calibration object for stereo-video. Distance between screens 420 mm.*

Figure 2*. Camera mount for stereo-video transects. Technical details: base separation- 70mm, inward facing angle of 8°. Fitted with compass to navigate underwater and adjust and control swimming direction during transects.*

V. References of the general introduction

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Mid-trophic generalists dominate reef fish community impacted by overfishing

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1. Abstract

Overfishing is one of the most severe threats to oceans globally and predates all other human impacts on the marine environment. A common tool to manage fisheries sustainably are marine protected areas (MPAs). However, to achieve the desired results effective management plans integrating continuous monitoring need to be in place. This study assessed the MPA effect of nine sites within the Santa Luzia marine reserve, by employing diver-operated stereo- video transects along with an assessment of the benthic composition to account for natural variability. Specifically, differences to a previous assessment in 2009 were evaluated in terms of reef fish relative biomass by trophic group, relative densities and frequency of species using multivariate analyses and change of community descriptors (species richness, diversity, and evenness). In 2022, the community was dominated in terms of biomass and density by two pomacentrids of the genus Chromis and three omnivorous sparid species of the genus Diplodus. A pronounced shift from a more specialized community in 2009 with high proportions of the biomass at the lower and upper end of the trophic spectrum, to a more homogenous community dominated by mid-trophic generalists was observed. There was no significant difference between the benthic cover composition and fishing intensity is the only environmental predictor that was weakly related to community composition. In the virtual absence of natural variation accompanied with over 20% loss of species richness and significantly higher evenness, the reef fish community of Santa Luzia exhibits signs that previously have been related to high fishing pressure. The functional redundancy of reef fishes was heavily impacted, and the implementation of more effective management measures is necessary to restore the reef fish community and ensure ecosystem functioning.

Keywords:

Conservation MPA Trophic groups Reef fish overfishing

2. Introduction

Overfishing, one of the most severe threats to oceans, predates other human disturbances such as pollution, degradation of water quality, anthropogenic driven climate change and causes of ecological extinction in - not only, but especially - coastal areas globally. The depletion of fish stocks transcends beyond threats opposed on target species, as it can prompt structural and functional changes throughout the food web and can even cause the loss of entire trophic level, negatively affecting the resilience of the ecosystem (Jackson et al., 2001).

A common tool to restore fish stocks and promote sustainable fisheries is the establishment of marine protected areas (MPAs). MPA benefits the conservation of biodiversity, climate mitigation and resilience, disaster risk reduction and improved fisheries due to an increase in fish biomass and density not only within the MPA (Halpern, 2003; Côté et al., 2001), but also beyond MPA boundaries, as larvae and adults are exported due to the spillover effect (Di Lorenzo et al., 2020). The MPA effect varies with level of protection and enforcement, latitude, MPA size, and age (Soykan et al., 2015; Côté et al., 2001) and is species- and fish size-dependent; commercial value and life-history traits of a species are good indicators for the effect on a given species (Claudet et al., 2006).

Historically, resource management focused on single species or sector and only in the last decades managements started to consider socio-ecological connections, shifting towards resilience-based management approaches (McLeod et al., 2019). Ecological resilience refers to the ability to resist threats, recover from disturbances and adapt to changes (Holling 1973, Nyström and Folke 2001). The functional redundancy within a community is an important predictor for a system's ecological resilience and can potentially cause a delay in an altered ecosystem response and the onset of a disturbance, such as fishing (Jackson et al., 2001). A high ecological resilience preserves the maintenance of an ecosystems key functions and processes and is crucial in an ever-changing, less predictable world.

Adaptive management improves decision-making in the face of uncertainty, it is centred around a 'learning by doing' strategy and encourages managers and stakeholders to make future decision based on observed effects of their management strategies. When assessing the effect of implemented strategies, difficulties are faced in the application of a true experimental design, such as the Before-After-Control-Impact design which minimizes confounding effects, because of monetary cost and stakeholder engagement (Tony, 2020). Most studies assessing MPA effects are set up in a Control-Impact design as before data is often not available. When assessing areas within and outside the MPA, spatial variation may be confounded with reserve effects; vice versa the assessment in a before-after design may confound temporal variation with reserve effects (Jackson et al., 2001). The integration of ‘before’ data (when available) is crucial in a field where the shifting baseline syndrome is insidious and widespread (Pauly, 1995).

The selective effect that fishing has on the size structure of a population is well understood (Wilson et al., 2010; Andersen & Pedersen, 2010) and biomass is considered a powerful indicator, showing greater statistical power than abundance values (Soykan et al., 2015). Two commonly used indices, species richness and diversity, do not always show the effect of an MPA and might not adequately represent shifts in the fish community (Bellwood et al., 2006; Soykan et al., 2015). However, diversity is often associated with, but not indicative of functional redundancy (Bellwood et al., 2003; Hoey & Bellwood, 2009). Ecosystem health and the maintenance of key processes is more precisely evaluated when trophic structure and community function are considered in the analysis.

One hypothesis regarding the influence of fishing on the fish community structure is widely known as ‘fishing down marine food webs’ and describes the process of fisheries targeting smaller fish, after the depletion of large predatory fish with high commercial value, gradually moving towards smaller species with a low trophic level (Pauly et al., 1998). This has effects on food web interactions, as lower abundances of predatory fish reduce the predation pressure on the next smaller size class, an increase in abundance of that size class follows, leading to a higher predation pressure on its prey population, thus food limitation for the predators, limiting growth (Andersen & Pedersen, 2010). Contradicting this paradigm, Graham (2017) identified an increase of the trophic level with lower biomass, partially due to great proportions of low-trophic level fish at high biomass levels and low fishing intensity. Alongside occurs a proportional increase of mid-trophic level individuals in fished regions, likely a consequence of the release from predation pressure (Lamb & Johnson, 2010; Mumby et al., 2012). The effects of fishing on the trophic structure of a fish community are less well understood in more compound ecosystems with complex trophic links, such as coral reefs.

This study addresses the main question of how MPAs impact fish community structure, using as model the rare opportunity to compare fish community information in before and after a long-term conservation effort was conducted. To evaluate the effect of Santa Luzia MPA in Cabo Verde, this study reassesses the reef fish relative biomass and abundance in terms of (1) community structure (species richness, diversity and evenness), (2) trophic function, (3) community composition, and (4) absolute frequencies of species distribution, and investigates differences in between study sites and to a study by Freitas (2019) in the same sites in 2009. This study also considers natural variability by accounting for changes in benthic habitat composition between the sites and years, and assesses the effects of habitat complexity, water surge, and fishing intensity.

3. Material and Methods

3.1. Study Area

Cabo Verde is a country formed by an archipelago (also known as Cape Verde) located in the eastern central Atlantic (Figure 3.1), 300 nautical miles off the coast of Dakar (Senegal), the closest point on the African mainland (where a cape named Cap Vert occurs, often originating mistakes in species records). The archipelago is of volcanic origin, consists of ten islands and various islets which are divided into the Barlavento (Windward) group to the north and the Sotavento (Leeward) group to the south. The Barlavento group is situated at the southern limit of the cold Canary Current and a tropical climate prevails on all islands. The reefs are composed off volcanic rocks, major coral reef structures are absent, and the coral species diversity and richness are lower than in other tropical reef systems (Monteiro et al., 2008), therefore generally referred to as coralline community.

Santa Luzia Island (16°45′ N, 24°44′ W) is the only uninhabited, and smallest island of the archipelago with a land area of 34,27 km^2. Belonging to the Barlavento group, Santa Luzia is located 9,26 km to the east of São Vicente Island with the biggest port of the country placed in Mindelo. In 1990, a protected area with the category Integral Reserve was established, today the Santa Luzia/ Branco/ Raso Natural Reserve covers 454,62 marine km^2 and 40,65 terrestrial km^2. Santa Luzia is among the Critical Ecosystem Partnership Fund’s priority key biodiversity areas (CEPF, 2019) and the surrounding waters are traditionally important to artisanal fisheries of the surrounding islands São Vicente, Santo Antão and São Nicolau. The MPA goals are the promotion of biodiversity-friendly and sustainable fisheries co-management agreements to enhance compliance with protection measures through the designation of no-take zones, seasonal fishing bans and the adaptation of practices and gear (United Nations, 2022). The only previous assessment of Santa Luzia’s fish community were conducted in 2009, using underwater visual census.

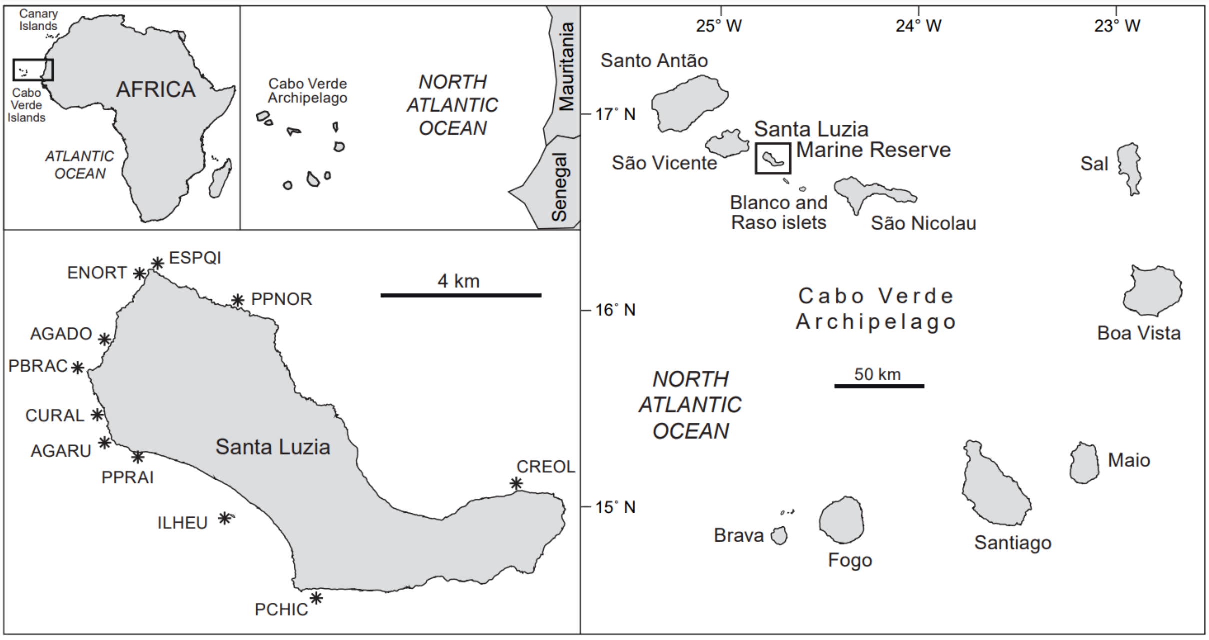

Figure 3.1. *Map showing the geographical position of the Cabo Verde Archipelago in the eastern central Atlantic Ocean and the study sites in the Santa Luzia Marine Reserve, including nearby islands and islets (as in Freitas et al., 2019). The 11 studied reefs (stars) at Santa Luzia Island were: Água Doce (AGADO), Água Ruim (AGARU), Curral (CURAL), Enseadinha Norte (ENORT, only in 2009), Espequinho (ESPQI), Ilhéuzinho (ILHEU), Ponta Branca (PBRAC), Ponta Chica (PCHIC, only in 2009), Ponta Creolo (CREOL), Ponta Praia (PPRAI) and Ponta Preta Norte (PPNOR).*

3.2. Survey procedure

The survey took place from September 14 to September 21, a total of 9 sites were assessed, which also were subject in the 2009 assessment (ILHEU, PPRAI, AGARU, CURAL, AGADO, PBRAC, ESPQI, PPNOR, CREOL). Unlike previous assessment, this study is using stereo diver-operated video (stereo-DOV), opposed to underwater visual census (UVC). Stereo DOV has numerous advantages, such as a decrease in (inter-)observer bias, minimize bias due to misidentification, more accurate and precise length estimates and therefore a more precise biomass estimate than those of experienced diver scientists (Harvey et al., 2002), and a more precise estimation of the total study area (Cappo et al., 2003). All of which give this method a greater statistical power and make it a more suitable non-destructive method to detect changes in fish populations (Goetze et al., 2015). It also presents opportunities in standardization over long time series and gives a permanent video record, that can be used and reanalyzed in future studies that might also consider other aspects or variables not investigated here, such as fish behaviour. Additionally, it allows sampling by less experienced personnel and allow for surveying and monitoring at lower cost and could lead to more effective management of MPAs.

The transects (20 x 2m) were run parallel to shore. Swimming with the current, the fish were filmed with two GoPro Hero4, mounted to a camera mount (base separation 70mm, facing inward by 8°). The diver operating the stereo-video swam ahead, while another diver unwound the transect tape and followed closely behind. The swimming speed was aimed at 3s/m (= 20m/min) (Goetze et al., 2019).

The benthic community structure was assessed with 20 photo quadrants (25 x 25 cm) per transect, which were taken in 1m intervals. For the analysis of the photo quadrants, the Coral Point Count with Excel extensions (CPCe 3.6) program (Kohler & Gill, 2006) was used. 25 randomly placed points were selected in each photograph to estimate the relative abundance or surface cover (in %) of each substrate type. They were classified into 10 functional categories: macroalgae, turf algae, crustose coralline algae (CCA), hard corals, zoanthids, millepores, other invertebrates, rhodoliths, bare rock, and sand and rubble.

For each transect, the depth and water temperature were noted, according to the dive computer. The complexity of the substrate was classified on a scale from 1 (low) to 5 (high) in a video assessment.

3.3. Video Analysis

Fish lengths were measured in VidSync (Neuswanger et al., 2016) from snout to fork (fork length (FL)), as the fork was the characteristic that could also clearly be distinguished in sites with poor visibility. For some individuals (n= 2938), the length was assumed using the overall average of all individuals of the same species from all sites. The majority of these fish were unmeasured due to their shoaling behaviour (*C.lubbocki* (n=652), *C.multilineata* (n=1569), *T.pavo* (n=705) and *D.lineatus* (n=4), which complicates the clear distinction of the same individual in both (left and right) frames, other species were hidden in (*S. imbricatus* (n=5) , C. capistrata (n=1) and *C. rostrata* (n=1)) or not clearly distinguishable from (*C. atlantica* (n=3)) the habitat. Fork length estimates were converted to total length using length-length relationships established by Oliveira (2015), due to the body shape of some species no conversion was necessary. In the case of *T.pavo* a relationship between the measured length and the total length was established from high visibility transects and then applied to all individuals. Total length (TL) estimates of each fish were converted to weight (W) using the species-specific allometric length-weight conversion: $W = aTL^b$.

When species-specific parameters (a, b) were not available, those of a closely related fish were applied (references as in Freitas et al., 2019: Halpern and Floeter (2008), Pereira et al. (2012), Oliveira et al. (2015)). The sum of all individuals of each species provided the biomass estimate for each transect. Information on trophic level was obtained from FishBase (Froese & Pauly, 2023), when information on trophic level was not available, that of the closest relatives was used.

3.4. Statistical Analysis

For the comparison of the obtained data to the assessment of the reef fish community in 2009 (Freitas et al., 2019), cryptobenthic species were removed from the previous dataset.

All statistical analyses were performed with R, version 4.0.5 (R Core Team, 2021) and methods within the packages vegan (Oksanen et al., 2019), clustsig (Whitaker & Christman, 2014), and car (Fox & Weisberg, 2019).

3.4.1. Differences in trophic function

Relative abundances and biomass of trophic levels and groups (carnivores, territorial herbivores, roving herbivores, mobile invertebrate feeders, sessile invertebrate feeders, omnivores, piscivores and planktivores) were compared. Note that only results of relative biomass are shown, as they appear to be more indicative than relative densities.

3.4.2. Community descriptors: species richness, diversity, and evenness

To assess general differences in the reef fish communities, three indicators, species richness (N), Shannon Wiener diversity (H') and evenness (Hill's ratio = H'/ N) were determined through the diversity function in R. All indicators were tested on normality (Shapiro Wilk's test) and homogeneity of variance (Levene's test) and according to these results (α= 0,05) either a parametric Welch's t-test (diversity) or a non-parametric Wilcoxon-Mann-Whitney- Test (richness, evenness) were performed to assess the significance of differences between the years 2009 and 2022. Site specific differences between the years were assessed using ANOVA or the non-parametric Kruskal-Wallis test.

3.4.3. Differences in community composition

To analyse the community composition, two multivariate analyses, hierarchical cluster analyses and non-metric multidimensional scaling (nMDS) were performed on site averages of relative density. The analysis is based on the Bray-Curtis dissimilarity coefficient and the appropriateness of the NMDS result was assessed through a Shepard diagram in addition to goodness of fit, both functions within the package vegan. Environmental variables (fishing intensity, water surge, habitat complexity and relative cover of corals, algae, zoanthids and CCAs) were fitted to the NMDS using the function envfit.

After calculating the cophenetic correlation and Gower (1986) distance for both variables, it was determined that the best fitting clustering algorithms are the unweighted pair group method with arithmetic mean (UPGMA), which groups an object based on the average of the dissimilarities between the object and all members of the group (Borcard et al., 2018). For the identification of significant ($p < 0.05$) clusters, the simprof test, according to Clarke et al. (2008) was used.

The species that contribute the most to dissimilarities in communities between the years were calculated using the function simper within the package vegan.

3.4.4. Dominant species frequencies

The species determined through simper (n=13) were highly abundant species in both years or species of commercial value. Hence, these species were selected for an assessment of their relative distribution within the year. To assess the relative distribution of species among the years by species the absolute frequencies were calculated:

$$absolute\ frequency_{species\ x} = \frac{abundance_{\ species\ x\ \ at\ site\ y}}{total\ abundance_{\ in\ year\ z}},$$

to reduce the influence that one (i.e. highly abundant) species might have on another. Differences between the years were assessed in a PERMANOVA using the adonis function within the vegan package in R.

3.4.5. Effect of habitat composition

To determine whether natural variation causes differences between the reef fish communities of the different years a PERMANOVA on the relative benthic coverage of the categories algae, corals, zoanthids, CCAs, invertebrates and substrate (averaged by site) was performed. Additionally, a dataset based on the absolute densities of the previously mentioned 8 trophic groups for each transect of 2022 was created. Before performing a PCA, the data was double square root transformed and the PCA was fitted with the six benthic categories using the function envfit, to assess correlations of benthic cover and trophic function of the reef fish community.

4. Results

4.1. Community composition in 2022

During the 2022 field campaign 4822 individuals were identified from 43 stereo-DOV transects (Table 4.1), of which 1854 were measured (Appendix Table 8.2). A total of 32 species of 14 families were documented. The most species-rich families were Pomacentridae (7 species) and Labridae (6 species), followed by Sparidae (4 species). Four families were represented by two species and seven families only had a single representative.

Only four species accounted for 91,31% of all fish recorded in the 2022 study. The most abundant species were *C. multilineata* (41,2%), *T. pavo* (26,26%) *C. lubbocki* (17,73%) and *D. lineatus* (6,11%).

Most of the biomass (90,17%) consisted of ten species. Four out of the five most important species in terms of biomass were endemic to Cabo Verde. Three sparid species, *D. lineatus*, accounting for 28,75% of and *D. prayensis* (9,04%) and *D. fasciatus* (4,88%) are endemic species with low commercial value and accounted for almost half of the total biomass . A quarter of the total biomass was attributed to two pomacentrid species *C. multilineata* (17,04%) and the endemic *C. lubbocki* (8,88%), with low and no commercial value, respectively. *T. pavo* with no commercial value contributed to 4,2% of the total biomass. Four species with commercial value (*S. cretense* (6,6%), *C. taeniops* (4,72%), *B. speciosus* (3,84%) and *M. fusca* (2,2%)) were listed in the ten most important species for total biomass.

The trophic level with the highest average biomass per transect were omnivores (1901, 17 ± 271,37 g/40m^2), followed by planktivores. The average biomass of mobile invertebrate feeders (509,54 ± 71, 65 g/40m^2), carnivores (366, 05 ± 60,99 g/40m^2) and roving herbivores (361, 87 ± 69,58 g/40m^2) combined was similar to the biomass of planktivores (1180,21 ± 199,56 g/40m^2). Three groups showed low average biomass per transect: piscivores, territorial herbivores and sessile invertebrate feeders (in declining order).

In terms of density, Planktivores were the most important trophic group (68,33 ± 11,42 ind./40m^2), other notable groups were mobile invertebrate feeders and (32,40 ±4,29 ind. /40m^2) and omnivores (10,09 ± 1,16 ind./40m^2). All remaining groups showed an average density lower than 2 individuals per transect.

4.2. Differences in trophic function

Both density and biomass were compared to the previous assessment of the fish community of Santa Luzia in 2009. Here only biomass is presented as it is commonly considered a stronger indicator in regard to fisheries and clearly portrays the differences between the reef fish communities over time in this assessment (Figure 4.2 top). The greatest difference between the years was in omnivores, which experienced a threefold increase in relative biomass. Roving herbivores decreased twofold and planktivores also decreased by almost half. There were only two planktivore species, *Chromis multilineata* and the endemic *Chromis lubbocki*, both of which appear in large schools and have been found to introduce biases according to their presence in transects, termed the *Chromis effect* (Freitas et al., 2019). Accordingly, both species have been removed from the data depicting the distribution of absolute biomass over trophic

Table 4.1. *Comparative composition of reef fishes among sites in the Santa Luzia Marine Reserve (Cabo Verde) in 2022, showing the density of individuals per species (overall and per site), and overall estimated biomass per species. The commercial value, trophic level and trophic group of each species are also presented. Numbers in bold indicate the 10 most abundant fish species (by density or biomass). Com. = commercial value: C = commercial species, LC = low commercial value, and NC = non-commercial species. Species endemic to Cabo Verde are highlighted with *.*

				All sites		Reef Sites Density, mean (SE) (ind. 40m^{-2})								
Family and species	Com.	Trophic level	Trophic group	Density, mean (SE) (ind. 40m^{-2})	Biomass, mean (SE) (g 40m^{-2})	PPRAI	AGARU	CURAL	PBRAC	AGADO	ESPQI	PPNOR	CREOL	ILHEU
Holocenthridae														
1 *Myripristis jacobus*	L	3,4	Carnivore	0,47 (0,03)	55,36 (4,82)	0,78 (0,41)	0,60 (0,54)	0,33 (0,27)					1,50 (1,20)	
2 *Sargocentron hastatum*	L	3,5	Carnivore	0,33(0,02)	53,49 (2,74)		0,20 (0,18)			0,80 (0,18)	0,75 (0,41)	1,00 (0,47)		
Aulostomidae														
3 *Aulostomus strigosus*	N	4,2	Piscivore	0,05 (>0,01)	7,32 (0,83)		0,20 (0,18)							0,50 (0,35)
Serranidae														
4 *Cephalopholis taeniops*	C	4,4	Carnivore	1,07 (0,03)	**185,08 (5,35)**		1,20 (0,66)			1,20 (0,33)	2,00 (0,35)	1,83 (0,50)	1,83 (0,60)	
5 *Mycteroperca fusca*	C	4,3	Piscivore	0,07 (0,01)	**100,90 (15,21)**					0,60 (0,54)				
Pricanthidae														
6 *Priacanthus arenatus*	C	4,0	m.Invert.	0,05 (>0,01)	25,89 (2,83)			0,33 (0,27)					0,17 (0,15)	
Haemulidae														
7 *Parapristipoma humile*	C	3,6	m.Invert.	0,14 (0,01)	49,14 (4,84)					1,20 (0,66)				
Sparidae														
8 *Diplodus fasciatus**	L	3,5	Omnivore	**0,51 (0,02)**	**222,32 (8,85)**	**0,11 (0,10)**	**1,20 (0,33)**		**1,33 (0,72)**	**1,40 (0,54)**	**0,50 (0,25)**		**0,17 (0,15)**	**0,50 (0,35)**
9 *Diplodus lineatus**	L	2,8	Omnivore	**7,00 (0,14)**	**1308,96 (27,11)**	**3,56 (1,22)**	**13,60 (2,17)**	**5,00 (3,30)**	**12,33 (0,72)**	**9,20 (3,60)**	**9,00 (2,89)**	**1,33 (1,05)**	**8,50 (1,12)**	**4,00 (0,0)**
10 *Diplodus prayensis**	L	2,8	Omnivore	**1,72 (0,05)**	**411,50 (13,04)**	**1,78 (0,73)**	**3,00 (1,02)**	**0,33 (0,27)**		**1,20 (0,66)**	**2,00 (0,61)**	**0,17 (0,15)**	**3,00 (1,41)**	**3,00 (0,71)**
11 *Virididentex acromegalus**	C	3,4	Carnivore	0,07 (>0,01)	42,08 (3,67)	0,11 (0,10)					0,25 (0,22)	0,17 (0,15)		
Mullidae														
12 *Mulloidichthys martinicus*	C	3,2	m.Invert.	**0,49 (0,05)**	53,80 (6,02)	**0,33 (0,22)**	**3,60 (2,15)**							
13 *Pseudupeneus prayensis*	C	3,2	m.Invert.				1,20 (0,66)					0,17 (0,15)		
Chaetodontidae														
14 *Chaetodon robustus*	N	3,3	s.Invert.	0,02 (>0,01)	0,66 (0,10)		0,20 (0,18)							
Pomacanthidae														
15 *Holacanthus africanus*	N		Omnivore	0,12 (>0,01)	7,09 (0,52)	0,33 (0,22)						0,33 (0,19)		
Pomacentridae														
16 *Abudefduf hoefleri*	N	2,7	Omnivore	0,14 (0,01)	16,57 (1,45)	0,22 (0,14)							0,50 (0,46)	0,50 (0,35)
17 *Abudefduf saxatilis*	N	3,8	Omnivore	0,16 (0,01)	21,22 (1,55)	0,33 (0,22)	0,20 (0,18)							1,50 (0,35)
18 *Chromis lubbocki**	N	3,0	Planktivore	**20,56 (0,87)**	**432,14 (17,00)**	**24,44 (13,64)**	**23,20 (9,18)**	**8,00 (3,40)**		**49,00 (30,86)**	**18,25 (9,41)**	**8,50 (6,70)**	**0,67 (0,61)**	**75,50 (18,74)**
19 *Chromis multilineata*	N	3,0	Planktivore	**47,77 (1,22)**	**775,69 (19,74)**	**89,44 (18,96)**	**24,4 0(7,58)**	**32,00 (13,14)**		**32,20 (20,00)**	**83,00 (34,33)**	**60,67 (13,01)**	**0,33 (0,19)**	**86,00 (24,04)**
20 *Similiparma hermani**	N	2,5	Omnivore	0,33 (0,01)	12,23 (0,59)			0,33 (0,27)		0,80 (0,18)			1,00 (0,24)	1,50 (0,35)
21 *Similiperma lurida*	N	3,5	Omnivore	0,02 (>0,01)	0,06 (>0,01)							0,17 (0,15)		
22 *Stegastes imbricatus*	N		terr.Herbi.	**1,63 (0,05)**	21,90 (0,70)	**1,00 (0,61)**	**0,40 (0,22)**	**0,67 (0,54)**			**3,50 (0,90)**	**3,17 (1,42)**	**3,67 (0,56)**	**1,00 (0,71)**
Labridae														
23 *Bodianus speciosus*	C	3,6	m.Invert.	0,44 (0,01)	**174,93 (6,37)**	0,33 (0,22)	0,40 (0,22)	1,00 (0,47)		0,40 (0,22)	0,75 (0,22)	0,50 (0,20)	0,33 (0,19)	0,50 (0,35)
24 *Coris atlantica*	N	3,5	m.Invert.	**0,67 (0,04)**	4,46 (0,25)	**0,56 (0,52)**	**2,20 (0,77)**	**2,67 (1,78)**	**0,33 (0,27)**	**0,40 (0,36)**		**0,17 (0,15)**	**0,17 (0,15)**	
25 *Scarus hoefleri*	C	2,0	rov.Herbi.	0,02 (>0,01)	9,75 (1,47)		0,20 (0,18)							
26 *Sparisoma choati*	C	2,0	rov.Herbi.	0,09 (>0,01)	1,99 (0,21)	0,11 (0,10)							0,33 (0,30)	0,50 (0,35)
27 *Sparisoma cretense*	C	2,9	rov.Herbi	**1,09 (0,03)**	**304,91 (9,98)**	**1,00 (0,31)**	**2,40 (1,04)**	**0,67 (0,54)**			**1,50 (0,56)**	**2,50 (0,66)**	**0,50 (0,20)**	
28 *Thalassoma pavo*	N	3,5	m.Invert.	**30,44 (0,63)**	**191,42 (3,58)**	**17,22 (4,25)**	**57,20 (16,70)**	**14,33 (7,66)**	**17,33 (13,34)**	**30,60 (6,03)**	**59,75 (14,17)**	**30,67 (10,76)**	**20,67 (3,30)**	**36,50 (19,45)**
Acanthuridae														
29 *Acanthurus monroviae*	C	2,5	rov.Herbi.	0,21 (0,01)	45,21 (2,94)		0,20 (0,18)			0,40 (0,36)		0,33 (0,30)	0,33 (0,19)	1,00 (0,0)
Monacanthidae														
30 *Aluterus scriptus*	N	2,8	Omnivore	0,05 (>0,01)	4,75 (0,52)					0,20 (0,18)				0,50 (0,35)
Tetradontidae														
31 *Canthigaster capistrata*	N	3,5	Omnivore	0,05 (>0,01)	*NA*	0,11 (0,10)					0,25 (0,22)			
32 *Canthigaster rostrata*	N	3,3	Omnivore	0,02 (>0,01)	*NA*	0,11 (0,10)								

level (Figure 4.2 bottom). Most of the biomass in 2022 was allocated in level 2,8 and can be attributed to two sparid species (*Diplodus lineatus, Diplodus prayensis*). In 2009, the biomass was more equally distributed and over half of it was allotted in trophic level 3,4 or higher. Out of the 36 species only present in 2009, 33 had a trophic level of 3,4 or higher.

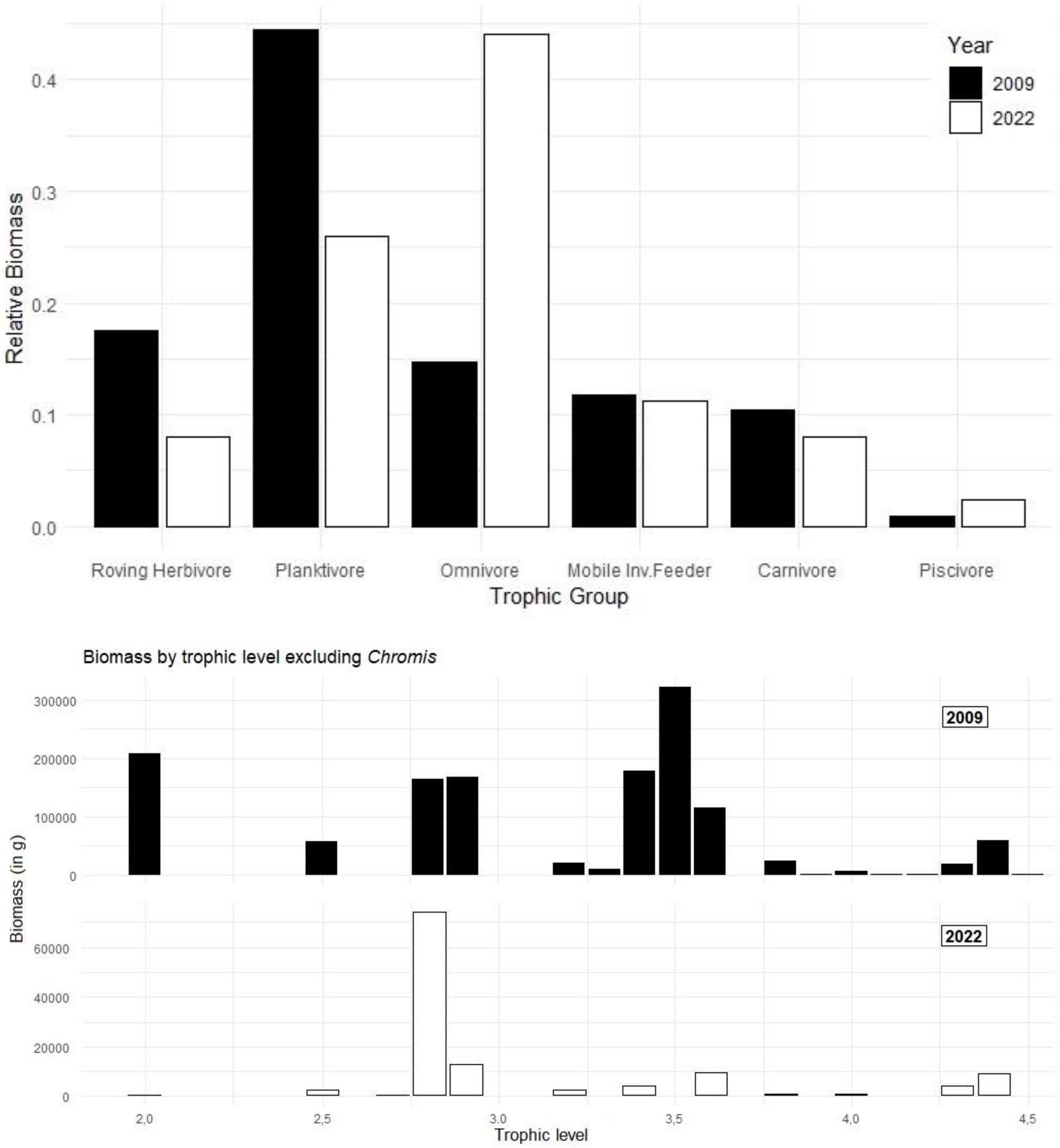

Figure 4.2. ***top****: Relative biomass of trophic groups, summarized by year. Territorial herbivores and sessile invertebrate feeders were evaluated but removed due to low numbers.* ***bottom****: Absolute biomass by trophic level, 2009 in black and 2022 in white. Highly abundant species of the genus Chromis were removed from the dataset*

Simultaneously there is a greater contribution of level 2,0 to the biomass in 2009 compared to 2022, which was attributed to four species (*Scarus hoefleri*, *Kyphosus incisor, Girella stuebeli,* and *Sparisoma choati*), the last three were virtually absent in transects of the 2022 assessment. Additional to these roving herbivores, two more species (*Acanthurus monroviae* with a trophic level of 2,5, and *Sparisoma cretense* with 2,9) of this functional group declined in their proportional biomass to the reef fish community over the years.

4.3. Community descriptors: species richness, diversity and evenness

The observed species richness was 10,18 ± 2,99 species per transect in 2009 and decreased significantly (Wilcoxon-Mann-Whitney-Test: $p < 0,0001$; Figure 4.3, Appendix Table 8.1) by over 20% to 8,12 ± 2,87 species per transect in 2022. The Shannon-Wiener diversity index decreased slightly, but not significantly (Welch's t-test: $p = 0,10$; Appendix Table 8.1; Figure 8.1) from 1,32 in 2009 to 1,21 in 2022, whereas the species evenness (Hill's ratio) increased significantly (Wilcoxon-Mann-Whitney-Test: $p < 0,01$; Appendix Table 8.1; Figure 8.2).

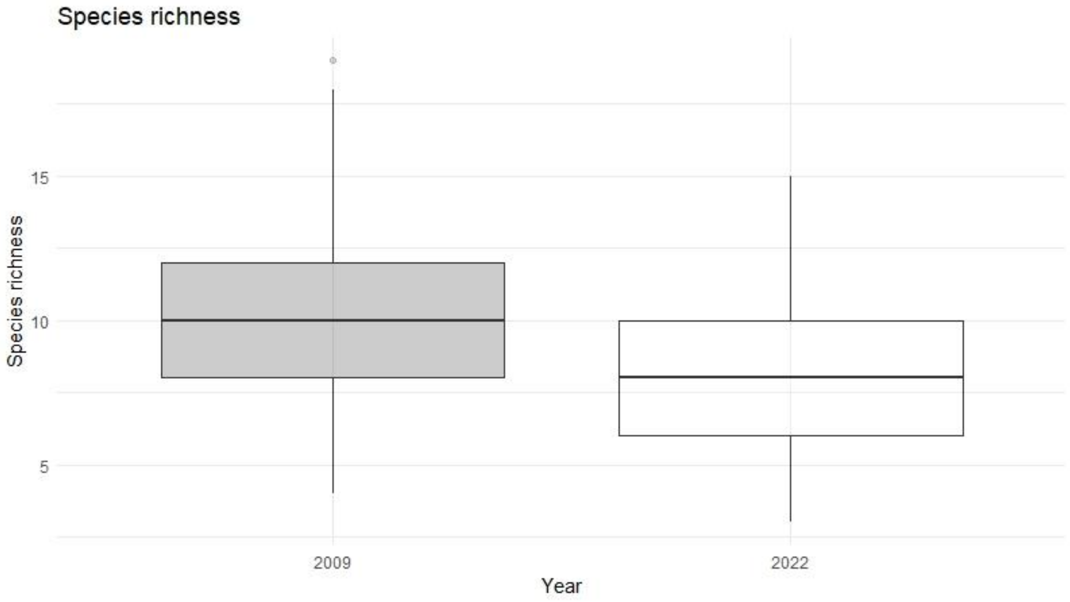

Figure 4.3: *Species richness by year*

Species richness declined in all sites (Appendix Figure 8.3), with significant findings for three sites: CREOL, PBRAC and PPRAI (all $p < 0,01$).

The differences in Shannon-Wiener diversity by site showed more variation than the yearly comparison (Appendix Figure 8.4). Only one site, AGARU, showed a higher diversity (H'= 1,54; $p = 0,04$) than 2009 (H'= 1,20). It was also the most diverse site in 2009, followed by CREOL (H'= 1,53), which exhibited a similar diversity to 2009. Four sites decreased in diversity since 2009 and scored the lowest overall diversity: PBRAC (H'=0,75), CURAL (H'=

1,02), PPRAI (H’= 1,03), and PPNOR (H’= 1,15), but with significant findings only for PBRAC ($p < 0{,}01$). In 2009, PPRAI was the site with the lowest diversity (H’= 1,16).

The Hill’s ratio, describing the evenness, increased from 2009 to 2022 in every single pairing (Appendix Figure 8.5), with significant differences at the sites CREOL ($p < 0{,}01$) and PPRAI ($p = 0{,}02$).

4.4. Differences in community composition

The hierarchical clustering in combination with simprof determined four clusters with non-random structure that further group into two distinct communities based on year (Figure 4.4; Appendix Figure 8.7). All points from 2009 were located along the negative side of NMDS1 axis, one single station AGARU built a separate cluster from the remaining stations and had the lowest NMDS1 value and highest sampling effort of all stations. Within the second cluster (in red), ILHEU was the most distinct site with the highest NMDS2 value, all other sites grouped with a dissimilarity lower than 60%. The second cluster further distinguished along the NMDS2 axis with corresponding branches within the dendrogram. ESPQI and PPRAI were separated from the remaining stations of 2009, but relatively dissimilar from each other. The next pair consists of CURAL and PCHIC and was more closely related than the last five stations to each other (AGADO, PBRAC, PPNOR, CREOL, and ENORT). These were further distinguishable among the NMDS1 axis, with PBRAC and AGADO grouping together with the lowest NMDS1 values and ENORT being distinct from PPNOR and CREOL with the highest NMDS1 value from the sites of 2009. Two clusters were identified from 2022 sites, one located at the right side of the NMDS. This cluster consisted of PBRAC, CURAL and ILHEU, the sites with the lowest transect numbers in 2022, and displayed higher dissimilarity within its cluster than that of the 2009 community. With lower, but positive NMDS1 values, the second cluster of the 2022 community was further distinguished along the NMDS2 axis and separated into two branches. The first branch, with higher NMDS2 values consisted of CREOL, PPRAI, and ESPQI. CREOL and PPRAI paired closely together and ESPQI was less distant to the first cluster of 2022 while based on a comparably low number of replicates. The second branch consisted of AGARU and PPNOR that showed the closest similarity out of any pair within the 2022 community, and AGADO which is more dissimilar with an even lower NMDS2 value.

The environmental fit is poor for every variable except fishing intensity (Appendix Table 8.3). For fishing intensity the findings are not significant for $\alpha = 0{,}05$ ($p = 0{,}063$), but would be for $\alpha = 0{,}10$. It should also be noted that the poorly fit variables of relative algae and zoanthid cover are both weakly associated with a positive NMDS 1, corresponding to sites of 2022. All other parameters (fishing intensity, water surge, complexity, and relative coral and CCA cover) are concurrent with a negative NMDS 2, in accordance with sites of 2009.

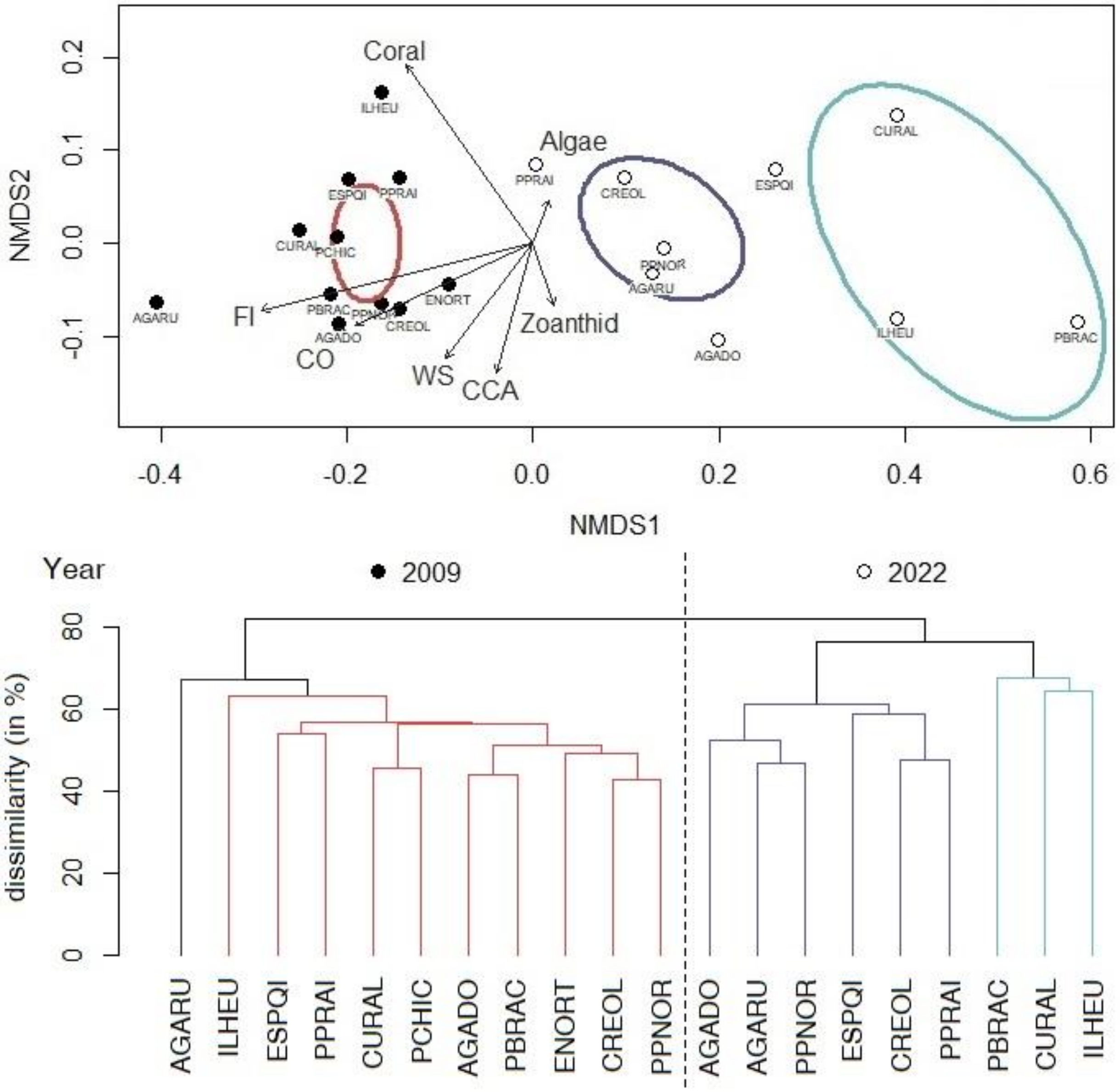

Figure 3.4. top: *NMDS and* ***bottom:*** *clustering. NMDS (stress = 0,08) with fitting of environmental variables and clusters determined through simprof (bottom). Ordiellipses in respective colour represent SE of each cluster. Sites of 2009 are marked with a black dot, sites of 2022 in white.*

Out of the thirteen species contributing to the most dissimilarity between the fish communities of 2009 and 2022 (Table 4.4), three species with high commercial value were ranked in the top five: *C. taeniops* (72,93%), *S. cretense* (69,81%), and *A. monroviae* (59,26%), and a fourth species with high commercial value *B. speciosus* also significantly accorded to the dissimilarities. The five most abundant non-commercial species significantly contribute to the dissimilarities, but range in their importance (high to low): *C. multilineata, C. atlantica, S.imbricatus, C. lubbocki,* and *T. pavo.* One species with low commercial value, *S. hastatum*, but with high importance for only the 2009 community in terms of abundance and biomass, highly (63,00%) contributes to the dissimilarities between the years. With a lower, but significant contribution were three species of the genus *Diplodus*: *D. fasciatus* (45,82%), *D. prayensis* (34,48%), and *D. lineatus* (20,04%).

Table 4.4. *Species contributing to the highest dissimilarities (in %) between the reef fish communities of 2009 and 2022, with commercial value (none (N) – low(L) – high(C)).*

	Species	Commercial Value	Dissimilarity (in%)
1	*C. taeniops*	C	72,93
2	*S. cretense*	C	69,81
3	*C. multilineata*	N	66,55
4	*S. hastatum*	L	63,00
5	*A. monroviae*	C	59,26
6	*C. atlantica*	N	55,21
7	*S. imbricatus*	N	51,06
8	*D. fasciatus*	L	45,82
9	*C. lubbocki*	N	40,53
10	*D. prayensis*	L	34,48
11	*B. speciosus*	C	28,37
12	*D. lineatus*	L	20,04
13	*T. pavo*	N	11,05

4.5. Dominant species frequencies

To avoid any biases that could have been introduced by summarizing into site averages or through the dominance of one or a few species, species frequencies were calculated by transect and the dataset was narrowed down to only include dominant species (Table 4.5).

A stratification of transects by year along the NMDS2 axis is apparent (Figure 4.5, Appendix Figure 8.8). Transects of 2009 are scattered around the origin of the coordinate system, whereas transects of 2022 are located at a higher NMDS 2 and a lower NMDS1. In the NMDS the points and standard deviations of the years appear with little overlap and the PERMANOVA found statistically significant differences between the years for $p < 0,001$ (Appendix Table 8.4).

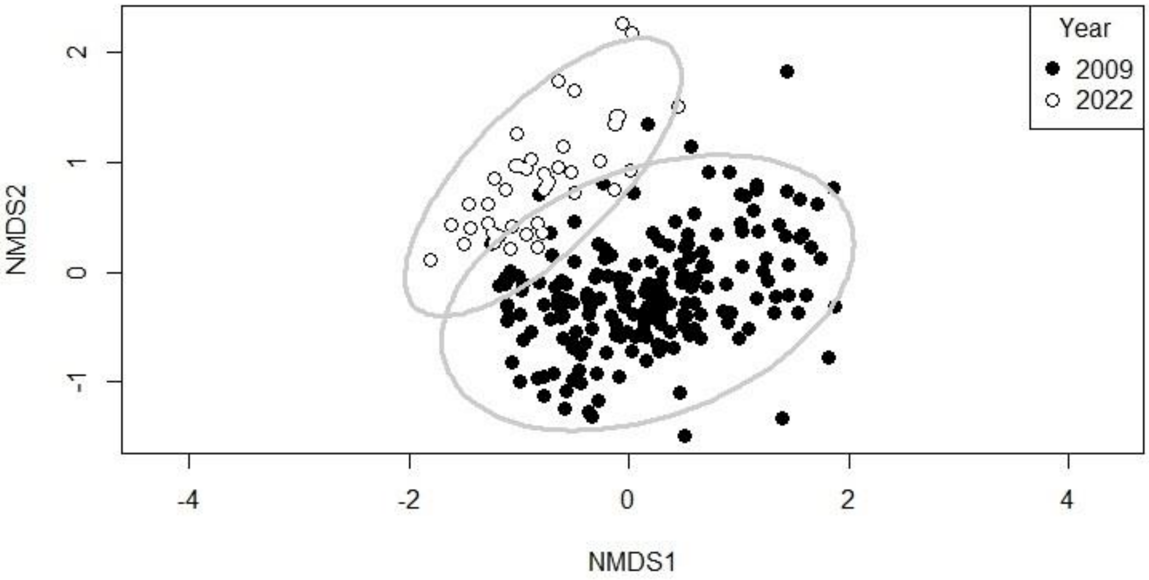

Figure 4.5. *NMDS on relative distribution of dominant species. NMDS stress = 0.18. SD in grey ellipses.*

4.6. Effect of habitat composition

No statistically significant difference was found in the relative cover of the categories algae, coral, zoanthid, CCAs, invertebrates and substrate (Appendix Table 8.5).

Out of the six assessed categories, four are fitted appropriately to the PCA on densities of trophic groups (Appendix Table 8.6). The environmental fitting of corals and CCAs is statistically significant ($p < 0{,}001$ and $p < 0{,}05$ respectively), and the fit of the variables zoanthids and substrate is not significant but with $p < 0{,}1$.

In the first quadrant of the PCA (Figure 4.6) are omnivores which are associated with a high relative cover of substrate. Within the second quadrant are the environmental variables zoanthid and invertebrate cover, that demonstrate a weak link to planktivore density. In the origin are the low abundant trophic groups piscivores and sessile invertebrate feeders. CCA and coral cover are fitted into the third and fourth quadrant respectively, roving herbivores and mobile invertebrate feeders are associated with CCAs, territorial herbivores with coral cover and carnivores are linked to both, CCA and coral cover. No trophic group is directly linked to the weakly fitted variable of relative algae cover.

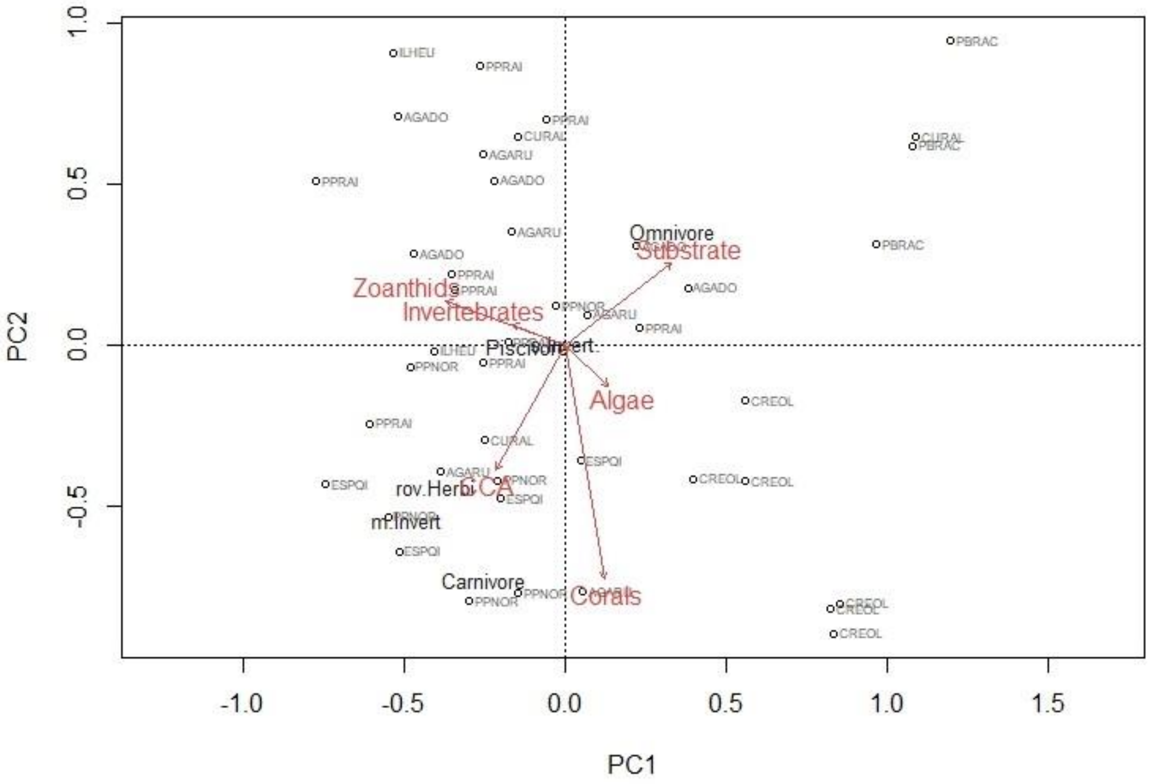

Figure 4.6. *PCA on absolute densities of trophic groups in 2022, fitted with relative benthic cover.*

5. Discussion

5.1. Shift in reef fish community

The Santa Luzia reef fish community experienced a loss of species of over 20%. At the same time the evenness (Hill's ratio) increased significantly over time. This indicates the loss of less abundant, rare species and a higher dominance of a small proportion of the original species pool. Other Atlantic islands that share similar features of high isolation and endemism appear to have ecologically simple reef fish communities characterized by low species richness (Luiz et al., 2015). However, phase shifts to the here observed extent have previously been related to habitat degradation and a species loss of this magnitude will have an ecological significance to any community (Jones et al., 2004). Reef communities with high species richness have a higher potential for functional redundancy across different key functions and consequently may have a higher chance of recovery if one species is lost from a functional group (Bellwood et al., 2004).

For Shannon-Wiener diversity, no significant difference between 2009 and 2022 was found for $\alpha=0,05$, however the p-values are close to 10% so an increased sampling effort in 2022 might have delivered evidence for a significant decrease in abundance. Nonetheless, diversity and richness are not indicative of shifts in the community and might not be adequate indicators when assessing MPA effects (Bellwood et al., 2006; Soykan & Lewison, 2015). Previous studies suggest that indicators considering a species functional role and the functional redundancy within a community are more powerful in terms of ecosystem maintenance and resilience (Hoey & Bellwood, 2009; Rasher & Hay, 2010).

All multivariate analyses clearly distinguish the communities by years. Some biases could have been introduced to the analyses of community composition by site as the first NMDS axis appears to be weakly correlated to the number of transects within each site and year. The apparent distinction between the years could originate from differences in sampling effort. Accordingly, the year and stations with high sampling effort (2009) are located at low NMDS1 values and low sampling effort correspond to high NMDS1 values. In regard to the community composition, a higher sampling effort is likely to introduce more rare species into site averages. This additional, albeit small numbers could be a source for higher dissimilarities between the years. To avoid these biases when working with site averages, the data should be subjected to bootstrapping before performing multivariate analyses. However, assessing only dominant species frequencies by transect, the years are statistically significant different in their community composition. Any apparent stratification of the samples could therefore also reflect the previously established trend of loss of species richness or other shifts in community composition.

The species responsible for the highest dissimilarities between the years are either highly abundant species with no commercial value (*C. multilineata, C. lubbocki, C. atlantica. T. pavo* and *S. imbricatus),* dominate the biomass in 2022 (with low commercial value: all three present species of the genus *Diplodus*) or are species of high commercial value (*C. taeniops, S. cretense, A. monroviae, B. speciosus*; and one species of low commercial value: *S. hastatum*).

Assessing the relative biomass by trophic group, the most notable shift is an increase of omnivores, accompanied by a decline of roving herbivores and planktivores. This can be attributed to two species, the endemic Lubbock's chromis *Chromis lubbocki*, and the brown chromis *Chromis multilineata*. The latter is highly abundant across Atlantic islands and dominating the reef fish communities in terms of density (Trindade island: Pinheiro et al., 2011; São Tomé Island: Maia et al., 2018; Fernando de Noronha Archipelago: Krajewski & Floeter, 2011; St Peter & St Paul's Archipelago: Luiz et al., 2015). In Cabo Verde, this dominance is shared with the endemic *C. lubbocki*, both pomacentrids are highly sociable and demonstrate schooling behaviour (Freitas et al., 2019). The presence of large schools can already cause inter-observer bias in UVC's alone, as observers are unable to count fish in large schools directly and generally tend to overestimate mobile fish and transect boundaries (Pessanha Pais & Cabral, 2018). Simultaneously, in video transects the field of view is limited to the camera orientation, transect boundaries are clearly defined, but fish in the water column might be undetected. Especially large schools of pelagic fish might only be partially detected and underestimated in video-based methods. A decline in relative biomass could possibly derive from biases between the two methods and would particularly show at this order of magnitude with several hundred individuals in a school of fish.

After the removal of *Chromis* in a complementary analysis on absolute biomass by trophic level, two omnivorous, endemic sparid species (*D. lineatus* and *D. prayensis*) dominate the biomass in 2022. In the Atlantic, this family is more speciose and dominant in more temperate opposed to tropical waters, these highly mobile fish are less reliant on reef substratum for protection and can shift diets seasonally depending on food availability (Floeter et al., 2004). This dominance of generalists in terms of biomass has previously been documented in other isolated reef systems with high rates of endemism and low species richness in the equatorial Atlantic (Luiz et al., 2015).

In 2009, the distribution of biomass is more homogeneous across the trophic spectrum, with a large proportion of biomass allocated in trophic level 3,4 or higher. Out of the 36 species only present in 2009, 33 species are associated with this fraction of the community, indicating that these higher trophic levels are unproportionally affected by species loss. A lack of variety of predators has previously been associated with species-poor communities (Halpern & Floeter, 2008). However as per the author's definition, also the 2009 community would be considered a species-poor community, suggesting that there must be an alternative explanation for the drastic decline in predator biomass and species richness. Large, predatory fish are widely targeted by global fisheries, the depletion of targeted stocks evokes a shift in landings from large piscivores to smaller planktivorous and invertebrate-feeding fish, resulting in a mean decline of trophic level termed as "fishing down marine food webs" (Pauly, 1998). Depending on fisheries targets, fishing can cause trophic cascades up and down the food web, and a high functional redundancy can mitigate human impacts such as fishing on ecosystem impacts and weaken trophic cascades (Andersen & Pedersen, 2010; Halpern & Floeter, 2008).

Besides a decrease of species-rich mobile invertebrate feeders, carnivores and piscivores, a notable decline of roving herbivore biomass is apparent. With three algae-consuming species (*K. incisor, G. stuebeli,* and *S. choati*) virtually absent in the 2022 assessment, and a strong decrease in the remaining roving herbivore species, the perpetuation of their function to the ecosystem is put at risk. A strong decline of parrotfish (*Sparisoma*) biomass has previously been observed in fished areas within the Caribbean, following a shift of fisheries targets to parrotfish after the depletion of preferred groupers and snappers (Mumby et al., 2012). However, the harvesting of these macroalgae grazers can prompt negative feedback loops within the reef system promoting macroalgae growth, which negatively affects coral growth and reef fish recruitment (Mumby & Steneck, 2008). Once established large macroalgae stands can be difficult to remove because of herbivore behaviour and food preferences, and consequently stabilize the macroalgae-dominant reef state (Hoey & Bellwood, 2011).

These findings of a strong decline of biomass at both ends of the trophic spectrum are contradicting Pauly's "fishing down the food web" paradigm, but coherent with community shifts in fished reefs in the Atlantic (Mumby et al., 2012; Lamb & Johnson, 2010) and Indian Ocean (Graham et al., 2017). At low biomass (representing fished communities) mid- trophic fish dominate. This can even result in an increase of the overall trophic level at lower biomass, as at high biomass the trophic structures are increasingly bottom heavy (Graham et al., 2017). Not only do fisheries target both ends of the trophic spectrum, but because reef herbivores of trophic lower levels, like *Sparisoma* grow large in body size, they are not predated on by smaller, mid-trophic level omnivores or carnivores. The pathways within a reef system are highly complex and top predators feed on all trophic levels, which only highlights their importance for a healthy ecosystem (Graham et al., 2017).

From a more specialised, species-rich community with a higher diversity of predators that provide functional redundancy and ensure ecosystem functioning even when human impacts such as fishing are present, the Santa Luzia reef fish community shifted to a species-poor, more homogenous community characterised by high biomass of mid-trophic generalist species, with implications to ecosystem functioning (Halpern & Floeter, 2008).

5.2. Link to habitat

Shifts in the reef fish community are in some cases explained but natural variation within the habitat. In the Canary Islands, blanket-forming zoanthids gained dominance over the reef habitat and prompted shifts in the fish community; an overall reduction of total fish abundance and richness is apparent, herbivores are especially affected and experience a reduction of numbers at a higher relative cover of zoanthids, whereas omnivores are more abundant (Moreno-Borges et al., 2022). Herbivores that are adapted to macroalgae, are lacking food and shelter in zoantharian habitats. Conversely, a high density of macroalgae especially when growing into large stands has previously been found to deter herbivorous fish as they struggle to detect predators amongst the canopy, but predator movement is largely unrestricted (Hoey & Bellwood, 2011). Territorial herbivores are strongly linked to coral cover, the dominant territorial herbivore in this study is *S. imbricatus* and has been linked to coral microhabitats, where they cultivate algae between coral patches and are known to display aggressive defending behaviour towards other herbivores (Canterle et al., 2020).

The strong link of omnivores and substrate can be explained through their ability to forage in a wide range of habitats as they can utilize various food sources. Through their high adaptability, these generalist species are more resilient to changes within the environment and other impacts, and are at a reduced risk for extinction, especially compared to specialist species (Luiz et al., 2015). The most important species in terms of biomass and density in the Santa Luzia reserve are highly mobile fish species of the genus *Diplodus* and *Chromis*, which are also known to be less reliant on the reef substratum for protection (Floeter et al., 2004). This could result in less competition for space and could possibly explain why the reef fish community, is not strongly affected by the benthic composition as observed in Santa Luzia but also shown in other Atlantic islands (Luiz et al., 2015; Krajewski & Floeter, 2011).

While the assessment was performed based on broad categories, it is unlikely that a benthic assessment with higher taxonomic resolution would result in a correlation between biotic variables and reef fish community composition. Additionally, the benthic composition does not differ statistically significant between the years. Thus, the dominance of habitat-independent generalists that do not prefer a specific type of benthic cover can not be explained by habitat variation within the Santa Luzia marine reserve.

5.3. Conclusion

This study has observed a drastic shift within the reef fish community over the span of thirteen years. Natural variation based on benthic habitat composition was excluded from possible explanations for such a shift. Although not assessed in this study, other impacts such as pollution are unlikely due to the isolation of the island. However, the reef fish community displays characteristics of a community that has been subjected to the impacts of fishing. While Santa Luzia is a marine reserve, fishing with traditional techniques (line and hook) is allowed. Whether other techniques are being used or the extent of fishing is putting excessive strength on the fish stocks is unclear, however the valuable resources of Santa Luzia are harvested beyond sustainable levels. A threshold to maintain piscivore fisheries on coral reefs has previously been determined for the Indian Ocean (Graham et al., 2017), but great caution should be applied when transferring these numbers to naturally low-diversity, more temperate systems. Furthermore, thresholds for sharp irreversible shift may also vary with climatic conditions (Scheffer et al., 2005). With increasing impacts due to climate change and a reef fish community that has been drastically shaped by excessive resource extraction, the implementation of an ecosystem- or resilience-based management plan is crucial. The establishment of a no-take zone in the northwest of the island should be considered to allow the fish community to recover and fish stocks to replenish. Close monitoring is advised to allow for well-informed decision-making. This study demonstrates the value of new, less traditional techniques such as stereo-video and their ability to provide a valuable database, effective to detect shifts within the reef fish community even in comparison to other methods.

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8. Appendix

Table 8.1. *Statistical test results for the indicators species richness, Shannon-Wiener diersity index and evenness (Hill's ratio). Each indicator was tested on normality (Shapiro-Wilk's test), subsetted by year. According to the results a test on homogeneity of variances was performed (Bartlett test for normally distributed data, Levene's test for data deriving from normal distribution). According to the normality and homogeneity of variances the parametric Welch two sample t-test or its non-parametric alternative Wilcoxon.Mann-Whitney-Test was performed. Significant p-values in bold.*

		Species richness	Shannon-Wiener diversity index	Evenness (Hill's ratio)
Shapiro Wilk's test for normality	2009	W = 0,97989 **p = 0,006089**	W = 0,99175 p = 0,3242	W = 0,98144 p = 0,101
	2022	W = 0,96706 p = 0,2495	W = 0,97948 p = 0,6271	W = 0,96802 p = 0,2698
Test on homogeneity of variances		Levene's test F-value = 0,1811 p = 0,6708	Bartlett test K-squared = 0,81017 p = 0,3681	Bartlett test K-squared = 3,9112 **p = 0,04797**
Statistical test		*Wilcoxon-Mann-Whitney-Test* W = 5907 **p = 6,308e-05**	*Welch two sample t-test* t = 1,666 df = 66,833 p = 0,1004	*Wilcoxon-Mann-Whitney-Test* W = 3108 **p = 0,005576**

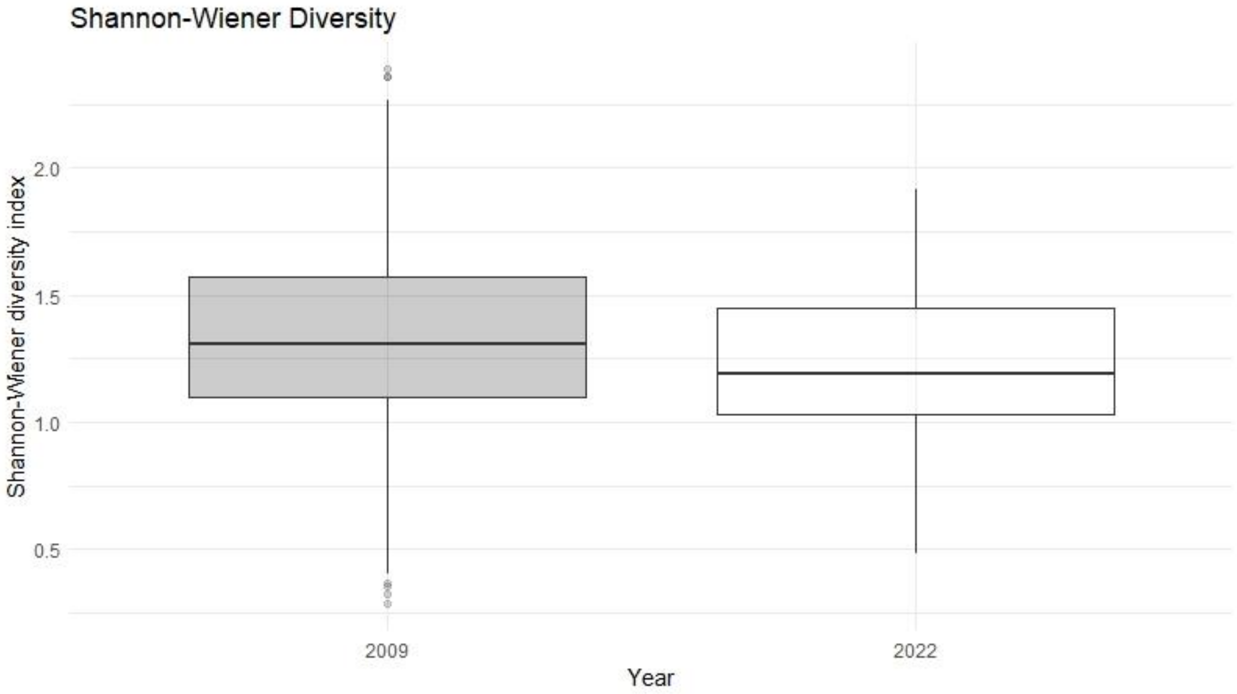

Figure 8.1. *Shannon-Wiener diversity index by year.*

Table 8.2. Composition by biomass of reef fishes among sites in the Santa Luzia Marine Reserve in 2022, showing the estimated biomass of individuals per species (per site). The commercial value, trophic level and trophic group of each species are also presented. Numbers in bold indicate the 10 most important fish species (by biomass).

Family and species		Com.	Trophic level	Trophic group	Biomass, mean (SE) (g 40m^{-2})								
					PPRAI	AGARU	CURAL	PBRAC	AGADO	ESPQI	PPNOR	CREOL	ILHEU
Holocenthridae													
1	*Myripristis jacobus*	LC	3,4	Carnivore	56,09 (31,11)	39,94 (35,72)	50,45 (41,20)					254,13 (198,81)	
2	*Sargocentron hastatum*	LC	3,5	Carnivore		33,87 (30,30)			142,06 (39,52)	112,52 (74,39)	161,74 (84,07		
Aulostomidae													
3	*Aulostomus strigosus*	NC	4,2	Piscivore		19,09 (17,07)							109,57 (77,48)
Serranidae													
4	*Cephalopholis taeniops*	C	4,4	Carnivore		**150,64 (89,18)**			**254,79 (81,40)**	**406,02 (65,58)**	**303,70 (101,71)**	**350,47 (118,19)**	
5	*Mycteroperca fusca*	C	4,3	Piscivore					**867,79 (776,18)**				
Pricanthidae													
6	*Priacanthus arenatus*	C	4,0	m.Invert.			134,35 (109,69)					118,44 (108,12)	
Haemulidae													
7	*Parapristipoma humile*	C	3,6	m.Invert.					422,62 (207,25)				
Sparidae													
8	*Diplodus fasciatus*	LC	3,5	Omnivore	**101,19 (63,73)**	**471,25 (149,09)**		**330,35 (180,29)**	**785,09 (287,35)**	**194,49 (101,92)**		**44,42 (40,55)**	**165,95 (177,34)**
9	*Diplodus lineatus*	LC	2,8	Omnivore	**488,22 (150,18)**	**1999,46 (360,39)**	**686,32 (425,58)**	**2182,27 (217,01)**	**1984,16 (776,86)**	**2073,76 (658,55)**	**361,22 (286,80)**	**1898,54 (214,88)**	**757,00 (112,40)**
10	*Diplodus prayensis*	LC	2,8	Omnivore	**169,18 (70,91)**	**891,71 (411,75)**	**179,97 (146,94)**		**400,19 (219,19)**	**665,59 (197,25)**	**17,00 (15,52)**	**644,52 (292,27)**	**818,64 (94,83)**
11	*Viridentex acromegalus*	C	3,4	Carnivore	47,81 (45,08)					190,63 (165,09)	102,81 (93,85)		
Mullidae													
12	*Mulloidichthys martinicus*	C	3,2	m.Invert.	42,97 (39,00)	385,36 (291,65)							
13	*Pseudupeneus prayensis*	C	3,2	m.Invert.		51,37 (20,63)					27,99 (25,55)		
Chaetodontidae													
14	*Chaetodon robustus*	NC	3,3	s.Invert.		5,64 (5,05)							
Pomacanthidae													
15	*Holacanthus africanus*	NC		Omnivore	15,71 (9,80)						27,22 (15,75)		
Pomacentridae													
16	*Abudefduf hoefleri*	NC	2,7	Omnivore	24,77 (15,56)							62,55 (57,10)	57,12 (40,39)
17	*Abudefduf saxatilis*	NC	3,8	Omnivore	47,41 (31,95)	15,11 (13,52)							205,20 (64,91)
18	*Chromis lubbocki*	NC	3,0	Planktivore	**478,04 (257,43)**	**566,47 (190,20)**	**569,24 (269,37)**		**903,67 (563,63)**	**306,69 (159,79)**	**145,36 (120,09)**	**10,50 (9,58)**	**1592,15 (514,76)**
19	*Chromis multilineata*	NC	3,0	Planktivore	**1448,93 (302,33)**	**400,48 (122,08)**	**546,40 (229,13)**		**500,06 (315,71)**	**1294,20 (547,09)**	**982,51 (204,19)**	**9,42 (6,60)**	**1521,90 (461,30)**
20	*Similiparma hermani*	NC	2,5	Omnivore			11,00 (8,99)		29,52 (8,06)			48,87 (16,44)	31,88 (21,37)
21	*Similiperma lurida*	NC	3,5	Omnivore							0,42 (0,38)		
22	*Stegastes imbricatus*	NC		terr.Herbi.	11,25 (7,13)	5,52 (3,02)	6,41 (5,23)			45,21 (8,66)	42,73 (17,34)	53,59 (10,66)	17,57 (12,42)
Labridae													
23	*Bodianus speciosus*	C	3,6	m.Invert.	**88,63 (59,88)**	**138,33 (84,76)**	**569,24 (232,99)**		**88,72 (78,46)**	**339,00 (104,53)**	**156,85 (91,27)**	**249,65 (148,29)**	**43,25 (30,58)**
24	*Coris atlantica*	NC	3,5	m.Invert.	2,53 (2,39)	20,68 (7,33)	14,13 (9,72)	0,31 (0,25)	3,04 (2,72)		0,14 (0,13)	1,06 (0,96)	
25	*Scarus hoefleri*	C		rov.Herbi.		83,85 (75,00)							
26	*Sparisoma choati*	C	2,0	rov.Herbi.	1,93 (1,82)							1,72 (1,57)	29,05 (20,54)
27	*Sparisoma cretense*	C	2,9	rov.Herbi	**273,07 (111,86)**	**333,45 (110,60)**	**377,07 (307,88)**			**643,47 (261,83)**	**753,94 (218,20)**	**126,29 (56,01)**	
28	*Thalassoma pavo*	NC	3,5	m.Invert.	**140,86 (34,50)**	**342,17 (88,83)**	**88,28 (36,05)**	**74,17 (59,63)**	**195,23 (29,56)**	**332,02 (77,14)**	**185,51 (58,41)**	**115,38 (17,84)**	**36,50 (19,45)**
Acanthuridae													
29	*Acanthurus monroviae*	C	2,5	rov.Herbi.		32,14 (28,75)			104,51 (93,48)		93,30 (85,17)	26,50 (16,59)	271,00 (1,10)
Monacanthidae													
30	*Aluterus scriptus*	NC	2,8	Omnivore					26,56 (23,76)				35,76 (25,29)

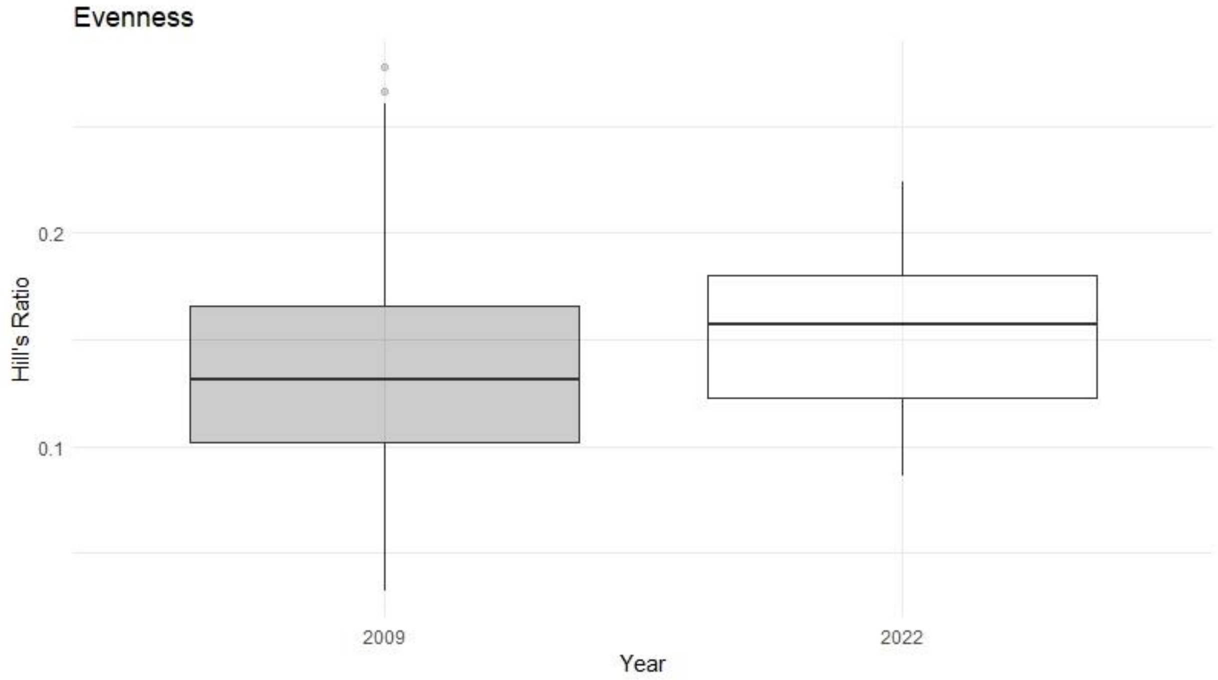

Figure 8.2. *Evenness (Hill's ratio) by year.*

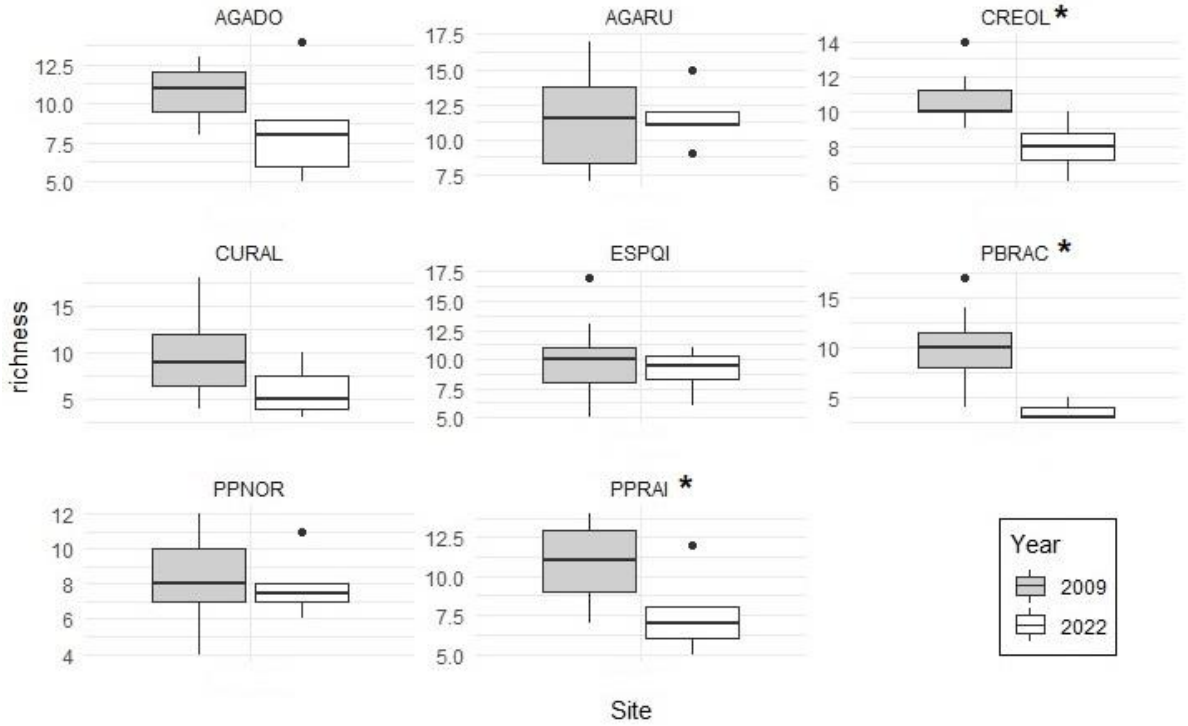

Figure 8.3. *Species richness for site specific pairings. Statistically significant differences (*) between 2009 and 2022 at the sites CREOL (p= 0,002399), PBRAC (p=0,008127), and PPRAI (p=0,001074).*

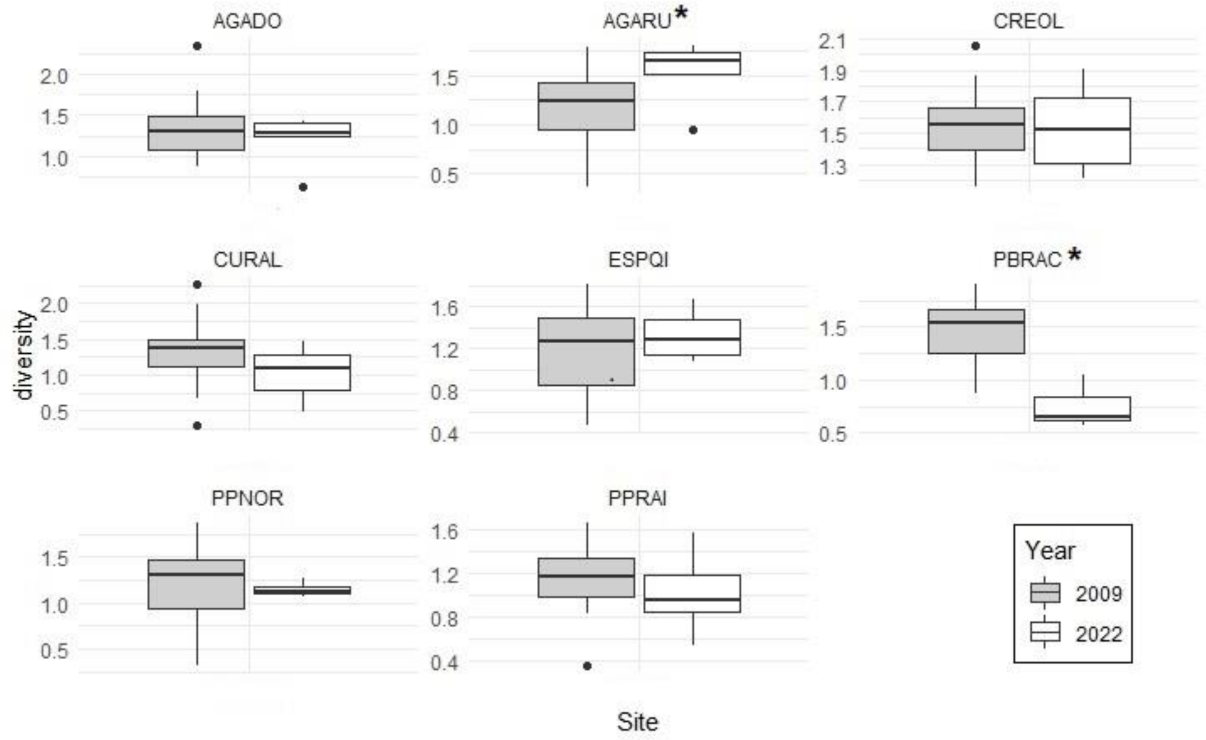

Figure 8.4. Shannon-Wiener diversity index for site specific pairings. Statistically significant differences (*) between 2009 and 2022 at the sites AGARU (p=0,03569) and PBRAC (p=0,008513).

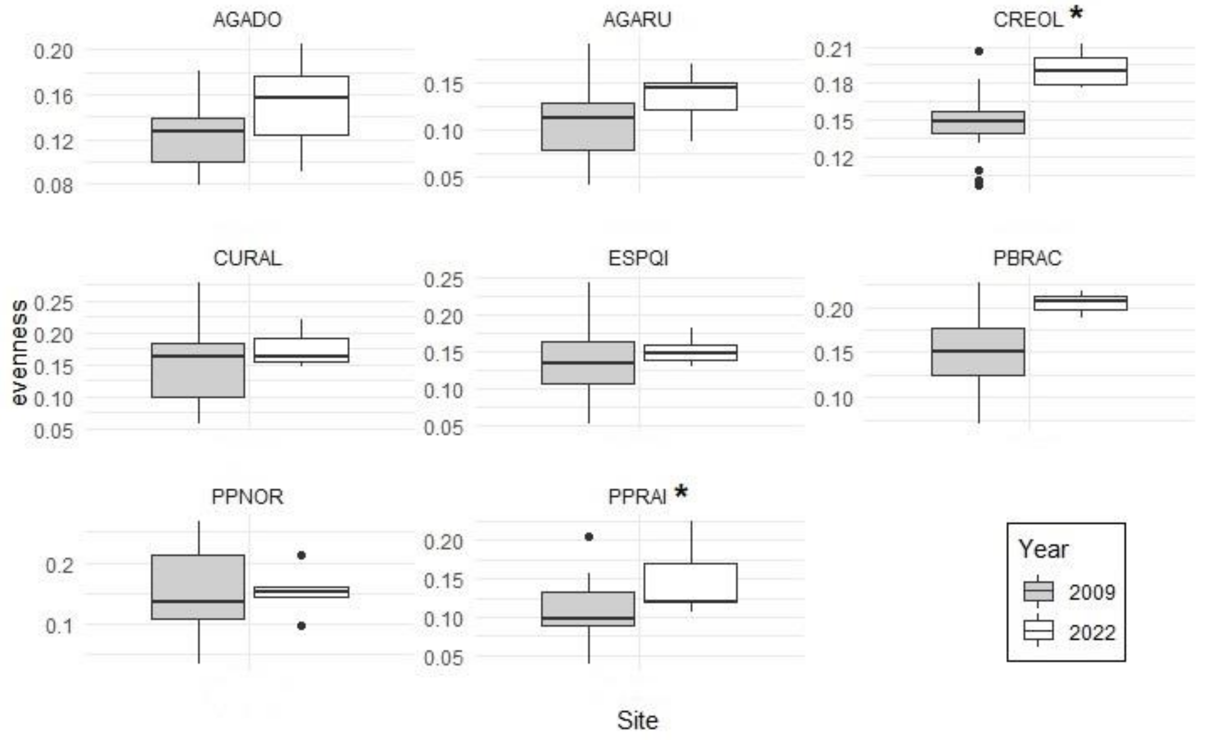

Figure 8.5. Evenness (Hill's ratio) for site specific pairings. Statistically significant differences (*) between 2009 and 2022 at the sites CREOL (p=0,006378), and PPRAI (p=0,01574).

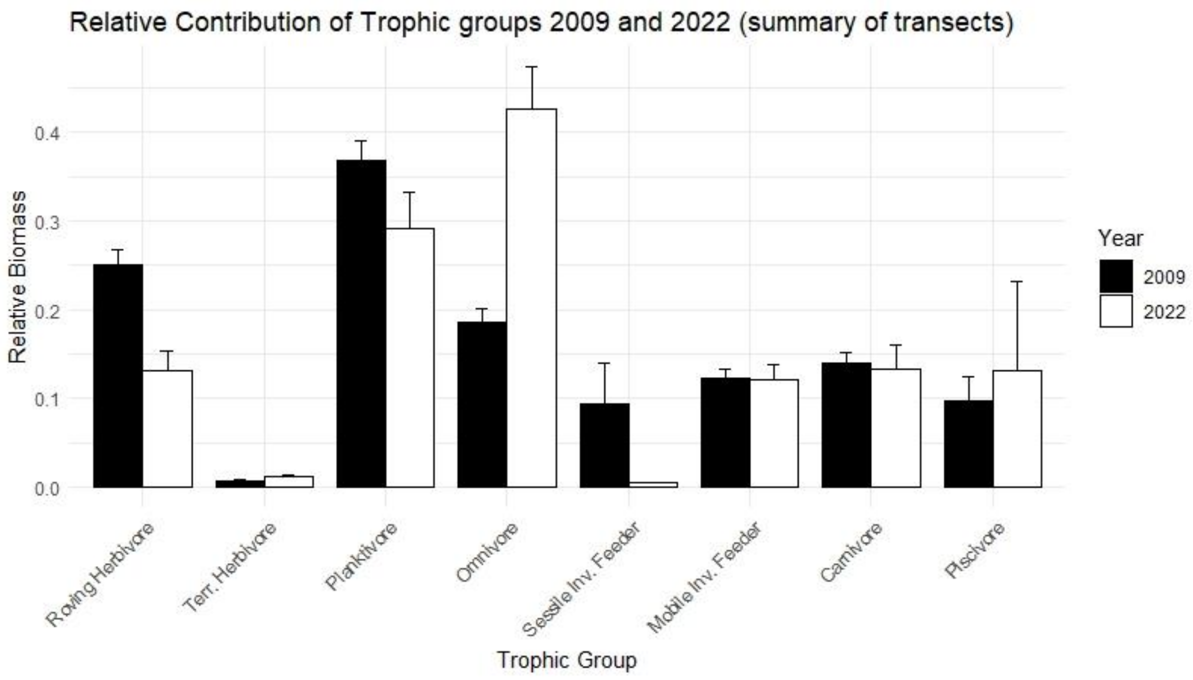

__Figure 8.64.__ Relative contribution of trophic groups in 2009 and 2022.

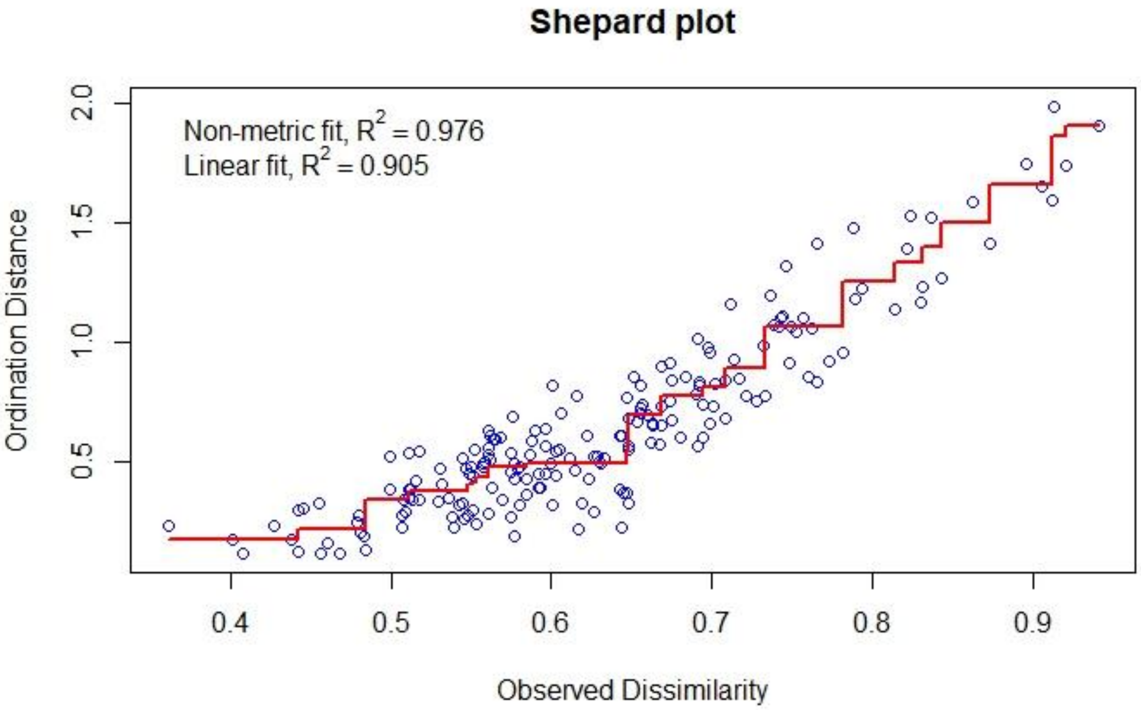

__Figure 8.5.__ Shepard Plot for NMDS on densities of all sampled species, averaged by site (NMDS stress = 0.08137056).

Table 8.3. *Fitting of environmental variables to NMDS (Figure 4.4). FI = Fishing intensity. WS = Water surge. CO = Complexity. Relative cover of four benthic categories: algae, coral, CCA and zoanthid. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

	NMDS1	NMDS2	R^2	p
FI	-0,97089	-0,23952	0,2833	0,063 (.)
WS	-0,60363	-0,79727	0,0754	0,542
CO	-0,90869	-0,41747	0,1383	0,275
Algae	0,32991	0,94401	0,0077	0,926
Coral	-0,58030	0,81440	0,1733	0,193
CCA	-0,27357	-0,96185	0,0661	0,583
Zoanthid	0,31555	-0,94891	0,0153	0,884

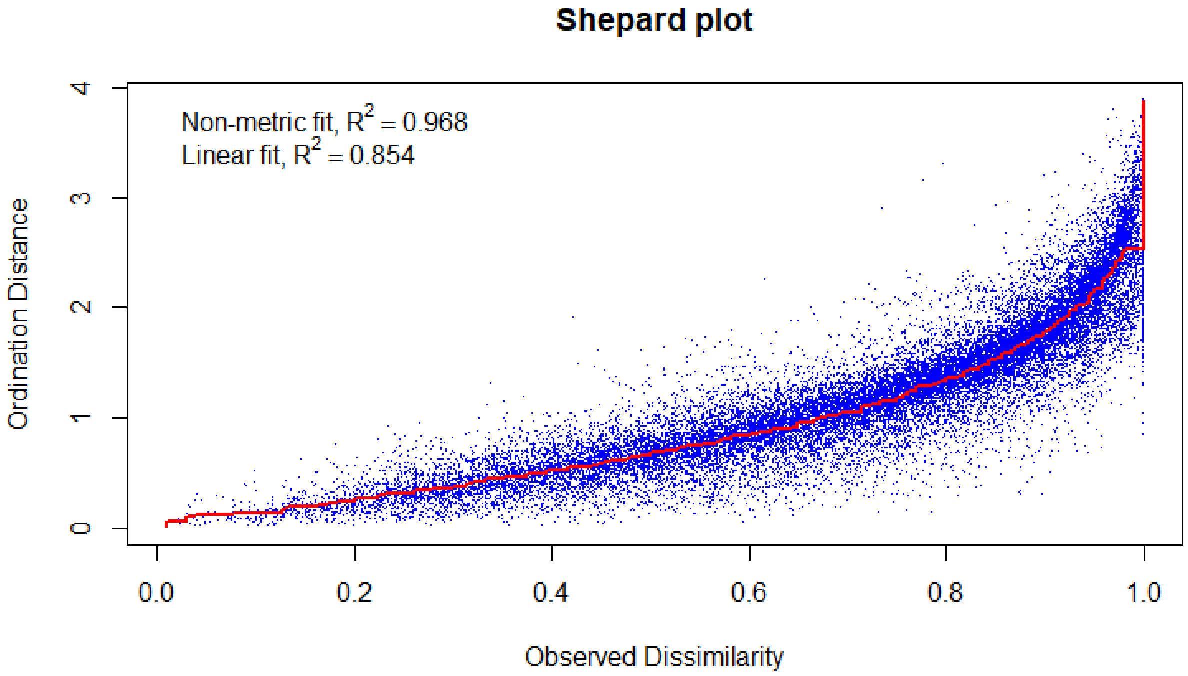

Figure 8.8. *Shepard plot for NMDS on dominant species frequencies, by transect (NMDS stress = 0.1783625).*

Table 8.4. *Results of PERMANOVA assessing differences in relative species distribution between the years 2009 and 2022. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

	Degrees of Freedom	Sum of Squares	R^2	F	p
Year	1	10,142	0,15039	42,305	0.001 (***)
Residual	239	57,295	0,84961		
Total	240	67,437	1,00000		

Table 8.5. *Results of PERMANOVA assessing differences in relative benthic cover between the years 2009 and 2022.*

	Degrees of Freedom	Sum of Squares	R^2	F Model	p
Year	1	0,02705	0,04015	0,7529	0.544
Residual	18	0,64668	0,95985		
Total	19	0,67373	1,00000		

Table 8.6. *Fitting of environmental variables to PCA (Figure 4.6). Variables are the relative cover of six benthic categories: algae, CCA, invertebrates, zoanthids, substrate and corals. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

	PC1	PC2	R^2	p
Algae	0,72606	-0,68763	0,0253	0,612
CCA	-0,48793	-0,87288	0,1457	0,045 (*)
Invertebrates	-0,92771	0,37330	0,0233	0,625
Zoanthids	-0,93580	0,35254	0,1157	0,079 (.)
Substrate	0,78951	0,61374	0,1288	0,068 (.)
Corals	0,16371	-0,98651	0,3993	0,01 (***)