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連結棲地品質與珊瑚礁魚類群聚跨生活史組成

Linking Habitat Quality to Reef fish Assemblage Composition across Life Stages

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摘要 - Chinese Abstract

珊瑚礁魚類群聚正面臨漁業活動、沿海開發與氣候變遷等重大威脅，導致棲地大規模喪失與如添入（recruitment）等關鍵生態過程的中斷。理解環境因子對魚類群聚的影響需進一步掌握棲地劣化的機制，而這也是當前研究中的知識缺口。本博士研究結合生物、地形與聲學指標，評估棲地品質對珊瑚礁魚類群聚不同生活史階段的影響。首先，我探討活珊瑚與死亡珊瑚如何影響不同生活史階段的魚類群聚。其次，我分析結構複雜度、底棲組成與珊瑚礁聲景在兩座島嶼上如何影響魚類添入。最後，我整合幼魚與成魚豐度、底棲覆蓋率與人為噪音，評估台灣第一座海洋保護區（Marine Protected Area, MPA）的棲地品質。

小尺度實驗（第二章）顯示，死亡的分枝狀珊瑚可為行動性高的魚類幼苗提供暫時性庇護；相對地，成魚則更依賴具有能量供應、結構穩定性與支持關鍵生態功能的活分枝狀珊瑚。

島嶼尺度調查（第三章）發現，魚類添入隨結構複雜度增加而上升，且在以絲狀藻類或軟珊瑚為主的礁體中顯著下降，凸顯硬珊瑚覆蓋在支持添入上的重要角色。此外，添入魚種的多樣性與夜間魚類合唱頻段的聲音強度呈正相關，顯示特定聲學線索在魚苗定居期間的重要性。

棲地品質評估（第四章）依據底棲與魚類群聚指標及人為噪音程度，辨識出「機會區」與「風險區」，其中一處高機會區目前未受保護，並針對兩處風險區提出管理策略。

未來研究應整合生態與聲學指標於多因子分析架構中，以更深入了解棲地品質如何形塑珊瑚礁魚類群聚，並支持更有效的保育策略。

關鍵字：添入、珊瑚礁魚、棲地劣化、珊瑚覆蓋率、結構複雜度、聲景

English Abstract.

Coral reef fish assemblages face significant threats from fishing activities, coastal development, and climate change leading to extensive habitat loss and disruptions to key ecological processes, such as recruitment. Understanding the influence of environmental factors on fish communities requires deeper insights into the mechanisms of habitat degradation, a knowledge gap in current research. This Ph.D. study integrates biological, topographic, and acoustic indicators to assess the effects of habitat quality on different life stages of reef fish assemblages. First, I examined how live and dead corals affect fish assemblages across life stages. Second, I investigated the role of topographic complexity, benthic composition, and reef soundscapes in shaping fish recruitment across two islands. Finally, I assessed habitat quality within Taiwan's first marine protected area (MPA) by integrating juvenile and adult fish abundance, benthic cover, and anthropogenic noise.

Small-scale experiments (Chapter 2) revealed that dead branching corals can provide temporary shelter for mobile fish recruits, whereas adults were more dependent on live branching corals that offer energetic input, structural stability, and support key ecological functions. Findings from island-scale surveys (Chapter 3) showed that recruitment increases with rugosity and is significantly reduced on reefs dominated by turf algae or soft corals—highlighting the role of hard coral cover in supporting recruitment. Additionally, recruitment richness was positively associated with nighttime sound levels at frequencies characteristic of fish choruses, suggesting the importance of specific acoustic cues during settlement. Habitat quality assessments (Chapter 4) identified "opportunity" and "risk" zones based on benthic and fish assemblage data and levels of anthropogenic noise, revealing a currently unprotected high-opportunity area and proposing management strategies for two high-risk sites. Future research should integrate ecological and acoustic indicators into multifactorial frameworks to better understand how habitat quality shapes reef fish assemblages and to support more effective conservation strategies.

Keywords: Recruitment, Reef fish, Habitat degradation, Coral cover, Complexity, Soundscape

Table of Contents

List of Figures

Chapter 1

General Introduction

1.1 Coral reefs

Coral reefs are among the most diverse ecosystems on Earth, supporting hundreds of thousands of associated species (Fisher et al., 2015). These ecosystems play crucial roles in providing essential functions and services in the marine realm, influencing the carbonate and nitrogen cycles (Brandl et al., 2019), primary productivity, nutrient cycling, and secondary productivity (Bellwood et al., 2018; Hatcher, 1990; Tebbett et al., 2024, 2025). These functions have local and regional impacts, such as increasing fish biomass (Bachtiar et al., 2023; Russ et al., 2020) and promoting connectivity between populations in different habitats (Carlson et al., 2021; Mumby, 2006). Coral reefs are also vital for human populations by supporting fisheries and tourism, protecting coastlines from wave action, and serving as a source of bioproducts (Moberg & Folke, 1999; Mora, 2008; Woodhead et al., 2019). These services depend on a healthy and diverse community of reef organisms, especially hard corals, algae, crustaceans, fishes, and other associated taxa (see Moberg & Folke, 1999).

1.2 Coral reef fish ecology

Fishes are the most taxonomically diverse group of vertebrates, with over 32,000 described species (Nelson et al., 2016), of which more than 5,000 are considered reef-associated (Victor, 2015). Reef fishes occupy a wide range of ecological niches, feeding on algae, plankton, corals, crustaceans, other fish, parasites, among other things (Ferreira et al., 2015; Suzuki et al., 2018). Their adult body sizes range from just a few centimeters to over 2 meters long, with home ranges as narrow as 1 m^2 or as wide as several km^2 (Chapman & Kramer, 2000). These features make reef fish assemblages vital components of coral reef ecosystems because they play essential roles in various ecological functions, such as nutrient cycling and transport (Brandl et al., 2019; Collins et al., 2024; Siqueira et al., 2021), increase secondary productivity (Bellwood et al., 2018; Morais & Bellwood, 2020), and exerting top-down control over many organisms, especially macroalgae (Hughes, 1994; Jessen & Wild, 2013; Lewis & Wainwright, 1985).

Reef fishes have strong and diverse ecological relationships with the substrate throughout most of their life history (Choat & Bellwood, 1991). Hard corals and topographic complexity provide reef fishes with a combination of energy resources and structural shelter that are crucial for their survival (Agudo-Adriani et al., 2019; Almany, 2004; Komyakova, 2018; Russ et al., 2020). Although hard coral cover and topographic complexity are important on their own, their combined effect has a greater influence on the richness and abundance of reef fishes (Coker et al., 2012; Komyakova et al., 2013). Additionally, heterogeneous substrates — including high coral diversity and other benthic organisms like calcareous algae, along with moderate levels of turf algae and soft corals — are known to enhance the diversity of associated reef fish communities (Bachtiar et al., 2023; Cabaitan et al., 2008). These diverse substrates support habitat specialists, such as obligate coral dwellers, as well as generalist bottom dwellers that swim and forage across different microhabitats within the reef (Munday, 2001; Streit et al., 2021; Wilson et al., 2008). Additionally, the needs of associated reef fish species can also vary with their life stage (Dahlgren & Eggleston, 2000; Félix-Hackradt, 2013). For instance, some species use different microhabitats according to life stage (Félix-Hackradt et al., 2014), while others change their diets as they grow (Bellwood, 1988; Chan et al., 2019). These ontogenetic changes highlight the importance of considering reef fish life cycles (Fig. 1.1) in ecological research.

1.3 Coral reef fish life cycle: from spawning to settlement

Reef fish exhibit different reproductive strategies depending on the species. The two main strategies involve either laying adhesive eggs on the reef substrate (Canan et al., 2011), or releasing pelagic eggs into the water column (Harrison et al., 1984), illustrating a trade-off between maximizing dispersal and survival (Hickford, 2003). After hatching, most fish larvae adopt pelagic habits as ichthyoplankton (Brogan, 1994). These larval stages can last from a few days to several months (Luiz et al., 2013; Victor, 1989), during which larvae may disperse from tens of meters to hundreds of kilometers (Abesamis et al., 2016; Hickford, 2003; Luiz et al., 2013; Sponaugle, 2015).

To return to a suitable reef substrate, reef fish larvae follow olfactory, visual, and auditory cues toward coral reefs (Lecchini et al., 2005, 2007, 2013; Parmentier et al., 2015; Simpson et al., 2004). The cues that fish larvae use to select suitable settlement habitats include: hard coral cover (Coker et al., 2012; Feary et al., 2007; Lecchini et al., 2013), topographic complexity (Almany, 2004; Cheminée et al., 2016; Coker et al., 2012), the presence of conspecifics (Lecchini et al., 2007; Levin, 1993), and reef sounds (Gordon et al., 2019; Lecchini, Shima, et al., 2005; Simpson et al., 2004). Although the relative importance of auditory, olfactory, and visual cues is still being studied, the growing scientific evidence suggests that fish larvae likely follow and need more than one cue to trigger settlement (Booth & Wellington, 1998; Lecchini, Planes, et al., 2005; Lecchini, Shima, et al., 2005; Sponaugle, 2015). For example, auditory cues may be more effective over longer distances (tens to hundreds of meters (Kaplan et al., 2015; Kaplan & Mooney, 2016; Simpson et al., 2002), while visual and chemical cues have been proven to work over smaller scales and clear waters (Igulu et al., 2011; Lecchini et al., 2007; Lecchini, Shima, et al., 2005).

Once the larva locates a suitable habitat through these environmental cues, settlement begins (Jones, 2015; Sponaugle, 2015). Shortly after settlement, most fish hide in small crevices or bury themselves in the sand to undergo metamorphosis and develop a benthic-associated morphology (Jones, 1990; Sponaugle, 2015). The point at which this metamorphosis is complete and young-of-the-year juveniles exit their shelter, becoming detectable to observers, is called recruitment (Félix-Hackradt, 2013; Keough & Downes, 1982). Recruitment is different from settlement, as it marks the specific time when fish become part of the local populations as demersal individuals (Matte et al., 2024).

1.4 Coral reef fish life cycle: recruits and juveniles

Juveniles are coral reef fish that have not yet reached sexual maturity and are often identified by their size, distinctive coloration, and behavior – used for camouflage or mimicry (Adjeroud et al., 2017; Dahlgren & Eggleston, 2000). Recruits are a specific stage of juveniles, consisting of recently post-settled individuals (see Fig. 1.2 A) (Adjeroud et al., 2017; Rankin & Sponaugle, 2014; Jenkins et al., 2009; Keough & Downes, 1982). During this stage, mortality rates can reach up to 60% per day, mainly due to predation (Goatley & Bellwood, 2016). Recruitment success depends on various factors, including random events (Lassig, 1983) and environmental influences such as competition for habitat (Munday, 2004; Sponaugle, 2015), predation (Almany, 2004a; Lecchini et al., 2007), substrate complexity (Connell & Jones, 1991), and live coral cover (Bonin et al., 2009; Booth & Beretta, 1994).

Recruits typically have different requirements than adults. For example, many species settle in nursery habitats such as mangroves, seagrass beds, or the backreef (Sponaugle, 2015). However, some species settle directly on the reef and may either join colonies of sedentary adults or avoid competition by occupying different microhabitats (Dahlgren & Eggleston, 2000; Félix-Hackradt et al., 2014). Additionally, most species need rapid growth after recruitment to reduce predation risk (Goatley & Bellwood, 2016). Some recruits adopt a different diet from the adults to meet the energetic demands of this life stage (Bellwood, 1988; Chen, 2002; Sponaugle, 2015). These traits underscore the importance of further recruit-focused research in community ecology studies.

Post-recruit juveniles are more experienced, notably larger than recruits (see Fig. 1.2 B), and often share similar habitats with adults (Adjeroud et al., 2017; Dahlgren & Eggleston, 2000; Félix-Hackradt et al., 2014; Grol et al., 2014). However, juveniles still maintain some ecological strategies to avoid predation, including alert behavior, stage-specific aposematic mimicry, and stage-specific schooling (Almany, 2004a; Bellwood & Choat, 1989; Hsiao et al., 2003). Moreover, juveniles are more sensitive to stressors such as habitat loss, water pollution, and anthropogenic noise (Egner & Mann, 2005; Ferrari et al., 2018). Due to these differences across life stages, it is inaccurate to assume that the relationship between reef fish assemblages and their substrate is the same for recruits, juveniles, and adults. Additionally, the survival of early life stages is crucial for reef fish populations as it supports their replenishment and maintenance (Almany et al., 2007; Leis et al., 1998; Lewis, 1997), which helps promote diversity in reef fish assemblages (Adjeroud et al., 2017).

1.5 Coral reef habitat quality

Habitat degradation has caused declines in reef fish assemblages worldwide (Christensen et al., 2014; Fontoura et al., 2020), even within MPAs (Bruno & Selig, 2007; Christensen et al., 2014), emphasizing the importance of habitat quality for reef fish. High-quality habitats should enhance replenishment rates by supporting the survival and reproduction of associated species (Johnson 2005, 2007). In coral reefs, high quality is often linked to the extent and diversity of coral cover, the biomass and variety of associated benthos, and nekton—especially coral reef fishes (Bruce et al., 2012; Díaz Pérez et al., 2016; Kaufman et al., 2011; Sheppard et al., 2023). Additionally, recent surveys highlight that underwater soundscapes are essential components of coral reef ecosystems, playing key roles in communication and reproduction (Myrberg, 1997; Popper et al., 2024; Roberts & Rice, 2023), as well as attracting new migrants and recruits (Gordon et al., 2019; Moulton, 1963; Simpson et al., 2002).

However, coral reefs worldwide have been extensively degraded by destructive and unregulated fishing (Christensen et al., 2014; McClanahan, 2018), coastal development (Zhou et al., 2017), as well as climate change, water pollution, and anthropogenic noise, which have recently become primary threats to coral reefs (Bruno et al., 2019; Fabricius et al., 2005; Nedelec et al., 2023). Together, these impacts have resulted in the loss of approximately 50% of the world's coral reefs (Bruno & Selig, 2007). For instance, rising seawater temperatures, ocean acidification, and extreme weather events due to climate change, lead to mass mortality events among corals and their associated fauna (Bruno et al., 2019; Fontoura et al., 2020). Eutrophication can trigger to rapid algal growth (Wenger et al., 2015), which shifts benthic dominance patterns and leads to the formation of alternative stable states (Ainsworth & Mumby, 2015; Hughes, 1994). The effects of anthropogenic noise pollution are still difficult to predict; however, research indicates it may hold negative impacts foraging, reproduction, settlement, and survival rates in various marine organisms (Cox et al., 2018; Hawkins & Popper, 2017; Nedelec et al., 2023).

These stressors directly impact coral reef fish assemblages. Although several measures have been implemented to reduce the effects of fisheries (see Allard et al., 2022; Gouezo et al., 2021; MacNeil et al., 2015), overfishing and habitat fragmentation still pose major problems worldwide (Mendes, 2024; Milne et al., 2021). Furthermore, the loss of coral cover can change the structure of reef fish assemblages (Morais et al., 2020) or directly decrease fish diversity and abundance (Brandl et al., 2020; Bruno & Selig, 2007; Russ et al., 2020). Likewise, shifts in substrate composition and functional homogenization often result in reduced biomass and functional losses within reef fish assemblages (Crisp et al., 2022; Reverter et al., 2022), causing ecosystem-level effects on the reef (Bellwood et al., 2018; Morais et al., 2020). These impacts can be intensified by noise stressors, which can impair communication, reduce foraging, spawning, and reproduction rates (Cox et al., 2018; Hawkins & Popper, 2017; Minier et al., 2024; Popper & Hawkins, 2019). Additionally, juveniles are especially impacted by habitat degradation and coral death which reduce their survival by limiting available habitat (Almany, 2004; Feary et al., 2007), while noise stressors can hinder settlement (Peng et al., 2015; Williams et al., 2024) and raise predation risk for juveniles (Cox et al., 2018; Jimenez et al., 2020; Nedelec et al., 2023). Nonetheless, the biology of early life stages remains less understood than that of adult fishes (see Sponaugle, 2015), highlighting a critical gap in our knowledge of coral reef fish community dynamics.

1.6 The importance of early stages to prevent habitat degradation

Despite their unique characteristics and growing research on early life stages (Sponaugle, 2015), most studies still overlook juveniles by excluding them from analyses (Helder et al., 2022; Liu et al., 2012) or disregard their ecological uniqueness by grouping all individuals together (Araújo et al., 2020; Mattos et al., 2023; Williams et al., 2015). Monitoring recruitment patterns and juvenile abundance is essential for understanding future population trends and assessing the recovery potential of coral reef habitats (Almany et al., 2007; Emslie et al., 2014; Fontoura et al., 2020; Holbrook et al., 2008). Therefore, filling the knowledge gap on how environmental variables impact early life stages is critical for promoting rich reef fish communities—especially in degraded habitats, where ecological processes and functions may be less predictable than in healthy systems (Fakan et al., 2025; Heinrichs et al., 2016; Roth et al., 2018).

Thus, investigating how reef fish assemblages at different life stages respond to habitat quality indicators can help identify potential responses to degradation. This study tries to improve our understanding on the effects of environmental and acoustic factors on reef fish assemblages, and how habitat quality shapes these relationships, reaching for more effective management strategies to preserve reef fish assemblages.

1.7 Objectives

Given the knowledge gap regarding the ecology of reef fish early life stages, especially in current scenarios of gradual habitat degradation, this study aims to:

1. Assess how live and dead coral influence recruit and adult fish assemblages

2. Determine environmental drivers associated with high recruitment across degradation gradients

3. Identify opportunity and risk sites by integrating ecological and acoustic indicators within a marine protected area

1.8 Thesis outline

Chapter 1: General introduction

Chapter 2: The role of live and dead corals in shaping fish assemblages across life stages

Chapter 3: Environmental and acoustic drivers of fish recruitment along degraded coral reefs

Chapter 4: Assessing opportunity and risk sites for reef fish conservation through ecological and noise indicators in a Marine Protected Area

Chapter 5: General Discussion

Figures

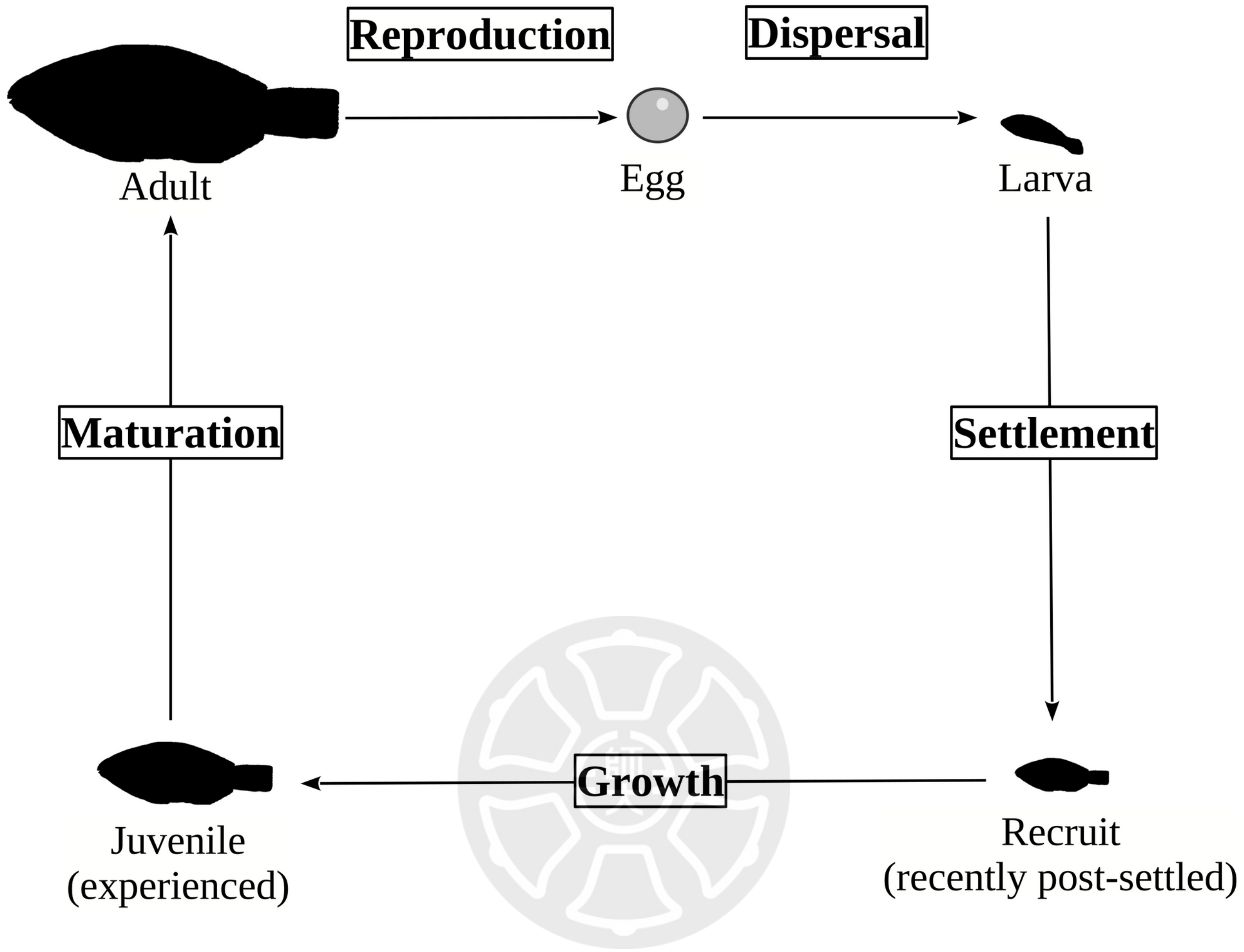

Figure 1.1: Life cycle of a reef fish. Adults are any sexually mature individuals living near the substrate. Larvae comprise planktonic pre-settlement stages. Recruits are recently settled individuals (days to weeks) which already have adopted a nektonic morphology. Juveniles are more experienced than recruits (months to years) but sexually immature.

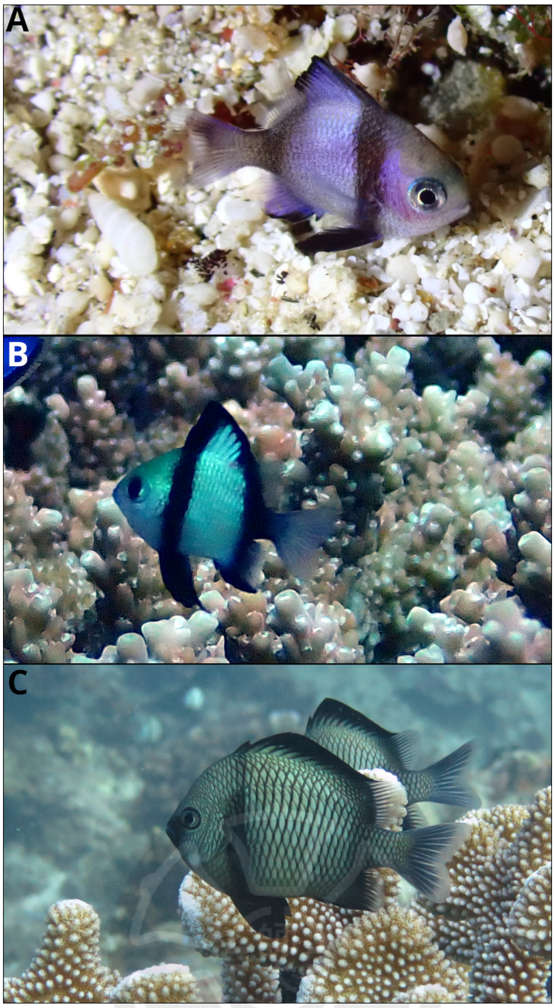

Figure 1.2: Examples of different life stages of the reef fish *Dascyllus reticulatus*. Recruit (A). Juvenile (B). Adult (C).

Chapter 2

The role of live and dead corals in shaping fish assemblages across life stages

2.1 Abstract

Coral reef fishes face unprecedented threats, as extensive habitat degradation compromises their ecological functions by modifying assemblage structure. It remains unknown as to how resistant reef fishes are to widespread losses in coral cover, and most studies tend to focus on adults, overlooking the important role of recruits. This study employed taxonomic and trait-based approaches to investigate how live and dead branching corals influence reef fish assemblages across life stages. Over one year, we monitored recruitment and the migration of post-recruits (juveniles and adults) on manually constructed 1 m² patches of live and dead branching corals in a degraded reef setting. Recruit assemblages, composed mainly of two trophic groups, exhibited similar abundance and richness in the complex structures of dead and live coral patches, compared to flat control areas. Conversely, post-recruit fishes were more abundant, species-rich, and functionally diverse in live coral patches, encompassing several trophic groups and a dominance shift between mobile and sedentary species. Our findings reveal that while dead coral structures can serve as temporary shelters for mobile recruits, live corals are essential for supporting long-term biodiversity and functional diversity. This study underscores the complementary roles of both live and dead corals in promoting reef fish recovery and highlights the value of integrative strategies for reef ecosystem restoration.

2.2 Introduction

In recent decades, fish assemblages along coral reefs have suffered extensively from habitat degradation triggered by anthropogenic activities (Bellwood et al., 2019; Garpe et al., 2006). This has led to a global reduction in reef fish biodiversity (Munday et al., 2008; Strona et al., 2021), biomass (Christensen et al., 2014), and the associated functions (Ainsworth & Mumby, 2015; Bonin, 2011; Emslie et al., 2008; Jones et al., 2004; Morais et al., 2020). Conversely, fishes are critical for reef dynamics, and changes in their assemblage structure may further precipitate coral reef decline (Brandl et al., 2020; Morais et al., 2022; Morais et al., 2020; Mouillot et al., 2014), risking a negative loop.

Several key ecosystem processes in coral reef functioning involve fishes (Brandl et al., 2019; Mouillot et al., 2013). Herbivorous and planktivorous fishes play an important role in the transfer of energy from low to high trophic levels, boosting secondary productivity (Bellwood et al., 2018; Morais & Bellwood, 2020; Tebbett et al., 2024). Furthermore, sedentary fish exert a strong local influence by helping nutrient recycling (Collins et al., 2024; Siqueira et al., 2021), whilst mobile species impact sediment distribution and nutrient transfer between habitats (Brandl et al., 2019; Tebbett et al., 2025). Additionally, healthy fish assemblages consist of diverse herbivorous fish populations that limit algal growth (Hughes, 1994; Jessen & Wild, 2013; Lewis & Wainwright, 1985) and help maintain stable coral cover (Mumby, 2006).

Few studies have investigated the capacity of coral reef fish to utilize dead corals (see Fakan et al., 2025; Streit et al., 2021; Wilson et al., 2006), with even fewer involving early life stages (Feary et al., 2007; Wismer et al., 2019). Due to the practical difficulties involved in studying small fishes in the field, many ecological surveys overlook recruits (e.g., Helder et al., 2022; Liu et al., 2024), thus failing to capture their ecological significance as the foundation for future assemblages (Halpern et al., 2005; Jones, 1990; Sponaugle, 2015). In many species, recruits inhabit distinct habitats (Félix-Hackradt et al., 2014; Grol et al., 2014; Kimirei et al., 2013) and require different diets (Bellwood, 1988; Chan et al., 2019) than adults, gradually adopting mature traits as they grow. The habitat use of recruits varies by taxa and environmental conditions, with some species depending on live corals (obligate live coral dwellers) (Bonin et al., 2009; Feary et al., 2007; Lecchini et al., 2013), while others prefer dead colonies or show no preference (facultative live coral dwellers) (Feary et al., 2007; Lirman, 1994). Furthermore, ontogenetic development influences the degree of preference for specific habitats (Komyakova et al., 2019; Lecchini & Galzin, 2005; Lirman, 1994).

As degraded reef habitats become increasingly prevalent worldwide (see Bruno et al., 2019; Bruno & Selig, 2007; De'ath et al., 2012), the capacity of dead corals to support a functionally diverse fish assemblage, compared to live corals, remains unclear. Furthermore, disturbances in coral reefs often lead to habitat fragmentation (Bonin, 2011), which accentuates the patchiness in these ecosystems (Bonin, 2011; McClanahan, 2022), creating a mosaic of variable biomass and productivity rates within the same reef (Agudo-Adriani et al., 2019; Syms & Jones, 2000). Responses to coral death and a fragmented habitat depend on a combination of species traits, spatial distribution in reef fish assemblages, and recruitment pulses (Syms & Jones, 2000). While some young, site-attached damselfishes appear relatively resilient to disturbances and coral mortality (see Wismer et al., 2019), the role of dead corals in maintaining and supporting functional fish assemblages in patchy reef habitats remains overlooked.

To address these knowledge gaps, we evaluate how live and dead corals impact reef fish assemblages on successive live stages and how habitat variations influence functional traits. We hypothesize that recruit and post-recruit (juveniles and adults) assemblages will exhibit different taxonomic and functional structures in live and dead coral patches. To test this, we conducted a year-long field experiment using patches of live and dead branching corals, comparing their associated reef fish assemblages to those observed along flatter degraded reef substrata.

2.3 Methods

2.3.1 Study site

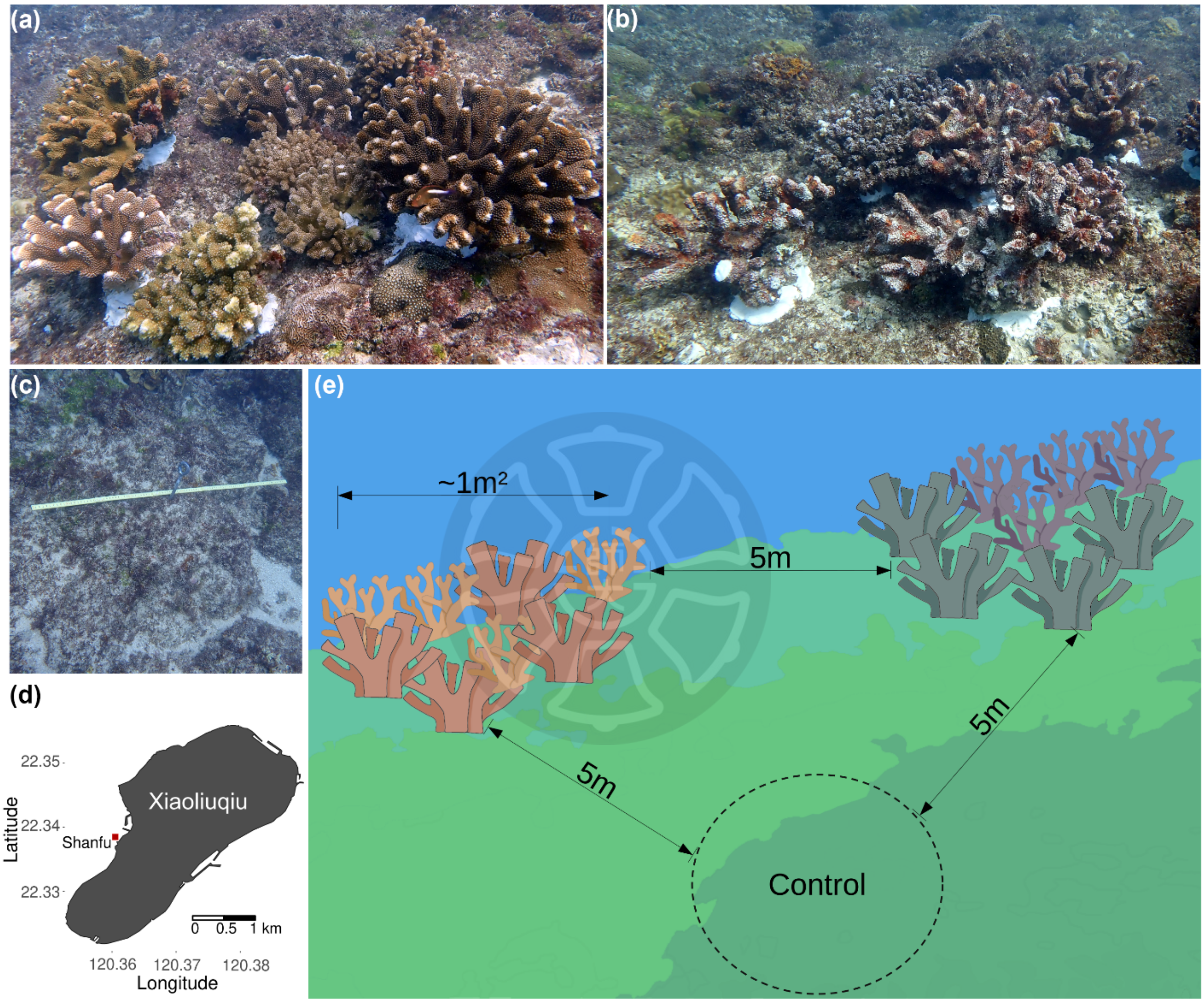

Figure 2.1: The present study employed four replicate blocks, each including three experimental conditions: a live coral treatment (a), a dead coral treatment (b), and a control (c), located near Shanfu harbor in Xiaoliuqiu (d). The 1 m^2 patches were placed approximately 5 m from each other (e). The replicate blocks were placed approximately 10 m apart from each other.

This study was conducted at Xiaoliuqiu Island in southern Taiwan, 22° 20' 24" N, 120° 22' 12" E. This 6.8 km^2 island was once home to diverse reefs with high coral and fish richness (Yang et al., 1975). However, intensive anthropogenic activities such as overfishing and coastal development have dramatically reduced biodiversity (Dai et al., 2009), causing severe declines in live coral cover (Lin et al., 2024; Yang et al., 2017). Despite a Marine Protected Area (MPA) established in 2000, with further zoning in 2014 prohibiting fishing activities, coral cover remains in decline, with no sign of recovery for both corals and the associated reef fish assemblage. In Shanfu Harbor, to the west of the Island (Fig. 2.1d), shallow-water reefs extend approximately 500 m along the islands' coastline and still host relatively high coral cover compared to other areas around the island (Lin et al., 2024; Mattos et al., *in review*). This site has a shallow slope (1-10 m) dominated by turf algae (less than 5% coral cover) on a relatively flat, hard substrate ("turf zone"), while a deeper area (10–17 m) still maintains moderate coral cover (~30 %) and a complex structure ("coral zone"). This allowed for a manipulation experiment to test the effect of patches of live and dead corals on shallow reef fish assemblages. This research was conducted under the permit number 11130157900 granted by the Pintung County Government.

2.3.2 Data collection

2.3.2.1 Experiment setting and monitoring

Between February 2022 and May 2023, we conducted a field experiment on the turf zone using live and structurally intact dead coral colonies from two different branching species: *Pocillopora eydouxi* and *Pocillopora verrucosa*. All colonies were collected from the surrounding area and transplanted to the experimental area. Colonies of *P. eydouxi* (~ 40–60 cm tall and ~ 40–70 cm wide) and *P. verrucosa* (~ 30–40 cm tall and ~ 40–60 cm wide) were carefully removed from their base using a crowbar. To ensure that live and dead coral patches held comparable structural complexities, we brushed the macroalgae from the dead corals with steel wire brushes, exposing branches and simulating recently dead corals. The original resident fish and invertebrates were also carefully moved to a new substrate before the transplantation. Each coral was then secured to the substrate with a 10 cm bolt and underwater epoxy. Four experimental blocks (i.e., four replicates) were constructed on the turf zone, each containing two experimental treatments, a live coral patch, a dead coral patch, and a flat reef area (control) (Fig. 2.1a-c). Treatment patches consisted of four colonies from each coral species, resulting in eight colonies per patch in a total area of approximately 1 m^2. The patches and control area were spaced ~5 m apart, forming a triangular shape in each replicate block (Fig. 2.1e). The control area was designated as a 1 m^2 circle on the flat substrate, and a peg was used to mark its center. Experimental blocks were positioned approximately 10 m apart, parallel to the coastline, at a depth of ~5 m.

The patches (treatment and control) were monitored for fish composition monthly, for the first 6 months starting from February 2022, expecting recruitment pulses and a stabilization of assemblage dynamics within that time. Monitoring in June 2022 was canceled due to adverse weather conditions. From August 2022 onward, patches were then monitored quarterly until May 2023 using an Underwater Visual Census (UVC) method adapted from Bohnsack & Bannerot (1986). In this approach, a diver swam around and above each patch for a maximum of two minutes, identifying and counting fish species foraging or sheltering in the patches. A trained researcher with over 10 years of experience in UVC and size estimation recorded the size of the recruits using a ruler for reference. For logistical reasons, a local collaborator conducted the field monitoring in April and July 2022 by recording two-minute Diver-Operated Videos (DOV) with a ruler as a scale bar to emulate the UVC method. This method has been extensively used and produces abundance counts similar to those of the UVC method (Wilson et al., 2018). Fish richness and abundance were unaffected by this difference (Fig. A1, Tables A1-A2).

Recruits, defined as recently settled individuals that have already transitioned to a demersal lifestyle (Jenkins et al., 2009; Keough & Downes, 1982), were identified based on coloration and the reported settlement size for the species or the closest taxa available up to subfamily. To avoid including older juveniles, any fish measuring more than 2 cm above the settlement size was excluded from the recruit category. Settlement size data was retrieved from the literature (Brothers et al. 1983; Leis 1984; Bellwood and Choat 1989; Wellington and Victor 1989; Chen 2002; Juncker et al. 2006; Leis et al. 2011; Leu et al. 2012, 2022; Grutter et al. 2017). This approach was considered conservative due to the rapid growth rates of recruits (Booth & Hixon, 1999; Leahy et al., 2015; Lou, 1993). All larger juveniles – i.e., beyond recruitment size - and adults were grouped into one category called "post-recruits" due to their similar mortality rates (Goatley & Bellwood, 2016) and habitat use (Kimirei et al., 2013) compared to recruits.

To compare temporal dynamics observed in the experimental patches and control zones to seasonal trends in the local ichthyofauna, we conducted quarterly surveys of fish assemblages in both the turf and the coral zones throughout the study. In each zone, three transect lines were randomly deployed 5 to 10 m apart, and fish were surveyed using a belt-transect UVC method (30 m x 2 m) to count and identify the recruits and post-recruits.

2.3.2.2 Habitat Assessment Scale

We scored patch structural conditions using a modified version of the Habitat Assessment Scale (HAS) from Gratwicke & Speight (2005) (Table A3). This method allows for assessing variables such as habitat rugosity, live coral cover, and the amount of refuge with minimum disturbance to the patches. Unlike Gratwicke & Speight (2005), we used "live coral cover" instead of "hard substratum", as the entire area is situated on hard substratum (refer to Table A3 for definitions). This approach enables the use of a single scale that integrates multiple variables.

2.3.2.3 Species traits

For our functional analyses, we selected two key traits: trophic group and mobility. A species' trophic group reflects their feeding habits, which influences the foraging grounds (Agudo-Adriani et al., 2019; Ferreira et al., 2015; Suzuki et al., 2018). Mobility mostly determines its level of association with the substrate. Sedentary species usually have small home ranges (< 5 m) and live in close association with the substrate, often with benthic organisms such as macroalgae, seagrass, sponges, or live corals (Waldner & Robertson, 1980; Wilson et al., 2008). Mobile species have a wider home range (up to 100 m), exploring a greater number of habitats without being restricted to a particular substrate type (Chapman & Kramer, 2000; Ferreira et al., 2015; Francini-Filho et al., 2010; Tebbett et al., 2025). Trophic and mobility traits were assigned at the species level and were not life-stage specific, as our goal was to examine potential trait-based selection when comparing the effects of live and dead colonies on recruit and post-recruit assemblages. This approach is correlative to recruitment ecology, as species traits could influence habitat selection by recruits (Booth & Wellington, 1998).

Trophic group traits were based on the definitions of Ferreira et al. (2004), with the addition of "cleaners" (for species whose diets are primarily from cleaning other organisms) and "corallivores" (for obligate coral feeders). Cleaners occupy a specialized niche, interacting with different fish species, often choosing coral heads as cleaning stations to maximize their access to clients (Grutter & Poulin, 1998). Corallivores differ from other sessile invertebrate feeders as they are generally associated with live corals, avoiding dead corals covered by algae (Brooker et al., 2016; Graham et al., 2009; Pratchett et al., 2006). In contrast, other sessile invertebrate feeders are often less specialized and feed on items available in wider substrate types (Ferreira et al., 2004). Trophic trait data were obtained from FishBase (Froese et al., 2014; last accessed December 2024) and other published fish guides (Allen et al., 2015; Lieske & Myers, 2001). Data were curated, and in cases where source information differed, we cross-referenced publications on the feeding biology of the species to ensure the accuracy of the data. Mobility traits were based on the definitions from Donati et al. (2019), which simply categorized species into high and low mobility. Low mobility includes sedentary and territorial species, which may exhibit significant vertical movement but have limited horizontal mobility. High mobility includes species with home ranges spanning tens of meters.

2.3.3 Data analysis

To test for differences in fish richness and total abundance between patches, we performed Kruskal-Wallis tests, followed by Dunn's tests. We then plotted smoothed conditional means which display the overall trend of the response variables, accounting for the variability between observations. Here we treat each patch monitored in a field survey as a sample – i.e., 12 samples per survey. To compare fish assemblages across treatments and controls, we first excluded all samples in which no fish were observed. We used Hellinger transformation to normalize the data and then computed two Bray-Curtis dissimilarity matrices, one for recruits and one for post-recruits. Then, two non-metric multi-dimensional scaling (nMDS) were produced to visualize the multivariate dispersion of recruit and post-recruit assemblages across treatments and controls. For the nMDS, we removed one sample out of 57 from recruit assemblages and three samples out of 83 in the post-recruit assemblages as these were outliers from the control area, with unusually high dissimilarity values that distorted the overall ordination (Fig. A2).

To test for multivariate differences in fish assemblage structure between blocks and patches, we further performed a stratified permutational analysis of variance (PERMANOVA) with 999 permutations based on the same similarity matrix. We stratified the permutations in the PERMANOVA by month to account for repeated measures, allowing permutations within months but not between months. The experimental treatments were used as the explanatory variables.

Significant differences between treatments were subsequently examined using pairwise comparisons. We could only run PERMANOVA for two out of five trophic groups in recruits and five out of nine groups in post-recruits, due to low abundances.

All data analyses were conducted using R software version 4.3.3 (R Core Team, 2024). The coin package version 1.4-3 (Hothorn et al., 2023) was utilized for the Kruskal-Wallis tests, and the FSA package version 0.9.6 (Ogle et al., 2025) for the Dunn's tests. We employed vegan version 2.6-2 (Oksanen et al., 2019) for data transformation, nMDS and PERMANOVA analyses, and used 'pairwiseAdonis2' for the pairwise PERMANOVAs (Martinez-Arbizu, 2020).

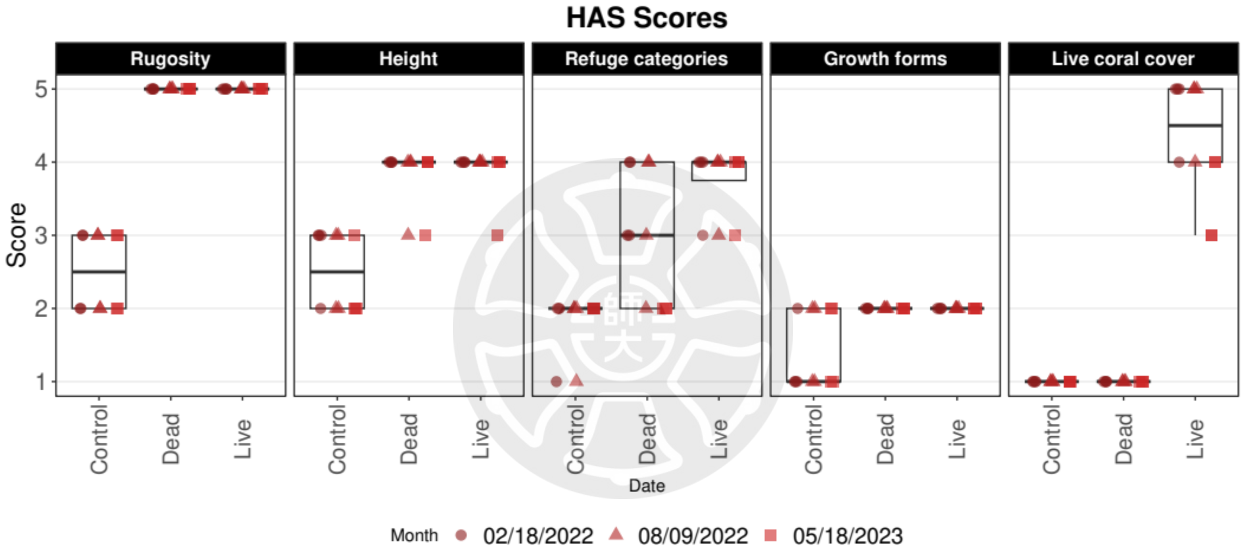

Figure 2.2: Habitat assessment scale (HAS) scores for the live and the dead coral patches and the control area at the initial (02/2022), mid (08/2022) and final (05/2023) months of the experiment. The scores follow Gratwicke & Speight (2005). See Table A3 for an explanation.

2.4 Results

HAS indicated that both live and dead coral treatments scored higher than the control areas (Fig. 2.2). Both treatment patches had similar values in most HAS variables; however, we observed some temporal variations, especially in the number of refuge size categories in dead coral patches, which decreased by half between the beginning and the end of the survey. Initially, both live and dead coral patches had refuges of 3-4 different sizes –very small, small, medium, and large refuges. Due to algal growth dead coral patches had only refuges of 2 different sizes –medium and large refuges – by the end of the experiment.

2.4.1 Effects of live and dead corals across life stages

Recruit and post-recruit assemblages varied seasonally (Fig. 2.3) following local dynamics (Fig. A3). There was a significant difference in the abundance and richness of recruits between coral patches and treatments ($p < 0.001$; Table A4), but not between live and dead coral treatments ($p > 0.05$; Tables A5 & A6; Fig. 2.3). The nMDS showed substantial overlap between recruit assemblages in live and dead coral patches (Fig. 2.4), while the PERMANOVA indicated marginal differences between these assemblages ($R^2 = 0.04$, $p < 0.05$; Tables A7 & A8).

The abundance and richness of post-recruit assemblages exhibited significant differences between live and dead treatments ($p < 0.001$; Tables A4-A6; Fig. 2.3). Results from PERMANOVA ($R^2 = 0.16$, $p < 0.01$; Tables A7 & A8) indicated significant differences in assemblage structure among live, dead, and control patches. Live coral patches differed from dead patches and control areas in greater magnitude (PERMANOVA, $R^2 = 0.14$ and 0.17, respectively), whereas weaker differences were observed between dead patches and control areas ($R^2 = 0.05$) (Fig. 2.4, Table A8).

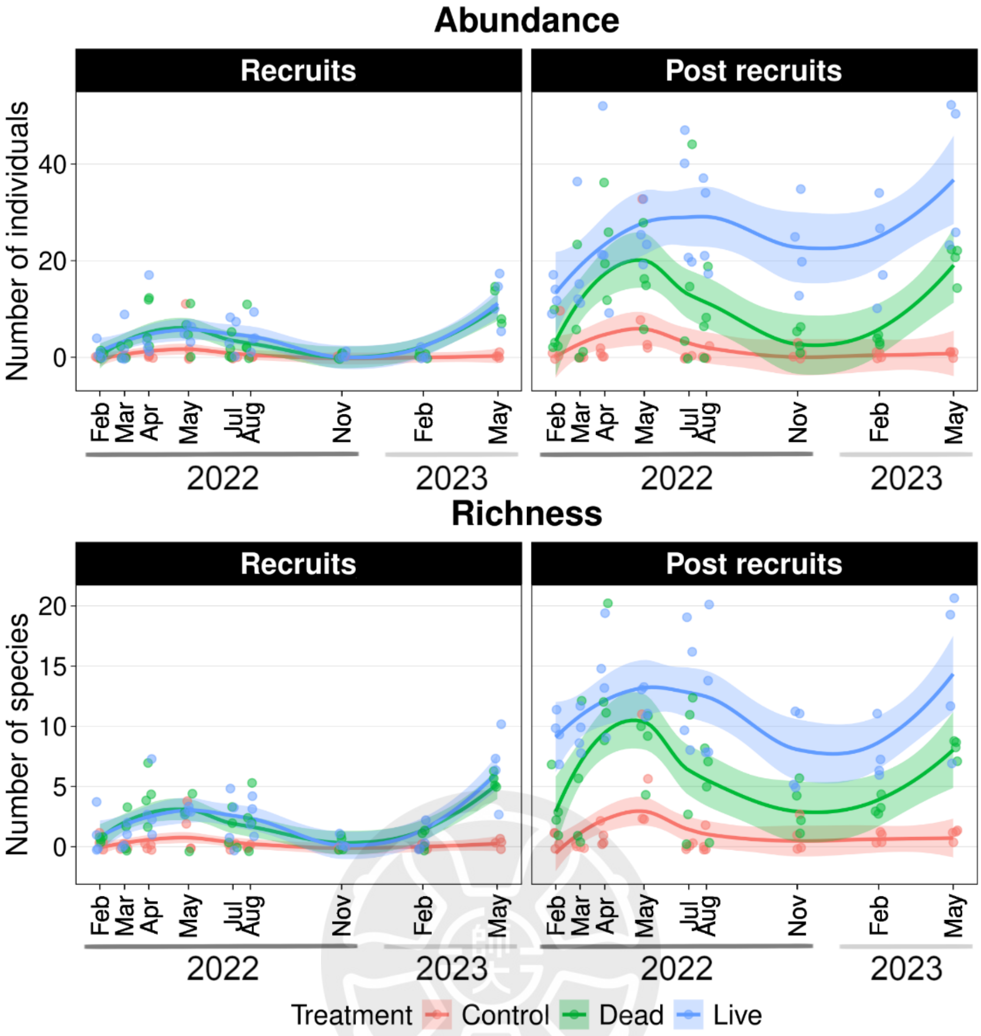

Figure 2.3: Abundance and species richness of recruit and post-recruit reef fish assemblages in live and dead coral patches and the control area over the one-year experimental period. Points represent individual samples, and the lines and shaded areas represent the smoothed conditional means with 95 % confidence intervals. Ticks at the x-axis are scaled by date.

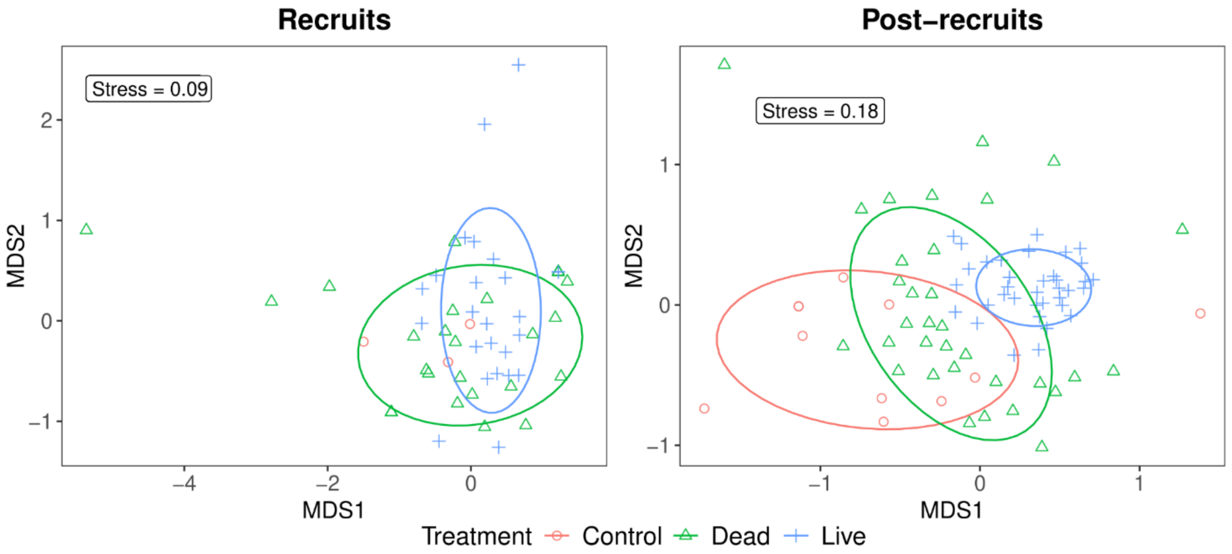

Figure 2.4: nMDS displaying the similarity of recruit and post-recruit reef fish assemblages in live and dead coral treatments and the control area, based on Bray-Curtis distance matrices from Hellinger-transformed data. Ellipses represent 69% confidence interval. Due to high collinearity between recruits' data points in the control area, the ellipse could not be calculated.

2.4.2 Influence of habitat on species traits

Throughout the experimental period, recruit assemblages in live and dead coral patches maintained a similar structure of low-mobility individuals and trophic groups (Figs. 2.5 & 2.6). The assemblage of high-mobility fishes exhibited weak but significant differences between live and dead coral treatments (PERMANOVA, $R^2 = 0.08$, $p < 0.01$, Tables A9 & A10). Mobile-invertebrate feeders and planktivores exhibited similar structure between live and dead coral treatments ($p > 0.05$, Tables A9 & A10) (Fig. 2.6). In general, recruitment densities per m^2 were higher in the experimental treatments than in the adjacent turf and coral zones (Fig. A3).

The variation in post-recruit assemblages between live and dead patches was mainly influenced by differences in species traits (Fig. 2.5 & 2.6). We observed significant differences between live, dead, and control patches across both mobility trait groups (PERMANOVA, $p < 0.01$). However, the coral patches had greater explanatory power in the low mobility group ($R^2 = 0.21$) compared to the high mobility group ($R^2 = 0.08$) (Tables A11 & A12).

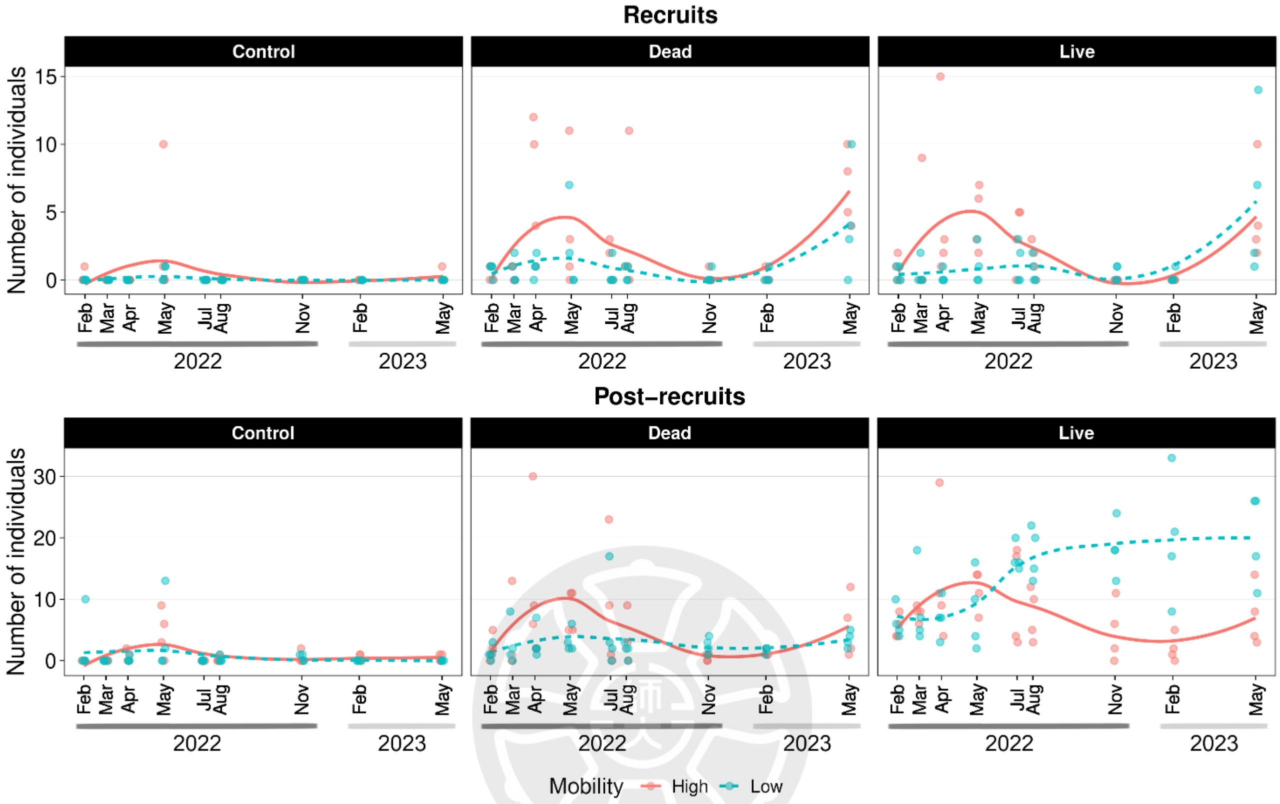

Figure 2.5: Mean abundance of recruits and post-recruits per month according to different mobility traits. Lines indicate conditional means, and dots indicate individual samples.

Low-mobility species dominated live corals, whereas dead corals were mainly dominated by high-mobility taxa (Fig. 2.5), which were primarily composed of mobile-invertebrate feeders (Fig. 2.6). Initially, the live coral patches were dominated by mobile invertebrate feeders and other highly mobile species but gradually shifted to a dominance of low mobility planktivore assemblages. Furthermore, the live coral patches exhibited higher abundances of carnivores and omnivores compared to dead coral patches. Four out of the five most abundant trophic groups exhibited significant differences between patches (PERMANOVA, $p < 0.01$, Table A11). With strong effects of live and dead coral treatments in planktivores and omnivores (R^2 = 0.47 and 0.31, respectively) and weaker effects on carnivores and mobile invertebrate feeders (R^2 = 0.08 and 0.05, respectively) (Table A13). The differences between control areas and dead patches were not significant for planktivore and carnivore species (PERMANOVA, $p > 0.05$) (Table A13).

2.5 Discussion

Recruit assemblages responded similarly to live and dead coral patches, both showing greater abundance and richness than the control areas. These assemblages were dominated by just two trophic groups and exhibited similar species composition between patches, highlighting the role of habitat complexity and underscoring the potential of dead corals as temporary shelters in degraded habitats. On the other hand, post-recruits displayed stronger habitat-specific responses. Live coral patches supported higher abundance, species richness and functional diversity, indicating that mature individuals benefit from the structural stability and increased resources provided by live corals.

Spatial distribution patterns of recruits are strongly influenced by the availability of shelter, primarily due to predation risk (Almany, 2004b; Steele, 1999). In our control areas, low complexity substrate offers little protection, leading to lower recruit abundance and richness (Booth & Beretta, 1994; Félix-Hackradt, 2013). In contrast, both live and dead coral patches support similar recruit assemblages, despite the higher carnivore densities in live coral patches. This suggests that shelter is the primary factor influencing recruit habitat choice in our coral patches, regardless of predator presence – a pattern consistent with previous observations (Almany 2004a). The relatively high complexity and structural protection possibly reduced young fish mortality (Almany, 2004b; Cabaitan et al., 2008; Cheminée et al., 2016), contributing to increased fish biomass (Beese et al., 2023). This highlights the potential role of live and dead coral patches in the recovery of reef fish assemblages.

The similarity between recruit assemblages in live and dead coral patches was primarily driven by the dominance of highly mobile invertebrate feeders. These fishes typically utilize several reef habitats for foraging and shelter (Lecchini & Galzin, 2005), including both live and dead corals (Almany, 2004a; Ferreira et al., 2015; Giffin et al., 2019; Johansson et al., 2012). While live corals support abundant associated fauna (Patton, 1994; van der Schoot & Hoeksema, 2024), dead corals also retain ecological importance, sustaining diverse assemblages of small invertebrates even after coral death (Head et al., 2015). This makes both habitats viable foraging grounds for mobile-invertebrate feeders (Bellwood, 1988; Chen, 2002; Choat, 1991; Kimirei et al., 2013; Lecchini & Galzin, 2005). Thus, for highly mobile species, dead corals could represent an important alternative to live corals (Giffin et al., 2019; Suzuki et al., 2018), especially in degraded areas where competition with territorial coral-dwellers could have detrimental effects (see Ben-Tzvi et al., 2009; Coppock et al., 2016; Jones, 1988).

The added habitat complexity created by dead and live corals in a mostly flat environment helps reduce competition, predation risks, and the impact of environmental stressors (Almany, 2004b). These benefits attracted post-recruit migrants from the surrounding reef in an aggregation effect (see Acosta & Robertson, 2002; Schroeder, 1987), leading to a higher fish density compared to the turf and coral zones, which feature a patchy distribution of complex and flat areas. This aggregation effect is more pronounced in live coral patches, which supported greater abundance, species richness, and number of trophic groups. This likely reflects the greater stability and persistence of live coral structures (Cheung et al., 2021; Darling et al., 2017), which contribute to sustained community richness over time.

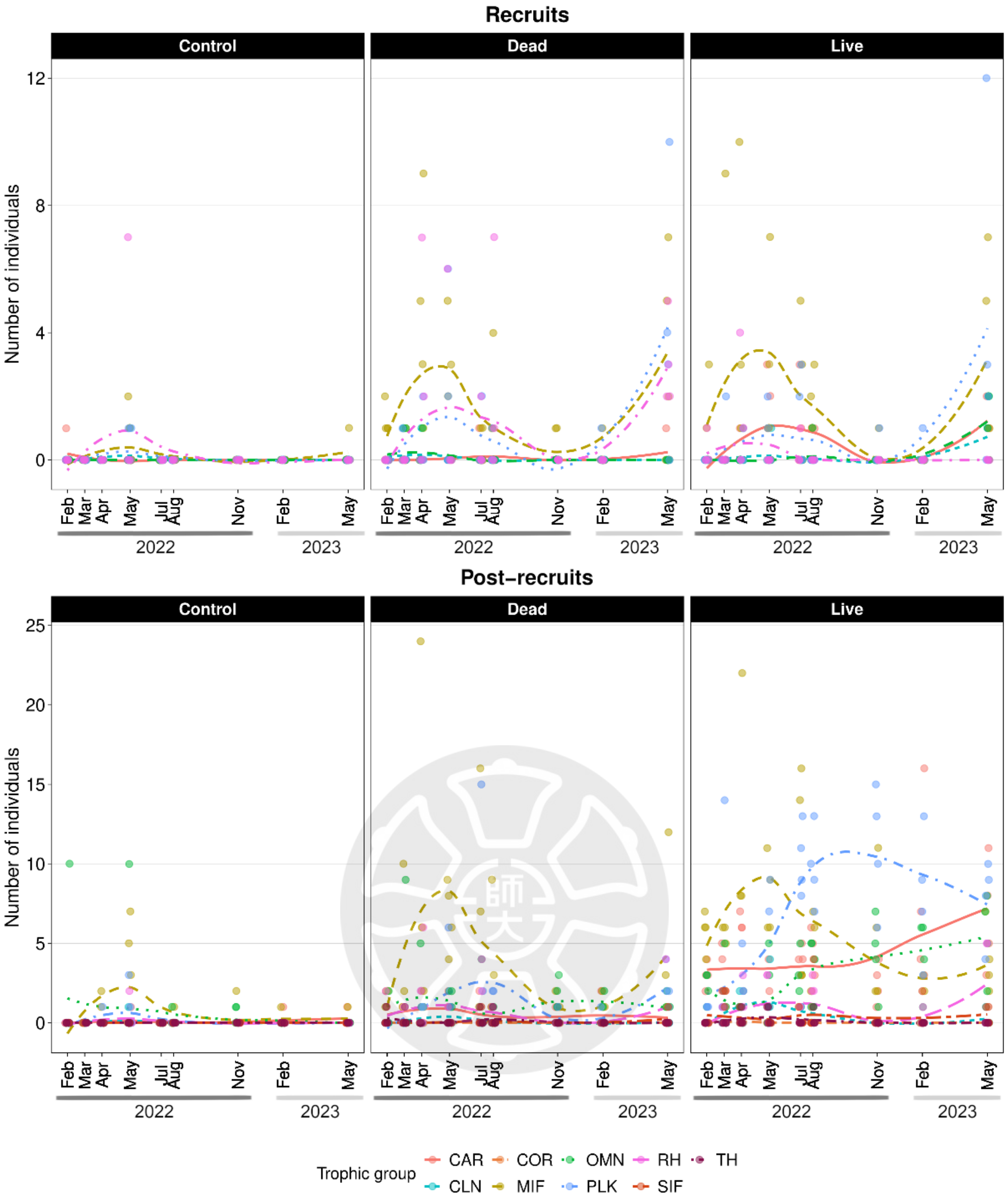

Figure 2.6: Mean abundance of recruits and post-recruits per month according to different trophic groups in the live and dead coral patches. Lines indicate conditional means, and dots indicate individual samples. Abbreviations: CAR = Carnivores, COR = Corallivores, CLN = Cleaners, MIF = Mobile-invertebrate feeders, OMN = Omnivores, PLK = Planktivores, RH = Roving herbivores, SIF = Sessile-invertebrate feeders, TH = Territorial herbivores.

Beyond structural benefits, live corals provide energetic and ecological resources, attracting both directly and indirectly associated species (Coker et al., 2013; Komyakova, 2018; Quimbayo et al., 2019; Yap et al., 1994). This includes mobile species with large home-ranges, like mobile-invertebrate feeders, which initially dominated live coral patches due to their mobile capacity and attraction towards coral-associated invertebrates (Chapman & Kramer, 2000; Ferreira et al., 2015; Suzuki et al., 2018). However, these patches gradually shifted to a planktivore-dominated assemblage, characterized by larger groups of low-mobility species (Floeter et al., 2006; Holbrook et al., 2000; Russ et al., 2020). These sedentary groups benefit from structural stability and are often found in association with live corals (Booth & Beretta, 2002; Cabaitan et al., 2008; Coker et al., 2012; Komyakova et al., 2013). In turn, this resource-rich environment attracted carnivores and omnivores that forage on the associated fauna and surrounding substrate (Kramer et al., 2015; Osuka et al., 2022; Stier & Leray, 2014). Hence, while relatively few reef fish species are strongly associated with corals (Siqueira et al., 2023), live corals attract a diverse array of species with varied traits, supporting higher functional diversity than dead corals or turf substrates (see Coker et al., 2013; Mouillot et al., 2014; Munday, 2004; Pratchett et al., 2011; Wilson et al., 2008).

The similar spatial and temporal trends observed in recruits and post-recruits of highly mobile species suggest that ontogenetic shifts in habitat use may be rare within this group, contrasting with previous findings (Giffin et al., 2019). Conversely, sedentary and planktivorous species exhibited shifts toward more specialized habitat use in post-recruit stages. These transitions might reflect changes from generalist recruits to specialized adults (Feary et al., 2007; Lirman, 1994) or the opposite (Booth & Beretta, 1994; Komyakova et al., 2019). The varying patterns in ontogenetic shifts across species and trophic groups highlight an important gap in our understanding of life-stage-specific habitat use. Particularly, more research is needed on the functional traits of early life stages, as most trait-based studies still focus primarily on adults.

While our study was limited to 1 m^2 patches composed of two *Pocillopora* spp. in a degraded reef zone, the findings provide valuable insights into habitat function across fish life stages. Despite spatial and compositional constraints, our design offers a controlled foundation for future research into habitat-specific recruitment at broader scales. For instance, fast-growing branching corals, such as *Pocillopora* sp., are linked to rapid coral cover recovery in the Indo-Pacific (Gilmour et al., 2013; Mulla et al., 2024). As shown here, even small patches of these corals support diverse fish assemblages spanning multiple trophic groups. Future studies should further explore how coral diversity, species identity, and patch size interact to shape recruit and post-recruit assemblages under varying reef conditions.

2.6 Conclusion

Our findings indicate that dead branching coral patches are not “graveyards”; rather, their retained complexity may serve as transitional shelters, helping to buffer the negative impacts of coral mortality on fish assemblages (Emslie et al., 2014; Morais et al., 2022). However, live corals remain irreplaceable for supporting functionally diverse assemblages across multiple trophic levels, a crucial component of ecosystem health (Graham et al., 2011; MacNeil et al., 2015). The patchy habitat configurations used here - often employed in restoration projects - could be important attractors for recruits and post-recruits supporting diverse functional traits, which ensures a link between bottom-up and top-down processes (Beese et al., 2023). Paired with fisheries management and coastal development controls, such habitat structures may foster positive recovery feedback. Future studies at larger spatial and temporal scales could build on these findings to clarify how fish from different life stages and functional groups respond to live, dead, and even coral rubble habitats, a commonly overlooked substrate. Integrating habitat-specific strategies - safeguarding live corals for their high productivity and functional importance, while also protecting dead corals from further fragmentation - could meaningfully enhance the resilience of coral reef fish assemblages in degraded ecosystems.

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Chapter 3

Environmental and acoustic drivers of fish recruitment along degraded coral reefs

3.1 Abstract

The global degradation of coral reefs threatens the persistence of fish assemblages, and protection-based management strategies alone may be insufficient to support their recovery. A key shortfall lies in the limited understanding of how habitat conditions shape fish recruitment along degraded reefs. In this study, we investigated how substrate composition, substrate rugosity, adult fish assemblages, and underwater soundscapes influence recruit abundance and richness. We found that rugosity was a consistent positive predictor of recruitment across degradation gradients. In contrast, benthic dominance by turf algae or soft corals was negatively associated with recruitment. While no clear relationships were found between adult and recruit assemblages, louder nighttime fish choruses—indicative of a healthy reef environment—were positively associated with recruit richness in less degraded reefs. These findings underscore the need to move beyond protection alone and adopt multidimensional approaches that account for both habitat structure and ecological signaling in degraded reef ecosystems.

3.2 Introduction

Coral reef fishes are increasingly threatened by environmental degradation driven by both natural and anthropogenic processes, resulting in significant habitat loss (Wilson et al. 2006; De'ath et al. 2012). These losses can reduce structural complexity (Alvarez-Filip et al. 2009) and alter benthic conditions (see Crisp et al. 2022 for a review), which in turn negatively affect the diversity and structure of reef fish assemblages (Pratchett et al. 2011; Brandl et al. 2020; Morais et al. 2020). A key consequence of these ecological changes is the disruption of recruitment dynamics, which are central to the recovery of fish assemblages from disturbances.

Fish recruitment refers to the process by which larval fish transition from the pelagic environment to benthic habitats, where they settle and begin juvenile development (Sponaugle 2015). Prior to settlement, larvae rely on a combination of visual, chemical, and auditory cues to locate suitable habitats (Lecchini et al. 2005, 2013; Wright et al. 2010; Igulu et al. 2011; Sponaugle 2015). Several key factors influence habitat selection, including hard coral cover (Coker et al. 2012; Lecchini et al. 2013), topographic complexity (Johnson 2007), the presence of conspecifics (Lecchini et al. 2007), and more recently described, reef soundscape (Mann et al. 2007; Parmentier et al. 2015). Settlers often respond to more than one cue simultaneously, for instance, high complexity and live coral cover have a stronger effect together (Cabaitan et al. 2008; Coker et al. 2012). Complex and healthy reefs also exhibit more evident acoustic cues (Lamont et al. 2022), mediating larvae orientation in conjunction with visual cues (Lecchini et al. 2005). Additionally, the presence of conspecifics might serve as a positive cue for suitable habitat or group protection (Hsiao et al. 2003; Lecchini et al. 2007; Wormald et al. 2013; Coppock et al. 2016). But the presence of adults also increases competition and predation (Almany 2004a; Ben-Tzvi et al. 2009).

Despite growing knowledge of the factors influencing fish recruitment, how these processes operate along a gradient of degraded reef environments remains poorly understood. Degraded reefs often lack the structural features and sensory cues that facilitate larval settlement, potentially impeding population replenishment (Grorud-Colvert and Sponaugle 2008; Sponaugle et al. 2012; Lecchini et al. 2013; Gordon et al. 2018). This gap is particularly concerning given that many conservation strategies specifically aim at restricting extractive activities, such as fishing (Bruno et al., 2019), overlooking the environmental attributes necessary for recruitment, which has been shown to enhance population recovery within Marine Protected Areas (Wen et al. 2013). Therefore, understanding the drivers of recruitment under degraded conditions is crucial for improving the effectiveness of conservation efforts.

In this study, we compared 17 reef sites with varying levels of habitat degradation to identify the local ecological factors associated with higher abundance and richness of fish recruits. Specifically, we focused on the influence of adult fish assemblages, substrate composition, and the reef soundscape to determine which habitat characteristics are most strongly linked to recruitment success and overall recovery potential.

3.3 Material and methods

3.3.1 Study sites and data collection

We collected data from two islands: Lyudao and Xiaoliuqiu. Lyudao is a volcanic island of approximately 12 km² located 33 km off Taiwan's southeast coast, influenced by the oligotrophic waters in the Kuroshio current (Tseng et al. 2012; Yen et al. 2022). It has rich coral reefs with an average of 40% hard coral cover (Ribas-Deulofeu et al. 2016). The island's economy is primarily based on tourism, and nearshore fishing activities are discouraged by the local government, although only two no-take zones exist along its coastline (Caicedo 2024). In contrast, Xiaoliuqiu is a 7 km² coral reef island located 13 km off the southwest coast of Taiwan which used to hold rich coral reefs in the past (see Yang *et al.* 2017). Currently, most reefs in Xiaoliuqiu are in relatively poor condition (5-20% live coral cover) (Yang et al. 2017) due to overfishing, tourism, and eutrophication (Dai et al. 2009). This motivated the establishment of a Marine Protected Area (MPA) along the island's coastline where fishing lines are the only gear permitted. The proximity to the main island puts Xiaoliuqiu under the influence of freshwater discharges and a larger human presence and tourist visitation rates subject this island to stronger anthropogenic pressures. Both islands are frequently impacted by typhoons, which can lead to major coral mortality (Chang et al. 2018).

We selected nine sites in Lyudao and eight sites in Xiaoliuqiu for data collection (Fig. 3.1). Except for the soundscape data, all other data were collected along the same transects at each site in May and June 2022 in Lyudao and in August 2022 in Xiaoliuqiu. At each site, four 20 m transects were placed randomly, following the reef's crest and parallel to the shore. The average working depth of the study sites was 8.2±2.7 m in Lyudao and 9.6±3.2 m in Xiaoliuqiu. The average depth difference between transects within each site was 2.9±1.6 m. A 5-minute waiting period between laying the transect lines and starting the census was strictly followed, to allow shy species to resume their swimming along the transects. A team of four divers conducted the entire data collection procedure. To minimize the influence of other divers on shy species, first, adult fish were recorded on video along four 20 m x 2 m belt transects using a GoPro HERO 9 in Water mode at 120 fps, 2.7K and 4:3 aspect ratio, with a narrow (27mm) lens mode (GoPro, Inc., San Mateo, CA, USA). The diver held the camera on a hand stick, swimming at constant speed of approximately 1 m/s and maintaining 1 m distance from the substrate, aligning the transect line at the center of the video. The transect width was determined using 1-m rulers on each side of the transect. The second diver focused solely on identifying and counting fish recruits (see details below) using Underwater Visual Census (UVC) (Bohnsack & Bannerot 1986) along four 20 m x 4 m belt transects. To adapt this method for small and reclusive recruits, the diver moved slowly along the line, swimming up to 2 m to each side, checking within holes or corals when needed to record the recruits hiding along the substrate. The diver used a foldable ruler (1 m long with 20 cm segments) as a reference to estimate the total length of recruits in cm, by carefully approaching the ruler as close as possible without startling the recruits.

Following the fish census, benthos cover was measured using the point intercept method, with 50 points marked at 40 cm intervals on transects. We took one photograph of the benthos under each point at approximately 20 cm of the substrate with an Olympus Tough TG-6 (Olympus Corporation, Tokyo, Japan). Lastly, substrate complexity and depth were measured using a HOBO depth logger (Onset Computer Corporation, Bourne, MA, USA), which recorded water pressure every second as the diver moved along the transects following the depth profile (Dustan et al. 2013). Soundscape data was collected with AUSOMS-mini (AquaSound Inc., Kobe, Japan; more information is available in Lin et al. 2021) set on the survey sites for 24 h. Due to the limitation of a single underwater recorder, we collected soundscape data on 13 of the 17 survey sites. These limitations were counteracted during the model-building process by determining sites as random factors (see section 3.3.3). Furthermore, additional recordings done in Chaikou and Shilan indicate that, within the same season, the 24-hour spectrograms show very similar patterns across years. Details of soundscape data collection are provided in Table B1.

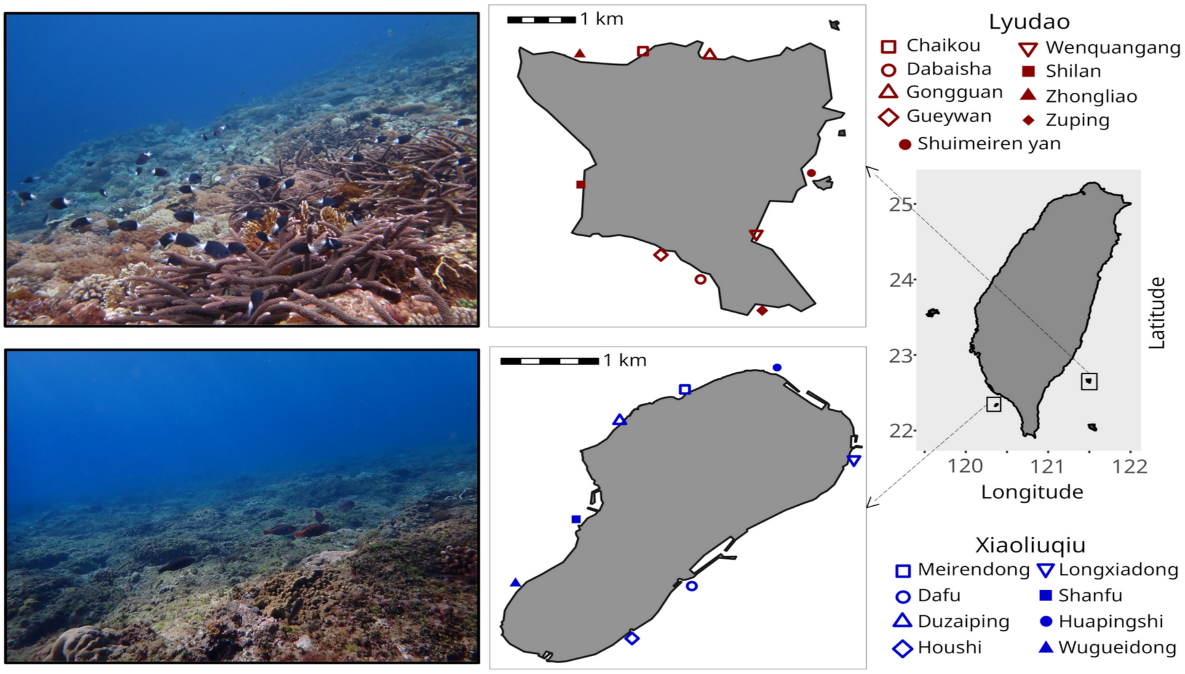

Figure 3.1: Maps of the study sites. Geographic location of Lyudao and Xiaoliuqiu relative to Taiwan, the location of the survey sites, and examples of reef conditions within each island (left panel photographs)

3.3.2 Data processing

Fish counts from the UVC data were further refined to exclude dubious observations and non-recruit juveniles. Recruits were defined as young-of-the-year individuals that have recently transitioned from a pelagic to a demersal lifestyle and are detectable by observers (Keough and Downes 1982; Jenkins et al. 2009). They are typically not much larger than the average settlement size for species and are more reclusive than experienced juveniles, who are larger and bolder. Individuals exceeding 2 cm above the settlement size were not classified as recruits to exclude non-recruit juveniles from the analyses. This conservative approach reflects the rapid growth rates of recruits (Lou 1993; Booth and Hixon 1999; Leahy et al. 2015). Average settlement sizes were obtained from previous publications (Brothers et al. 1983; Leis 1984; Bellwood and Choat 1989;

Wellington and Victor 1989; Chen 2002; Juncker et al. 2006; Leis et al. 2011; Leu et al. 2012, 2022; Grutter et al. 2017), and when species-specific data were lacking, the average size of species in the same genus was used.

Video data for adult fish richness and abundance were processed using Kdenlive™ (KDE e.V., Berlin, Germany) video editing tool to mark the 2 m width of the transect while the video was playing. All individuals in the video were identified to species level, except for nine unknown individuals that were not used in the analysis. Photographs from the point intercept method for benthos cover estimate were analyzed individually, and recorded benthos were classified into the following functional groups according to English et al. (1997): turf algae, macroalgae, soft corals, encrusting corals, massive corals, branching corals, foliose corals, table corals, and other benthos, in addition to bare rock and sand. The final dataset included the percentage cover of each functional group per transect. Substrate complexity per transect was calculated following Ribas-Deulofeu et al. 2021, which returns a rugosity index that simultaneously considers both fine (10-20 cm) and coarse scale (several meters). The average depth per transect was calculated based on the water pressure records from the depth logger.

Sound recordings were processed using soundscape_IR (Sun et al. 2022). First, we followed Lin et al. (2021) to visualize the spectral and temporal variations of underwater soundscapes using the technique of long-term spectrogram, which calculates median power spectral densities from each 1-min interval. Recording periods influenced by boat or scuba diving noise were identified and removed. After that, we extracted sound pressure levels (SPLs) from two frequency bands. The first frequency band is between 200 and 1500 Hz, corresponding to the band of fish choruses, and the second frequency band is between 2000 and 20,000 Hz, corresponding to the band in which crustacean snaps are detected (Lin et al. 2023). Given that soundscapes often vary across sites (Lin et al. 2021), we calculated signal-to-noise ratios (SNRs) by subtracting SPLs from the nighttime period (6 PM to 6 AM) - when most reef fish species settle - to the median SPLs during the day. Through this, we could clearly identify the louder sites at night and avoid bias due to site-specific soundscapes. Finally, we averaged the nighttime SNRs per site for each frequency band.

3.3.3 Statistical analyses

All statistical analyses were done using R software v. 4.3.3 (R Core Team 2024). We plotted a correlation matrix based on the Pearson correlation coefficient (Fig. B1 and B2) to observe the correlation between all response and explanatory variables and explore possible collinearities. We excluded the total hard coral cover from the model due to its high collinearity with coral cover in each functional group. Sand and rock were excluded from the analysis, as well as variables with very low percentages (e.g., other invertebrates and table corals). To account for the possible influence of depth on recruitment, we included the average depth per transect in the analyses. We then ran a Principal Component Analysis (PCA) for environmental variables to observe the differences between the two islands, using the package *FactoMineR* v. 2.11 (Husson et al. 2006). To better visualize the distinctions between islands, we plotted a histogram with the PC1 loadings of each island. To compare the differences in recruit assemblages between islands, we run a Non-metric Multidimensional Scaling (NMDS) using raw abundance count data. For that, we used the package *vegan* v. 2.6-8 (Oksanen et al. 2019) based on a Bray-Curtis distance matrix from raw abundance count data.

Environmental variables comprise transect-level predictors, i.e., depth, substrate rugosity, and substrate cover. Acoustic variables comprise site-level data with different dimensions from the other explanatory data. Due to this limitation, we treated soundscape data as a separated category and ran separate models to account for the particularities in the data structure. We used Random Forest (RF) to identify the best-fitted models for explanatory variables using the *randomForest* package v. 4.7-1.2 (Breiman 2001). Four separate models were built to estimate the influence of explanatory variables on recruit abundance and richness. In the first two models, we examined nine environmental variables (excluding acoustic variables) and their relationship to recruit abundance (Fig. B3) and richness (Fig. B4). In the next two models, we included acoustic variables along with the nine environmental variables (Fig. B5 and B6), excluding sites without soundscape data. We conducted 500 regression tree analyses for each model, testing three variables at each split. We then evaluated the combined contribution of the most important variables, selecting those that accounted for at least 75% of the variance in the response.

Following RF, we examined the relationship between the environmental variables selected by the RF models (Fig. B3-B6) and recruit abundance and richness using mixed-effect models (MEMs), which account for both fixed and random effects, modelling the variability among groups with hierarchical structures. This approach allowed us to use transect (replicates) and SNRs (repeated measures) from a hierarchical data structure (e.g., replicates:sites:islands) while maintaining a consistent analysis. Since our response variables were continuous and normally distributed, we used linear MEMs calculated with the package *lmerTest* v. 3.1-3 (Kuznetsova et al. 2017). For recruit richness and abundance, we ran two MEMs with the most important variables from RF model 1 (six variables in Fig. B3) and RF model 2 (six variables in Fig. B4) as fixed effects and sites as random effects. We also ran two MEMs including acoustic variables, from RF model 3 (seven variables in Fig. B5) and RF model 4 (seven variables in Fig. B6). To account for the effects of different islands, we included interactions between the variables and the islands. We tested multiple models with different combinations of factor-island interaction terms and selected the one with the lowest Akaike Information Criteria (AIC) as the final model. Summaries of the tested models can be found in Tables B2-B5, and the results of the MEMs are in Tables B6-B9. From the final MEMs, we extracted predicted values of recruit abundance and richness based on the fixed effects included in the model. These values were used to evaluate and visualize how changes in environmental or acoustic predictors influence the response variable, controlling for variability among sites.

3.4 Results

3.4.1 Characteristics of the study islands

There was a strong positive correlation between the abundance and the richness of reef fish recruits in both islands, with Lyudao showing greater variability (Fig. 3.2a). While recruit assemblages in both islands showed high compositional overlap (Fig. 3.2b), the PCA revealed clear environmental and ecological differences between islands (Fig 3.2c-d). The differences between islands were explained by several variables associated with the substrate, including the cover of branching, massive, and soft corals with high positive PC1 loadings (> 0.3), and turf cover with a strong negative loading (-0.56). On the other hand, rugosity, adult abundance and foliose coral cover were less relevant to the differences between islands but contributed strongly to PC2, which explained 19% of the variation between samples, indicating differences within islands. Adult richness and depth were similarly relevant for both axes.

3.4.2 Influence of local variables

Excluding acoustic variables, the RF models selected the rugosity index (hereafter referred to as rugosity), turf algae cover, soft coral cover, branching coral cover, and depth. These variables can explain approximately 26% of the variation in recruit abundance and 19% of the variance in recruit richness (Figs. B3 and B4). In addition, adult abundance was selected for recruit abundance and massive coral cover was selected for recruit richness (Figs. B3 and B4). The MEMs based on these selected variables show wide differences in the relationship between recruit assemblages and the environmental factors (Tables B6 – B9). In Fig. 3.3, we present the MEMs results from the factors with the strongest effects on recruit assemblages according to the MEMs estimate values (refer to Tables B7-B9 for estimate values). The results from environmental variables only display a positive relationship of rugosity with recruit abundance ($p < 0.01$, Table B7, Fig. 3.3) and a marginally positive relationship with recruit richness ($p = 0.07$, Table B9, Fig. 3.3). Soft coral cover, mostly from Lyudao, had a negative relationship with recruit richness ($p < 0.05$, Table B9, Fig. 3.3). In contrast, turf algae cover showed an island-specific non-linear pattern with recruit abundance (Table B7, Fig. 3.3): positive in Lyudao and negative in Xiaoliuqiu ($p < 0.05$). Adult abundance showed a weak but significant association with recruit abundance ($p < 0.05$, Table B7, Fig. B7). Depth showed no significant effects ($p > 0.05$, Fig. B7).

Considering acoustic variables, RF models place both fish choruses and crustacean snap sounds among the most influential variables (Fig. B5 and B6). Subsequent MEMs indicate that fish choruses had significant effects on recruit richness ($p < 0.05$, Table B9) and marginal effects on the abundance ($p = 0.07$, Table B7). These relationships were positive in Lyudao but weaker in Xiaoliuqiu (Fig. 3.4). At the same time, crustacean snaps had weak relationships to the abundance and richness alike (Fig. 3.4, Table B7 and B9).

3.5 Discussion

In this study, we examined 17 sites across two islands, representing a gradient of reef degradation. By integrating environmental, acoustic, and adult assemblage variables, we conducted a comprehensive analysis of the factors influencing reef fish recruitment. Our results showed that rugosity was positively associated with recruitment across both islands, while sites dominated by turf algae or soft corals tended to support lower recruitment rates. Incorporating soundscape data further revealed that nighttime fish choruses were positively linked to recruit richness, indicating a potential role for acoustic cues in enhancing recruitment. However, this effect was limited to the healthier reefs of Lyudao, suggesting that spatial patterns of recruitment are shaped by a combination of habitat features and ecological context.

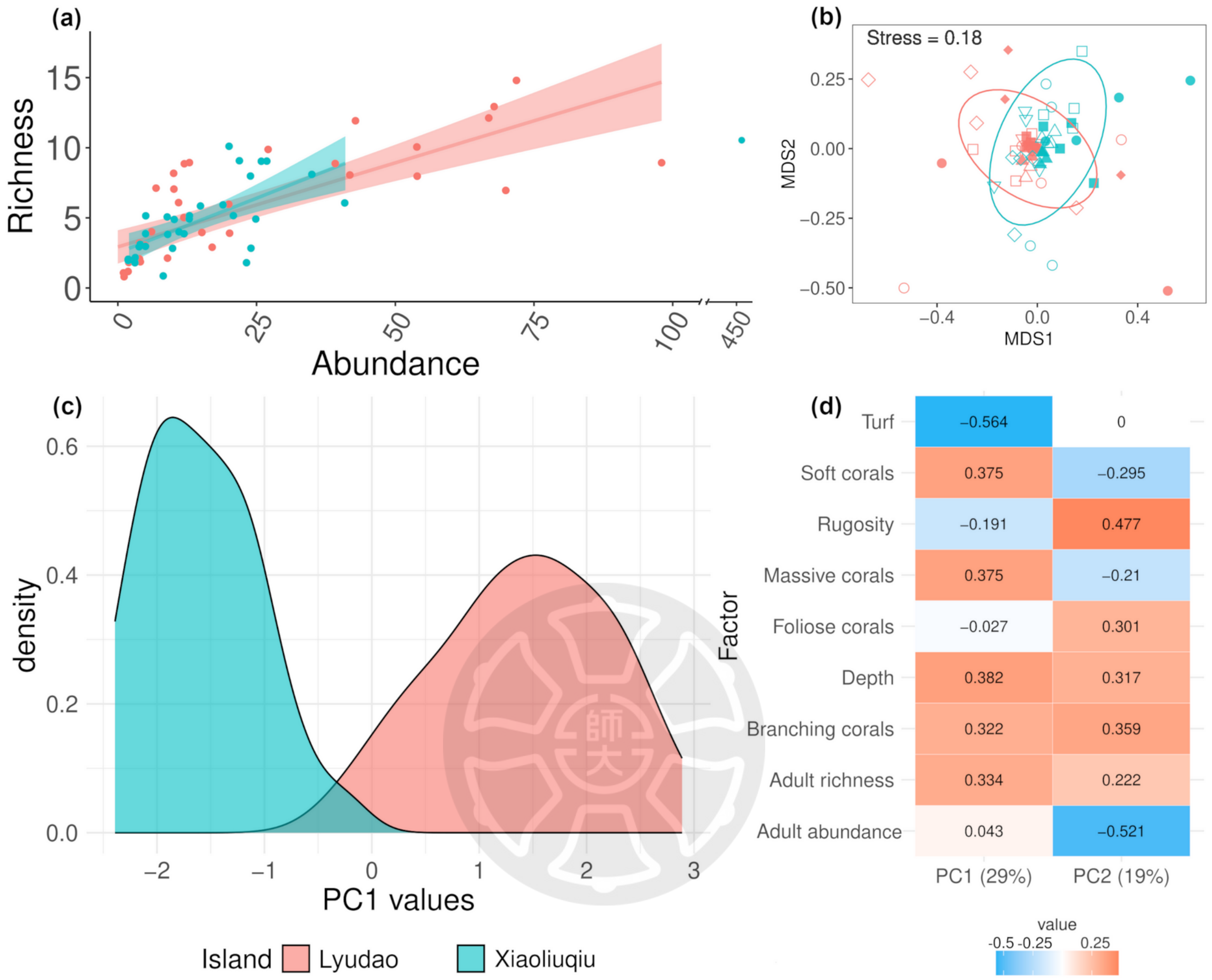

Figure 3.2: Comparative summary of the habitat conditions on each island. (a): Relationship between the richness and abundance of recruits in both islands, each point represents a transect. (b): NMDS comparing the recruit assemblages in both islands each point represents a transect. Ellipses indicate 95% confidence level. (c): Density plots of the PC1 loadings from the environmental and ecological variables used in the study. (d): PC1 and PC2 loadings of each environmental variable in the study.

3.5.1 Environmental factors

The effects of rugosity were consistently positive, enhancing recruitment rates across the degradation gradient. These findings align with previous studies on adult fish assemblages, which highlight the importance of structural complexity (Connell and Jones 1991; Almany 2004a; Graham and Nash 2013). In healthy coral reefs, rugosity is strongly associated with hard coral cover (Coker et al. 2012; Darling et al. 2017; Agudo-Adriani et al. 2019). However, structural complexity may persist through underlying substrate topography or remnants of dead corals (Emslie et al. 2014; Morais et al. 2022; Engleman et al. 2023), playing a crucial role in degraded reefs. In our study sites, rugosity was more influential than depth. Although depth effects on recruitment have been reported over broader gradients (>10 m) within reefs (Gutiérrez 1998; Leis and Carson-Ewart 2002; Smallhorn-West et al. 2017), depth variation in our sites was typically 5 m or less. At such shallow ranges, depth likely plays a lesser role than substrate composition, which is known to strongly influence settlement and recruitment (Booth and Beretta 1994; Cheminée et al. 2016; Coker et al. 2012; Leis and Mccormick 2002). Here, high rugosity benefits recruits independently of depth by providing shelter from predators (Almany 2004b), thereby supporting the potential for ecological recovery of degraded reefs.

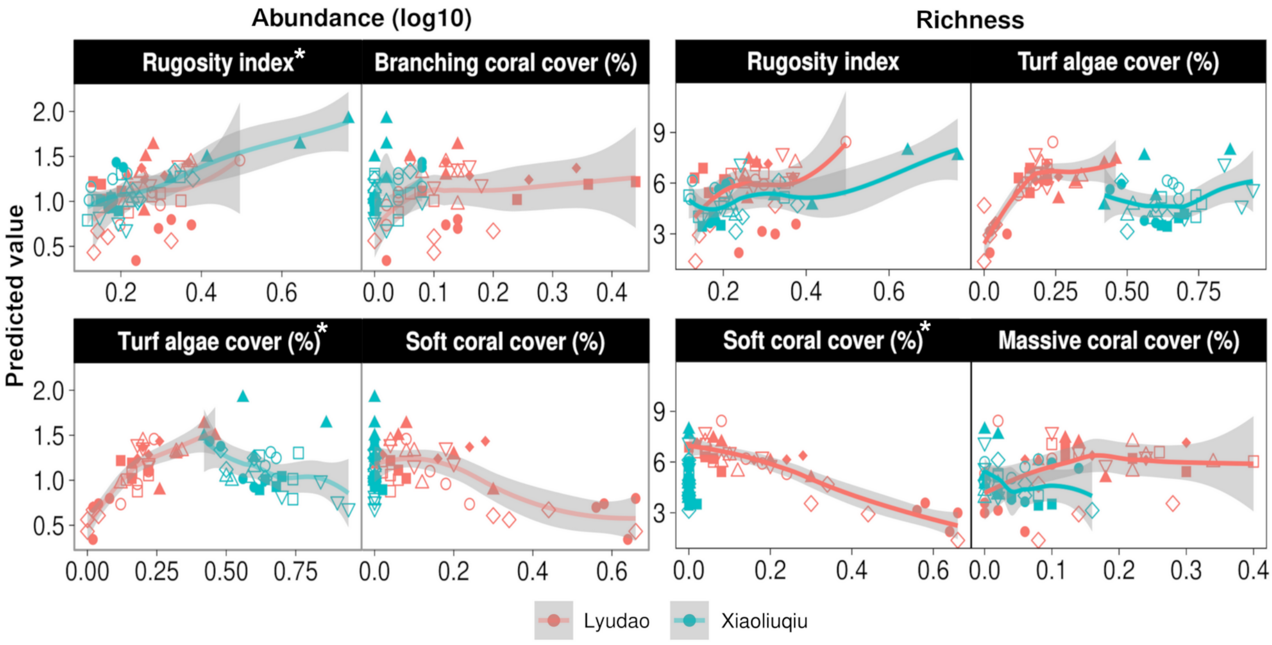

Figure 3.3: Relationship between environmental drivers and recruit assemblages. Plots showing the effect of four environmental factors with the strongest effects on the abundance and richness of recruits according to MEM estimates. Asterisks indicate that the factor was significant ($p < 0.05$) in the model. Dots represent data from individual transects. Lines indicate conditional means, and shaded areas indicate the 95% confidence intervals. Predicted values represent the expected response or recruit abundance and richness, given the observed environmental and acoustic conditions.

While hard coral cover is generally associated with higher recruitment rates (Bonin et al. 2009; Lecchini et al. 2013), the influence of other benthos remains less clear (Feary et al. 2007; Coker et al. 2012; Cheminée et al. 2016). To date, most studies on benthic phase shifts have focused on transitions from hard coral benthos to algal dominance (Hughes 1994; Kuo et al. 2012; Ainsworth and Mumby 2015; Bruno et al. 2019). However, recent studies have raised concerns about the increasing prevalence of fast-growing soft corals in oligotrophic waters (Cruz et al. 2015; Mezger et al. 2022; Tkachenko et al. 2022), especially in the Indo-Pacific (Mezger et al. 2022;

Reverter et al. 2022). Although soft corals are generally reported to have weak or neutral influences on fish assemblages (Syms & Jones 2001; Epstein & Kingsford 2019; Moynihan et al. 2022), our results suggest that the pulsating *Xenia* sp. found in Lyudao may negatively affect recruitment rates. Unlike rigid soft coral taxa (Syms & Jones 2001; Epstein & Kingsford 2019), *Xenia* sp. does not provide structural complexity, potentially reducing shelter availability for fish recruits (Mezger et al. 2022; Thobor et al. 2022). This highlights a potential challenge for managing reef fish assemblages in systems where soft corals dominate, even when algal cover is low.

Turf algal dominance has long been associated with negative effects on coral reefs (Norström et al. 2009; Ainsworth & Mumby 2015; Morais et al. 2020). Interestingly, our results show that low to moderate turf algal cover in Lyudao was associated with slightly higher recruitment, possibly due to increased habitat heterogeneity that benefits algal-associated fishes (Feary et al. 2007; Elma et al. 2023). In contrast, reefs in Xiaoliuqiu, where turf algal cover exceeded 45%, showed significant negative effects on fish recruitment, reflecting more severe degradation (Feary et al. 2007; Lecchini et al. 2013). Thus, simply protecting degraded reefs may not be sufficient to restore recruitment potential, leading to failure in the recovery of reef fish populations (Pickens et al. 2021: Canty et al. 2024). Improving habitat quality by addressing benthic composition may be more beneficial for supporting reef fish recruitment.

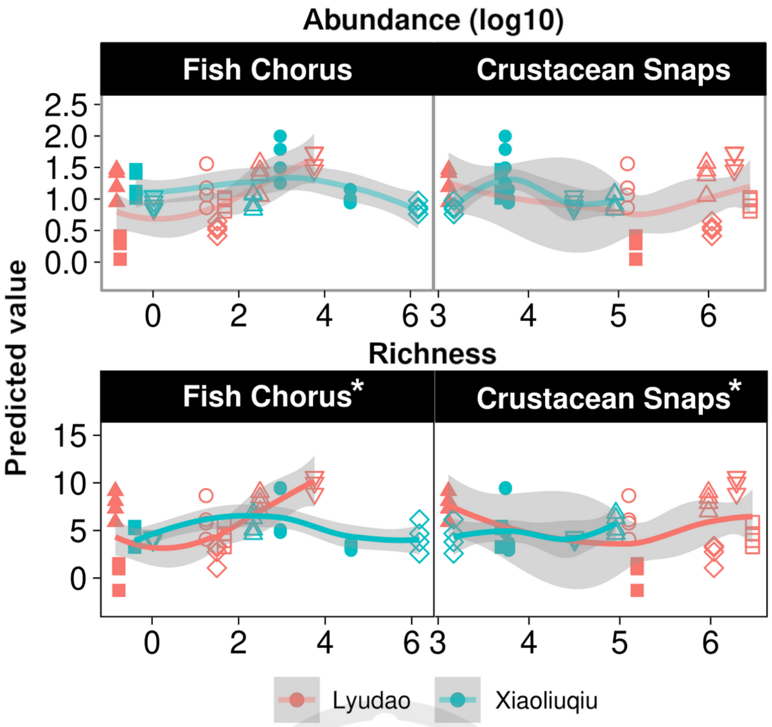

Figure 3.4: Relationship between acoustic drivers and recruit assemblages. Plots showing the effect of the acoustic factors on the abundance and richness of recruits. Asterisks indicate that the factor was significant in the model. Each point represents one transect, lines indicate conditional means, and shaded areas indicate the confidence intervals.

Here, we found generally weak associations between recruits and adult assemblages. This contrasts with species-level studies that report strong spatial associations between adults and recruits (Hsiao et al. 2003; Almany 2004a; Lecchini et al. 2007; Wormald et al. 2013; Coppock et al. 2016). For example, several species are known to settle on or near their natal reefs, often in proximity to conspecific adults (Jones 2015; Sponaugle 2015). However, our results indicate that such relationship might not be observed at the assemblage level, potentially due to interspecific interactions such as predation or competition (Almany 2004a; Ben-Tzvi et al. 2009; Coppock et al. 2016), and recruitment variability, since not all fishes are attracted to conspecifics (Roux et al.

2015; Coppock et al. 2016). Future studies should explore adult–recruit dynamics at both species and assemblage levels, particularly across gradients of reef degradation.

The variables considered in this study explain about 20–30% of the variation in recruitment patterns, indicating that other influential factors remain to be explored. While larval supply is believed to be similar around Lyudao and Xiaoliuqiu (Yen et al. 2022), local factors might influence larval movement at smaller spatial scales (Green et al. 2015). Additionally, local species pools could have a stronger impact on larval supply and settlement rates than offshore sources (Hamilton et al. 2021; Jones et al. 2005; Sponaugle 2015). Including oceanographic features—such as wider depth gradients, fine-scale current patterns, and larval dispersal dynamics—could enhance model accuracy and help account for the remaining variation in fish recruitment.

3.5.2 Soundscape influence

The influence of reef soundscape on fish recruitment remains relatively understudied. Some studies have primarily used playback experiments to demonstrate that healthy reef soundscapes can attract fish larvae and enhance recruitment (Simpson et al. 2004; Radford et al. 2011), but few have identified which specific components of the soundscape are driving these effects. Reef soundscape typically consists of a mixture of high-frequency crustacean snaps and low-frequency fish calls (Lin et al. 2023). In Lyudao, we found that nighttime fish choruses were positively correlated with recruit assemblages, suggesting that these low-frequency sounds may play a role in auditory settlement behavior of reef fish. Most reef fish settle at night (Sponaugle 2015), thus following nighttime fish chorus might be an important strategy to find suitable settlement habitats. Additionally, low-frequency sounds propagate more effectively than high-frequency ones and may provide spatial cues that influence larval orientation at local scales (Kaplan et al. 2015). These findings align with studies showing that reef soundscape characteristics reflect habitat quality and can serve as indicators of reef health (Gordon et al. 2019; Butler et al. 2022). Furthermore, acoustic enrichment has been shown to have positive effects on the settlement of reef building organisms (McAfee et al. 2023; Aoki et al. 2024), and fish choruses could have a similar effect on settling reef fish larvae. Therefore, investigating the prominence of fish choruses may offer a novel, non-invasive tool for identifying healthy reefs with higher recruitment potential.

In contrast, the influence of acoustic cues in Xiaoliuqiu was less evident. This may indicate that in heavily degraded reefs, other environmental factors—such as substrate composition or structural complexity—play a more important role in shaping recruitment patterns (Lecchini et al. 2005). Alternatively, settlement and recruitment may only be triggered in the presence of multiple cues (Jones 1990; Sponaugle 2015), and such process may be species-specific (Parmentier et al. 2015), further complicating efforts to identify clear causal mechanisms linking soundscapes to recruitment. Here, our soundscape data were limited to single 24-hour recordings per site, which may not reflect the temporal variability associated with lunar phases or peak settlement periods (Lin et al. 2021).

Despite these limitations, our approach of integrating acoustic, benthic, and adult assemblage data provides new insights into the complex interactions shaping reef fish recruitment. For instance, the SNR of fish choruses was not correlated with adult abundance or richness, suggesting that the acoustic patterns observed were not simply artifacts of adult density. Thus, it is crucial to consider multiple sensory cues in coral reef ecosystems, as these systems are shaped by an interplay of biotic and abiotic factors. Long-term, multi-dimensional monitoring that spans ecological and acoustic variables over varying temporal scales will be valuable for disentangling the drivers of fish recruitment and for advancing future reef conservation and restoration planning.

3.6 Conclusion

This study contributes to a growing understanding of how reef fish recruitment responds to environmental and soundscape gradients. Our findings highlight rugosity as a consistent positive driver of recruitment, even in highly degraded reef systems, underscoring the importance of structural complexity for ecosystem resilience. In contrast, benthic dominance by turf algae or soft corals—particularly taxa lacking structural rigidity—was associated with reduced recruitment, suggesting that not all benthic cover types equally support recovery. Importantly, our results also reveal the potential role of reef soundscapes in shaping recruitment patterns. The observed positive association between nighttime fish choruses and recruit richness in healthier reefs points to acoustic cues as possible indicators of recruitment potential. By combining benthic, biological, and acoustic variables, this study provides a more holistic perspective on the conditions that support fish recruitment. These findings suggest that conservation strategies focused solely on spatial protection may fall short without addressing habitat quality and sensory cues. Long-term, multi-modal monitoring will be essential for guiding restoration efforts and identifying priority areas for protection in increasingly degraded reef environments.

Acknowledgments

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Chapter 4

Assessing opportunity and risk sites for reef fish conservation through ecological and noise indicators in a Marine Protected Area

4.1 Abstract

Preventing habitat degradation requires comprehensive conservation and monitoring efforts to assess habitat quality and identify associated threats. Among these threats, anthropogenic noise pollution has become one of the most pervasive stressors affecting marine ecosystems in recent decades. In coral reefs, noise pollution impacts the behavior, reproduction, and settlement of reef-associated organisms. Moreover, noise can cross the boundaries of marine protected areas (MPAs), raising concerns about how to effectively mitigate its impacts. Here, we applied the concept of "opportunity zones" to identify high-biodiversity sites with minimal anthropogenic noise within Kenting National Park, the oldest MPA in Taiwan. We investigated two no-entry zones, three no-take zones, and three general-use zones. Ecological indicators included juvenile fish abundance, adult herbivore abundance, and substrate cover. Acoustic indicators were derived from signal-to-noise ratios in two biologically relevant frequency bands: 0.2–1.5 kHz for fish and 2–20 kHz for crustaceans. By integrating ecological and acoustic indicators, we identified a high-opportunity site that remains unprotected under current zoning regulations. Additionally, we found two "risk zones" where high coral cover and juvenile abundance coincide with elevated vessel noise, potentially leading to physiological and behavioral stress. Our results highlight the potential of combining ecological and acoustic assessments to locate quiet biodiversity hotspots and guide conservation measures. We recommend shifting recreational activities in no-take zones toward quieter, low-impact alternatives such as stand-up paddling, kayaking, and snorkeling to reduce noise pollution

while supporting sustainable tourism. This approach provides practical insights for improving spatial planning and management in MPAs.

4.2 Introduction

In recent decades, conservation biology has shifted from species-based approaches to habitat-focused campaigns, driven by growing awareness of the extensive impacts of human activities and the cascading effects of habitat degradation (Calizza et al., 2017; Krauss et al., 2010). Preventing habitat degradation remains challenging due to the variable and widespread nature of anthropogenic pressures (Keck et al., 2025; Soga & Gaston, 2024), as well as the inherent difficulty in assessing habitat quality in biologically complex and dynamic ecosystems (Brook et al., 2008; Dunn et al., 2009).

Coral reefs, among the most diverse marine ecosystems, support rich biological communities that rely on complex visual, chemical, and acoustic cues (Choat & Bellwood, 1991). Among these, underwater sound serves as a crucial long-distance sensory cue for reef organisms (Parks et al., 2014; Peng et al., 2015). For instance, coral and oyster larvae utilize acoustic cues from reefs to locate suitable settlement habitats (Lillis et al., 2013, 2016, 2018; McAfee et al., 2023), while some shrimps employ sounds for communication and habitat exploration (Hawkins & Popper, 2017). In coral reef fishes, acoustic communication helps mediate social interactions, reproduction, larval settlement, and predator avoidance in many species (Fay, 2009; Hawkins, 1986; Myrberg, 1980, 1997; Popper et al., 2024). Nevertheless, this acoustic reliance has raised concerns about the disruptive impacts of anthropogenic noise, particularly from boats. For instance, studies have reported that boat noise can reduce fish settlement and survival (Simpson et al., 2004, 2016a), disrupt acoustic communication (de Jong et al., 2018; Nedelec et al., 2023), and impair reproduction and parental behaviors (Cox et al., 2018; de Jong et al., 2018; Nedelec et al., 2022). Elevated noise exposures are also associated with increased stress levels (Amorim et al., 2022; Debusschere et al., 2016), reduced foraging efficiency (Cox et al., 2018), and weakened anti-predator responses, especially among juveniles (Ferrari et al., 2018; Price et al., 2023).

Regulating anthropogenic noise is challenging, as underwater sound can travel over long distances (Nedelec et al., 2023; Peng et al., 2015), making noise pollution a transboundary issue that extends beyond management borders (Cox et al., 2018; Hawkins & Popper, 2017; Juanes et al., 2017; Tyack, 2008). While shipping and commercial fishing vessels are well-known noise sources (Nedelec et al., 2023; Popper & Hawkins, 2019), recreational vessels such as speedboats and jet skis also contribute substantially to coastal soundscapes, particularly in biodiversity-rich tourist regions (Hawkins & Popper, 2017; Popper & Hawkins, 2019). These vessels generate broadband signals composed of engine noise and propeller cavitation (McKenna et al., 2024; Nedelec et al., 2023; Pine et al., 2016). This pervasive noise pollution poses a growing concern for marine protected areas (MPAs), which traditionally regulate extractive human activities but often allow vessel transit. For instance, MPAs near busy waterways (McKenna et al., 2024), even within integral protection zones, have been characterized by high sound pressure levels (SPLs) (La Manna et al., 2021). Such chronic noise exposure may compromise the ecological effectiveness of MPAs by interfering with crucial processes related to the replenishment of reef fish assemblages (de Jong et al., 2018; Jimenez et al., 2020; Price et al., 2023; Simpson et al., 2015, 2016a).

Designing and enforcing quiet marine sanctuaries is challenging, given the difficulty of altering established water lanes and the transboundary nature of underwater sound. One promising alternative involves identifying existing areas where high biodiversity overlaps with naturally low noise levels, referred to as “opportunity zones” (Williams et al., 2015). These zones provide potential refugia for marine biota with minimal regulatory changes, offering high conservation value with low implementation effort. In contrast, “risk zones” are areas where biodiversity is high but noise pollution is also severe, potentially requiring more intensive management. While this mapping of opportunity and risk zones is gaining attention for marine mammals in temperate habitats (El-Dairi et al., 2024; Erbe et al., 2018; Williams et al., 2015), its application to tropical coral reef ecosystems, especially in the context of small recreational vessel noise within MPAs, remains underexplored.

This study aims to identify opportunity and risk sites across different management zones within the Kenting National Park, Taiwan, by assessing the prevalence of noise indicators and their overlap with ecological indicators of reef health. To achieve this, we conducted soundscape and ecological surveys at eight sites representing three protection levels, using one-hour recordings during peak activity hours in the high season.

4.3 Methods

4.3.1 Study Area

Kenting National Park is an IUCN Category II protected area, encompassing both terrestrial and marine habitats, situated at the southernmost tip of Taiwan. The marine area spans over 150 km², encompassing coral reefs, rocky shores, and sandy beaches (Keshavmurthy et al., 2019). Two different management zones exist within the MPA of the park: Marine Ecological Protection Areas (MEPAs), which are no-entry zones where entry and use are limited to scientific and monitoring activities; and Marine Recreational Areas (MRAs), which are no-take zones where only extractive activities are prohibited. The area outside these zones is categorized as General Control Areas (GCA), where extractive activities are permitted under appropriate regulations (https://landgis.ktnp.gov.tw, last accessed June 12, 2025) (see Fig. 4.1).

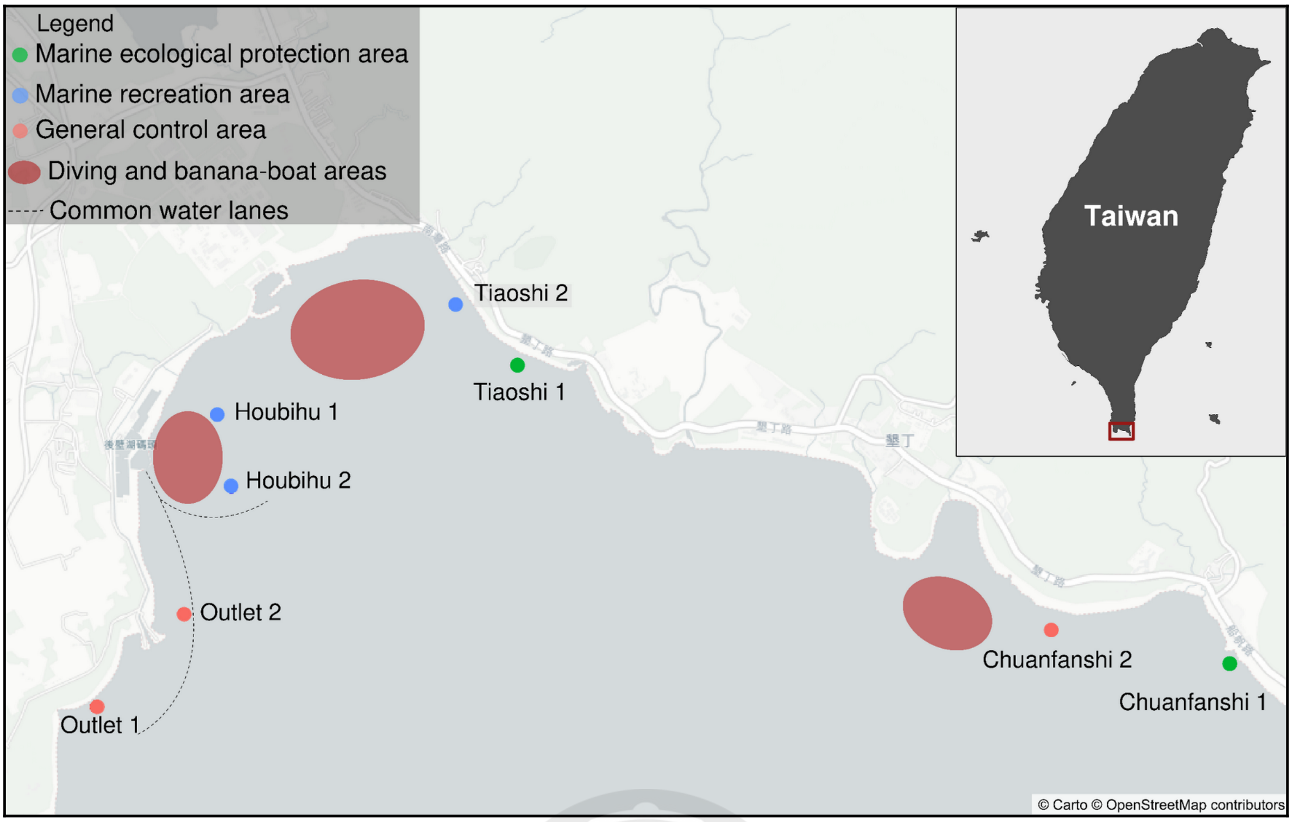

Figure 4.1: Map of the study area, located within Kenting National Park, in the southern tip of Taiwan. This map illustrates popular diving sites, banana boat zones, and water lanes relevant to the studied sites.

4.3.2 Data collection

During August 2022, we surveyed eight different sites, with two in the MEPAs, three in the MRAs, and three in the GCAs. At each site, we first placed an AUSOMS-mini hydrophone (AquaSound Inc., Kobe, Japan; more information is available in Lin et al., 2021) to record the noise from passing vessels over a one-hour period during peak tourist hours (10:00 a.m. to 2:00 p.m.). The working depth of the recorder varied from ~ 4.5 m to ~ 8 m. We placed the recorder at a distance greater than 30 meters from the nearest transect line and avoided swimming near the recorder to prevent interference from the open-circuit SCUBA noise.

Subsequently, four 20 m transects were placed randomly, following the reef's crest and parallel to the shore. Transect depth varied between 4 and 8 m, with averaging of 6.01±0.9 m. To minimize the influence of divers on reef fish assemblages, a 5-minute waiting period was enforced between laying the transect lines and starting the census. A team of four divers conducted the entire data collection procedure. First, adult fish were recorded using a GoPro HERO 10 (GoPro, Inc., San Mateo, CA, USA) video camera along four 20 m x 2 m belt transects; this approach allowed us to minimize the influence of other divers on shy species. The transect width was determined using 1-m rulers on each side of the transect. The second diver identified and counted fish juveniles (see details below) using Underwater Visual Census (UVC) (Bohnsack & Bannerot, 1986) along four 20 m x 4 m belt transects, using a ruler for reference to estimate fish size.

Following the fish census, benthic cover was measured using the point intercept method, with 50 points marked at 40 cm intervals along transects, and photographs of the benthos taken under these points using an Olympus Tough TG-6 (Olympus Corporation, Tokyo, Japan). Lastly, substrate complexity and depth were measured using a HOBO depth logger (Onset Computer Corporation, Bourne, MA, USA), which recorded water pressure every second as the diver moved along the transects following the depth profile (Dustan et al., 2013).

4.3.3 Data processing

Fish counts from the UVC data were later refined to exclude all observations from individuals that could not be identified at the species level. Juveniles were identified based on size and coloration. Video data for adult fish richness and abundance were processed using a video editing tool to mark the 2 m width of the transect while the video was playing. The individuals in the video were identified to species level, except for two specimens, which were excluded from the analyses. Fish species were categorized into five main trophic groups: Carnivores, Herbivores, Invertivores, Omnivores, and Planktivores, adapted from Ferreira et al. (2004). These major functions reflect significant assemblage trends and encompass important ecosystem functions essential for the reef's health (Adam et al., 2015; Ferreira et al., 2004; Green et al., 2009; Kramer et al., 2015; Sartori et al., 2021; Siqueira et al., 2021).

Photographs from the point intercept method for benthos cover estimate were analyzed individually, and recorded benthos were classified into the following functional groups according to (English et al., 1997): turf algae, macroalgae, soft corals, encrusting corals, massive corals, branching corals, foliose corals, table corals, and other benthos, in addition to bare rock and sand. The final dataset included the percentage cover of each functional group per transect. Substrate complexity per transect was calculated following Ribas-Deulofeu et al. (2021), which returns a rugosity index that simultaneously considers both fine (10-20 cm) and coarse scales (several meters).

Sound recordings were processed using soundscape_IR (Sun et al., 2022). First, we followed Lin et al. (2021) in visualizing the spectral and temporal variations of underwater soundscapes using the long-term spectrogram technique, calculating the mean power spectral densities from each 1-s interval. After that, we extracted sound pressure levels (SPLs) from two frequency bands. The first frequency band is between 0.2 and 1.5 kHz, corresponding to the band of fish calls (from here on low-frequency band), and the second frequency band is between 2 and 20 kHz (from here on high-frequency band), corresponding to the band in which crustacean snaps are detected (Lin et al., 2023). We then manually inspected the spectrograms and labeled each sampling period (1 s) to identify whether it represented ambient or vessel noise, excluding recording periods identified by scuba diving. To measure the level to which vessel noise exceeded the ambient sounds, we calculated signal-to-noise ratios (SNRs) by subtracting the SPLs from the vessel noise periods from the median SPLs of the ambient sound periods. We then calculated the average and standard deviation of vessel SNRs per site for each frequency band. We also calculated the average SNRs of boat and jet ski noise for reference.

4.3.4 Data analysis and dimension reduction

All statistical analyses were done using R software v. 4.3.3 (R Core Team, 2024). We first plotted a correlation matrix based on the Pearson correlation coefficient (Fig. C1) to observe the correlation between all ecological and acoustic variables and explore possible collinearities. Sand and rock were excluded from the analysis, as well as variables with very low percentages (e.g., other invertebrates and table corals). We divided our dataset into five groups, including ecological indicators such as juvenile fish assemblages, adult fish assemblages, and substrate characteristics, as well as noise indicators composed of low-frequency and high-frequency bands.

We chose key health indicators to characterize the environmental conditions of our study sites. Those indicators include juvenile abundance, herbivore abundance, and hard coral cover, following long-established health indices (Hafizt et al., 2023; Kaufman et al., 2011). Fish assemblage datasets were composed of abundance count data per trophic group, while substrate data included benthic cover and rugosity. For the juvenile and adult fish datasets, we utilized the *decostand* function, based on log10 transformations, from the vegan package v. 2.6-8 (Oksanen et al., 2019). Ecological indicators were derived by performing Principal Component Analysis (PCA) on fish and substrate variables to reduce the patterns of explanatory variables to two main dimensions, using the FactoMineR package v. 2.11 (Husson et al., 2006). The summary of the PCA results is presented in Tables C1-C3.

In order to keep the direction of benthic and acoustic indicators consistent with a logical habitat quality score, where higher scores reflect better habitat quality, we used the additive inverse of the vessel SNR (i.e. -1 × SNR) and the benthic PC1 loadings (i.e. -1 × Comp.1). The additive inverse of vessel SNR was then named as “quietness” score. We then standardize the PC loadings of fish, substrate, and quietness score before plotting radar charts using the scale function. This process scales the values according to the minimum and maximum values in each variable, creating a relative score where the highest values receive a score of 1 and the lowest receive a score of 0. We then used these scaled scores to calculate the relative opportunity and risk of each site by adapting the formula described in Williams et al. (2016). We used the mean of the ecological variables versus the mean of the quietness scores in the low and high-frequency bands to determine the final opportunity-risk index:

$$\bar{x}(\text{scaled ecological scores}) \times \bar{x}(\text{scaled quietness scores})$$

4.4 Results

Vessel noise varied markedly between sites. Overall, SNRs were higher in the low-frequency (0.2-1.5 kHz) than in the high-frequency band (2-20 kHz) (Fig. 4.2 and C2). Most diving and fishing boats generated noise concentrated below 5 kHz (Fig. C3). In contrast, speedboats and jet skis emitted broadband noise extending beyond 24 kHz, although their peak SNRs typically remained below 1.5 kHz (Fig. C4). Jet skis consistently showed high SNRs in both frequency bands, averaging 15 dB above ambient noise in the lower frequencies (Fig. 4.2). The temporal characteristics of noise also varied according to vessel type. Jet ski events were generally shorter, while noise from fishing, diving, and speed boats was more variable, ranging from a few seconds to several minutes (Fig. 4.2). Sites within MEPAs were relatively quiet, with only a single vessel noise event registered. MRAs exhibited mid-to-high SNRs, including the loudest site in the study area. GCAs exhibited a wide range of SNRs, spanning from low to high levels across sites.

Juvenile abundances in all trophic groups loaded positively on PC1, which explained 48% of the variance in the data (Table C1). The strongest contributors to this axis were planktivores (loading = 0.71), herbivores (0.49), and invertivores (0.43). This general pattern suggests that PC1 reflects an overall gradient in juvenile abundance and was subsequently used to determine habitat quality scores. The abundance of adult herbivores was the strongest contributor on PC2, which explained 27% of the variance in adult abundance data (Table C2). Although most of the other trophic groups also loaded positively in this axis, their contributions were relatively low, and PC2 loadings were used as an indicator of herbivore abundance. For substrate variables, PC1 (25%) reflected a gradient between hard coral-dominated and algae-dominated habitats and was used as an indicator of hard coral cover. On the other hand, PC2 (21%) captured a stratification between soft coral cover and rugosity (Table C3).

Most surveyed sites displayed low scores in at least one of the indicators. Only Outlet 1 stood out as the most favorable site, with high relative scores for relative juvenile abundance, adult herbivore abundance, coral cover, and quietness, indicating a well-balanced and high-quality habitat. Except for Outlet 1, other GCA sites showed lower habitat quality, with low scores across most indicators (Fig, 4.3). MEPAs tended to have low-to-intermediate juvenile abundance, but relatively higher adult herbivore abundance. These areas were also relatively quiet, but also showed low hard coral cover. MRAs typically exhibited relatively good coral cover, but varied widely in fish juveniles and adult herbivore abundance. Acoustic quietness conditions in MRAs were generally moderate to poor, especially at Houbihu.

The sites studied here exhibited a clear gradient in habitat quality, ranging from high-opportunity to high-risk areas. We identified three sites with intermediate to high opportunity scores. Among these sites, Outlet 1 displayed the highest opportunity score, being unprotected from extractive activities under the current zoning within Kenting National Park. On the other hand, the two Houbihu sites, located within MRAs, are at higher risk. While these sites showed high scores in ecological indicators, elevated levels of anthropogenic noise lowered their opportunity scores. The sites with the lowest opportunity score were located within GCAs, where existing anthropogenic noise overlaps with low habitat quality.

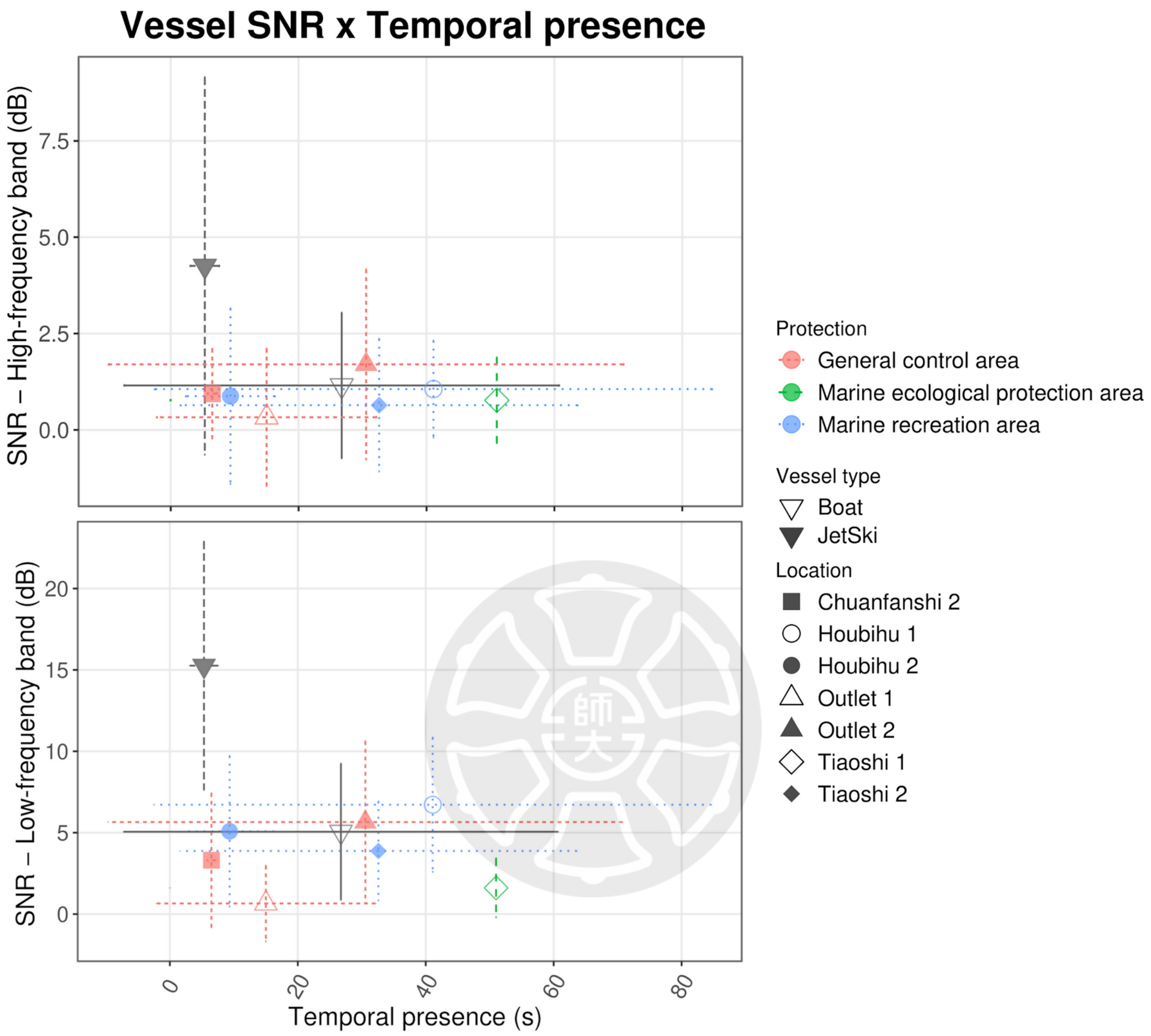

Figure 4.2: Signal-to-noise ratio (SNR) vs temporal presence of vessel noise events in Kenting National Park. The group "Boat" includes diving, fishing boats, and speedboats. Points are the average SNR, and bars are the standard deviation.

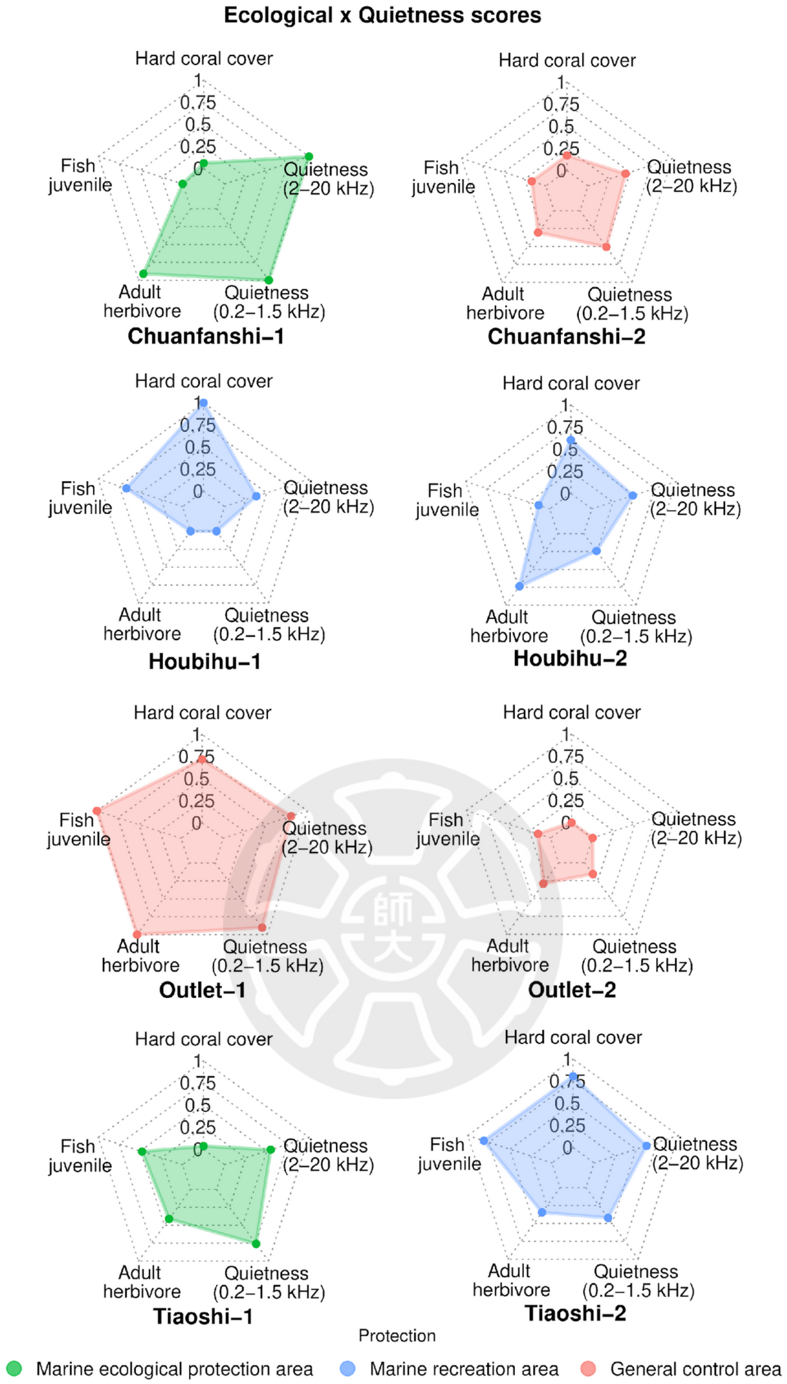

Figure 4.3: Radar plots displaying the relative scores of ecological and acoustic indicators at each study site. We used the loading values from PCAs to calculate the relative scores for the ecological variables and the additive inverse vessel SNR (i.e., -1 × SNR) to calculate the quietness scores.

4.5 Discussion

4.5.1 Habitat Quality: Opportunity and Risk Zones

We have identified a gradient in habitat quality across the surveyed sites, influenced by fish abundance, substrate cover, and exposure to anthropogenic noise. The combination of acoustic and ecological indicators revealed opportunity sites where high biodiversity coincides with low-intensity noise, as well as risk zones where diverse species encounter prevalent acoustic disturbances. Among the eight surveyed sites, Outlet 1 emerged as the highest opportunity zone, showcasing relatively high abundance of juveniles and adult herbivores, coral cover, and low noise levels. Notably, this site is situated within a GCA and is not protected from extractive activities. Other opportunity sites exhibited a mix of high and low score indicators, suggesting partial impacts. Among the high-risk sites, Houbihu 1 & 2 raise the greatest concern, as they contain relatively high coral cover and abundant fish assemblages (in different life stages, see Fig. 4.4), but also display high anthropogenic noise levels. This variability in opportunity and risk across different zoning categories highlights the necessity to move beyond simply designating protection status. Adaptive conservation strategies that reflect the actual habitat quality are essential for safeguarding biodiversity in commonly used coastal zones.

4.5.2 Opportunity Zones: Resilience drivers

Our results reveal an overlap between juvenile fish abundance and hard coral cover, underscoring the functional role of hard corals as shelters for fish during early life stages (Coker et al., 2012; Feary et al., 2007). Conversely, high turf and algae cover often have negative relationships with fish recruitment rates (Feary et al., 2007; Lecchini et al., 2013). Additionally, abiotic factors such as rugosity often interact with coral cover, enhancing recruitment rates and survival (Almany, 2004a; Cheminée et al., 2016; Coker et al., 2012). Thus, the role of opportunity sites extends beyond taxonomic conservation. For instance, quiet sites with high coral cover may attract greater recruitment rates, serving essential ecosystem functions by providing safe zones for future fish assemblages (Bell & Galzin, 1984; Coker et al., 2012; Komyakova et al., 2013). Short-duration recordings limit the scope of our analyses; however, long-term deployments should yield additional information regarding the biological aspects of the underwater soundscape, such as fish and crustacean sounds, which can be linked to habitat quality (Lillis et al., 2016; Lin et al., 2021) and fish recruitment (Gordon et al., 2019; Lecchini et al., 2005; Simpson et al., 2004). This reinforces the importance of considering multiple ecological and acoustic indicators and their interrelationships when assessing habitat quality, safeguarding essential ecological functions, and promoting higher resilience potential (Beese et al., 2023; Emslie et al., 2008, 2014; Glynn et al., 2014).

In addition to identifying opportunity zones with high-quality habitats, it is crucial to understand how these ecological indicators influence one another and change over time. Both MEPA sites here were relatively quiet but showed low coral cover and low-to-intermediate juvenile abundance, suggesting degradation from non-acoustic stressors such as thermal bleaching or land-based runoff (see Keshavmurthy et al., 2019). This implies that we should consider multiple stressors when assessing habitat quality in future surveys. Nevertheless, these sites also had an intermediate-to-high abundance of adult herbivores, which play critical roles in the top-down control of turf and macroalgal growth in coral reefs, promoting the maintenance and recovery of hard coral cover (Adam et al., 2015; Green et al., 2009; Hughes, 1994). Maintaining low noise pollution in these sites is essential to avoid disrupting potential recovery processes and safeguarding zones dominated by herbivores within Kenting National Park, which could function as a source of recruits to other reefs (Appeldoorn et al., 2003; Armsworth, 2002; Endo et al., 2019).

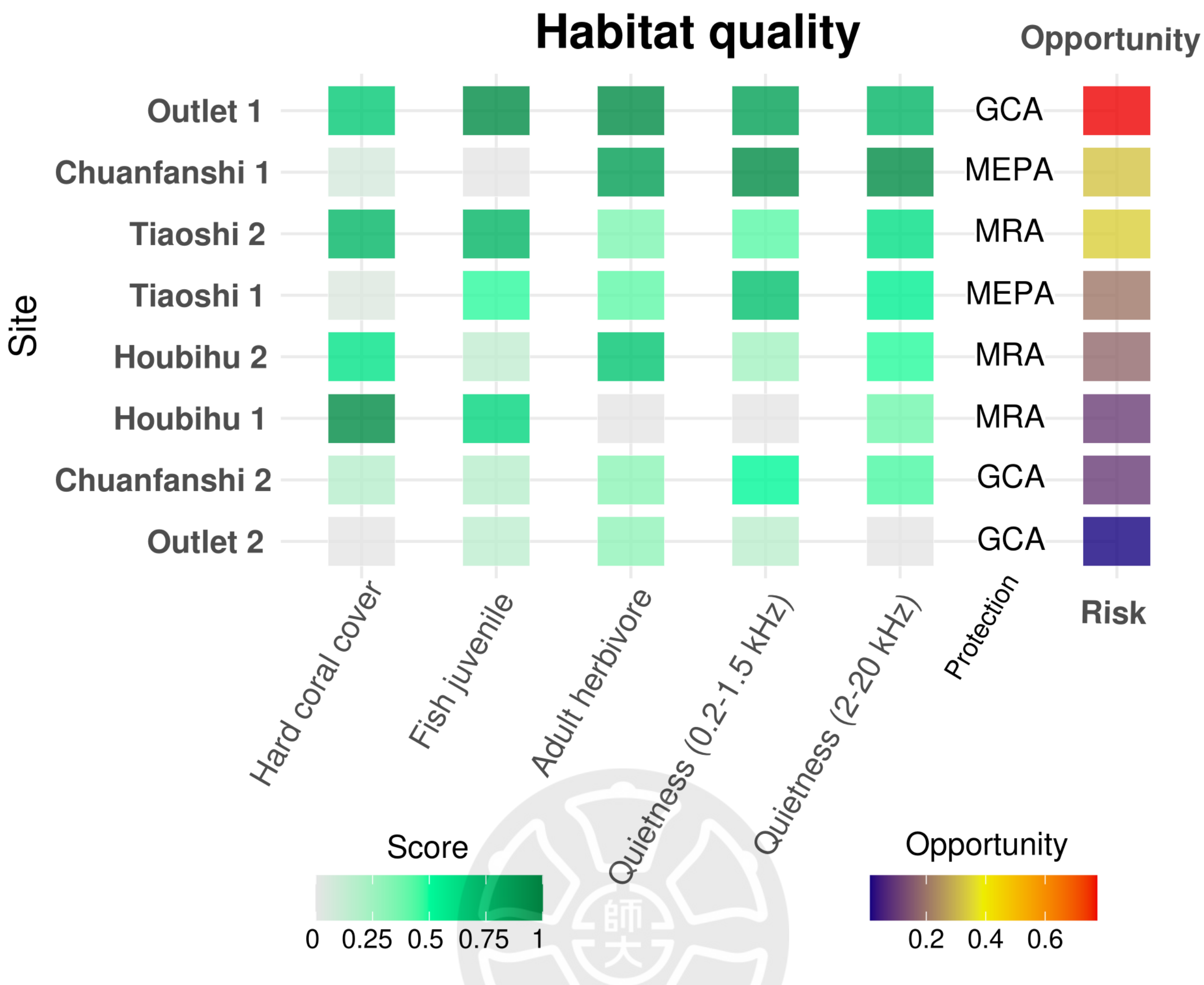

Figure 4.4: Summary of the relative scores for ecological and noise domains, displaying the relative opportunity and risk levels of each study site. We used the loading values from PCAs to calculate the relative scores for the ecological variables and the additive inverse vessel SNR (i.e., -1 × SNR) to calculate the quietness scores. GCA: General Control Area, MEPA: Marine Ecological Protection Area, MRA: Marine Recreational Area.

4.5.3 Risk Zones: Noise Stress and Potential Impacts

High-risk zones are characterized by the intersection of relatively high biodiversity and human-induced pressures. This pattern is exemplified by the two Houbihu sites, which ranked among the noisiest areas in our survey despite their relatively high coral cover and abundant juvenile fish.

These sites experience combined acoustic disruptions from recreational activities and nearby water lanes (see Fig. 4.1), which are frequently used by boats and jet skis. The latter pose particular disruptive potential in the high-risk sites observed here. Their broadband signals peaked within biologically relevant low-frequency bands (0.2–1.5 kHz), overlapping with key frequencies used by reef fishes for communication and orientation (Cox et al., 2018; Pine et al., 2016), potentially masking important auditory cues (Hawkins & Popper, 2017; Pine et al., 2016). Moreover, jet skis' ability to navigate shallow waters amplifies their local acoustic impact by shortening the distance between the vessels and the reefs below (Bittencourt et al., 2014; Peng et al., 2015). Houbihu sites are particularly vulnerable to this due to their shallow reefs (<1 m), which can only be navigated by jet skis. Additionally, their intermittent and unpredictable presence may trigger stronger stress responses than continuous shipping noise (Lessa et al., 2025; Nichols et al., 2015). Thus, the prevalence of these impacts could extend beyond behavioral levels and lead to ecological disruptions (Güney & Kinaci, 2024; Hawkins & Popper, 2017).

The effects of noise pollution on reef fish at the assemblage level remain poorly understood. Nevertheless, individual-based studies indicate potential disruptions to essential functions and processes, such as reproductive success, foraging rates, and responses to predators (Davies et al., 2024; Ferrari et al., 2018; Hawkins & Popper, 2017). Overall, sound disruption can decrease fish survival rates, especially among juveniles, thereby reducing potential resilience at impacted sites (Jimenez et al., 2020; McCormick et al., 2018; Simpson et al., 2015). Furthermore, noise pollution may also affect other animals, interfering with barnacle, oyster, and coral settlement (Aoki et al., 2024; Branscomb & Rittschof, 1984; Lillis et al., 2013, 2016, 2018; McAfee et al., 2023) and impacting interspecific social interactions (McCloskey et al., 2023; Nedelec et al., 2017). These community-level impacts could lead to alterations in trophic links (Minier et al., 2024; Simpson et al., 2016b), threatening key ecological functions.

Disrupting trophic links, settlement, and survival rates in functionally relevant species can lead to changes in reef assemblage structure (Ainsworth & Mumby, 2015; Bellwood et al., 2018; Booth & Beretta, 2002; Morais et al., 2020). For instance, low replenishment rates can decrease fish abundance and hinder top-down processes (Beese et al., 2023; Brandl et al., 2019), which, coupled with low coral settlement, may result in high algal dominance (Gordon et al., 2018; Hughes, 1994; Lönnstedt et al., 2014; Roth et al., 2018). Although noise from recreational vessels tends to decrease at night, when most reef fish species settle (Sponaugle, 2015), the potential ecosystemic effects may hinder reef fish resilience through indirect processes (Mouillot et al., 2013; Webb et al., 2021; Wilson et al., 2010). While our study captures only short-term acoustic snapshots, the localized and high-fidelity nature of recreational activities (Brander et al., 2007; Medeiros et al., 2007; Milazzo et al., 2002) raises concerns about the potential ecosystem effects of cumulative noise exposure, emphasizing the need to identify and manage risk zones within MPAs.

4.5.4 Toward Designating Quiet Zones for Improved MPA Effectiveness

Marine Protected Area (MPA) regulations in Taiwan, like in most regions, have traditionally focused on mitigating the impacts of extractive activities such as fishing and seabed mining. However, non-extractive stressors like noise pollution remain largely unregulated, particularly concerning small recreational vessels. This suggests that traditional MPA management strategies may be insufficient to address the pervasive nature of noise pollution. The current noise-related policies primarily emphasize the protection of marine mammals around commercial shipping routes (Peng et al., 2015; Tyack, 2008; Williams et al., 2015), overlooking the effects of noise pollution on reef ecosystems. Our study highlights the importance of data-driven conservation measures in reducing mismatches between protected status and habitat quality. For example, leveraging low-conflict opportunity sites where noise disruption is already minimal can provide managers with an excellent chance to implement stricter conservation measures or more ambitious restoration projects. These findings suggest that incorporating acoustic considerations into MPA design can improve the accuracy and effectiveness of spatial planning.

Applying the "opportunity" concept through a multispecies, multidimensional approach serves as a valuable tool for identifying promising conservation zones. For instance, based on our results, the area around Outlet 1 could be designated as a Marine Ecosystem Protection Area (MEPA), thereby creating a safe zone for local biodiversity and safeguarding species and functional groups in the region. Additionally, risk sites within MRAs could be better managed to reduce anthropogenic noise in local biodiversity hotspots. Rather than shifting their protection status, this could be achieved by altering the types of recreational activities permitted in the area. For example, we propose a shift towards quieter activities such as skin diving, freediving, stand-up paddling, and kayaking (see Fig. 4.5), which are popular marine activities with high tourist potential (Brander et al., 2007; Milazzo et al., 2002). Nevertheless, navigation rules should still be implemented in busy waterways, particularly on shallow reefs where the impacts of passing jet skis might disrupt key biological and ecosystem functions on coral reefs (e.g., Simpson et al., 2016a). This would offer a cost-effective, data-driven approach to facilitate MPA management, promoting the designation of efficient "quiet zones", a global conservation challenge.

Designing and managing protected areas has always been a challenging task, and transboundary stressors, such as noise, have increasingly complicated this task in recent decades. Previous proposals for quiet zones have primarily focused on marine mammals (Erbe et al., 2018; Parsons, 2017), leading to a knowledge gap regarding other marine organisms. Our findings demonstrate the relevance of this approach for broader marine biodiversity and suggest it could be expanded to include new organisms and ecosystems. Broader acoustic monitoring that accounts for diel and seasonal variation, as well as noise from other sources such as SCUBA diving, could further refine the identification of opportunity zones within Kenting National Park. An integrated approach that combines benthic condition, fish assemblage metrics, and acoustic disturbances can provide managers with actionable information to prioritize more effective interventions. With growing evidence that underwater noise causes significant habitat disruptions, incorporating soundscape assessments into conservation policies and MPA zoning will be essential for safeguarding coral reef ecosystems.

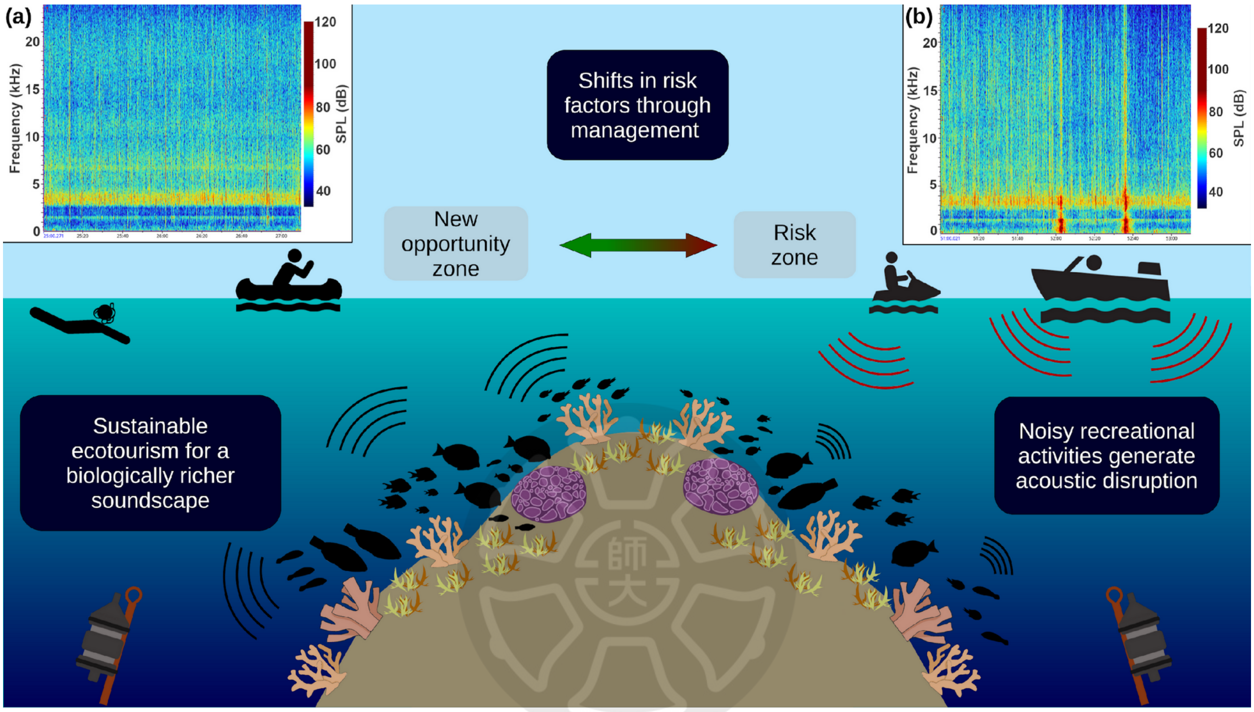

Figure 4.5: Proposed future scenarios derived from management strategies in no-entry recreational zones. (a) An example soundscape of a noise-free zone. (b) Example soundscape of a noisy zone with two jet ski events. Left: A managed recreational zone where quiet recreational activities are allowed and noisy activities are prohibited or discouraged, thereby preserving a healthy soundscape and minimizing acoustic disruptions. Right: A recreational zone where vessels and other noisy activities are allowed and unmanaged, disrupting the habitat soundscape and potentially causing ecosystem-level impacts.

4.6 Conclusion

There is growing evidence that anthropogenic noise negatively impacts coral reef fishes, potentially impairing crucial ecological processes. Identifying promising areas where management and conservation measures can protect local biodiversity while minimizing conflicts with human activities is essential for creating effective protected areas. Interdisciplinary surveys suggest that conservation efforts are more successful when integrated with socioeconomic aspects specific to the targeted area and ecosystem (Horta e Costa et al., 2022; Philip & Mukundi, 2024; Rees et al., 2021). Therefore, new tools and approaches, such as the "opportunity" assessment, are necessary to ensure healthy habitats. Although our scope was spatially and temporally limited, future, broader surveys could transform this relative assessment into more concrete guidelines for MPA management. Furthermore, this approach could be expanded to other organisms that are more sensitive to sounds during larval periods, such as corals and oysters (Aoki et al., 2024; Lillis et al., 2013, 2018; McAfee et al., 2023). Integrating acoustic assessments into environmental conservation measures provides a powerful tool for preventive zoning in Marine Protected Areas.

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Chapter 5

General Discussion

5.1 Summary and conclusions

Maintaining healthy habitats is not merely about preserving taxonomic diversity; it also involves safeguarding the ecological functions that support resilient communities. Therefore, investigating the processes and factors associated with resilience potential is crucial for understanding the effects of degrading reef habitats on resident assemblages (Wilson et al., 2006). Our results suggest that addressing this issue across different life stages and integrating various perspectives can provide promising pathways to resilient and better-protected coral reef fish assemblages.

Small-scale field experiments using *Pocillopora* spp. patches have demonstrated that dead branching corals can serve as temporary shelters for reef fish recruits by retaining rugosity, providing a buffer for reef fish assemblages during coral mortality events. However, the same experiment suggests that live branching corals are necessary to support a high abundance and functional richness of adult assemblages, which are essential for resilient coral reefs. These results underscore the close ecological ties between reef fish assemblages and corals, highlighting two different aspects of the bottom-up influence that branching corals have on reef fish assemblages.

Surveys along the coasts of Lyudao and Xiaoliuqiu revealed significant patterns regarding the influence of rugosity, substrate cover, and reef soundscapes on the abundance and richness of recruit assemblages. Consistent with the small-scale experiment, rugosity was positively associated with both richness and abundance, although the relationship was only significant for recruit abundance. Additionally, reefs dominated by turf algae exhibited significantly lower recruit abundance. Similarly, pulsating soft corals had a significant negative relationship with recruit richness. Finally, we demonstrate for the first time a possible link between the intensity of nighttime sounds, commonly dominated by fish choruses (Lin et al., 2021), and recruitment rates. Such findings highlight the need to consider habitat quality based on multifactorial analyses when designing conservation measures, as few studies have investigated the combined influence of visual, chemical, and auditory cues on recruitment rates (e.g. Feary et al., 2007; Lecchini et al., 2005).

The multidimensional approach we adopted to assess habitat quality in the reefs of Kenting provided important insights into the potential for improving MPA zoning. We have identified a quiet biodiversity hot spot which could be targeted in conservation measures as a healthy, potentially resilient site. We also propose alternative recreational use of seascapes, that could make risk zones into new opportunity zones. If adapted to specific local scenarios, approach could be an effective tool to manage conservation in conflict zones, promoting data-driven decision-making which accounts for social-ecological aspects

The early life stages of coral reef fishes are among the most important yet mysterious aspects of their life history. Studying the factors that shape the assemblage structure of young reef fishes is crucial for assessing local population status, forecasting future trends, and promoting resilience. We face unprecedented declines in reef fish assemblages, and gaining knowledge about the mechanisms involved in resilience processes is the most direct way to slow down habitat degradation. Nevertheless, all reefs worldwide have already been impacted to some extent, and we are just beginning to understand how the replenishment processes function in already affected reefs and at different levels of degradation (Bruno et al., 2019; Eddy et al., 2021). Understanding the small-scale influence of live and dead corals on reef fish assemblages is vital for planning more effective response measures to mass mortality events. Identifying the topographic, benthic, and acoustic drivers that influence recruitment can help reveal important recruitment trends, an essential aspect of reef fish life history. Finally, evaluating habitat quality through multidimensional approaches—including acoustic, structural, and ecological indicators—offers a promising tool for informed conservation planning.

5.2 Future directions

The results of our field experiment highlights the potential of small artificial patches—comprising live and dead corals—to attract and support diverse fish assemblages. We believe that the effectiveness of this design as a potential restoration tool could be used to minimize efforts and promote recovery in degraded reefs. Additionally, it is important to test the influence of live and dead branching corals in healthier and highly degraded sites, as the patterns observed here might differ in varying scenarios, and testing the use of dead coral patches could provide important insights for their potential to aid recovery of fish assemblages on highly degraded sites.

The multidimensional approach in chapters 3 and 4 serves as a baseline for studies attempting to integrate acoustic and ecological variables in the assessment of habitat quality in coral reefs. Long-term recordings of reef soundscapes and vessel noise should help strengthen the patterns found here and provide further insights to uncover which aspects of the reef soundscape can influence reef fish recruitment. Furtheremore, other studies could focus the potential implications of sound as a settlement cue in other areas, such as turbid water reeds, where visual cues might be less influencial. Our habitat quality score also offers a simple tool for evaluating the relative potential of different sites to support rich coral reefs. Expanding this approach to more sites, including other habitats, could help refine this method and extend its reach. We believe that integrative approaches, combining acoustic and ecological surveys with other tools, such as remote sensing and satellite data could be a powerful way to address conservation challenges in a rapidly changing world. For instance, interdisciplinary approaches could investigate the correlations between reef soundscapes and temperature, nutrients, primary productivity, turbidity and other factors. This kind of research will pave the way for new methodologies that account for the multidimensional nature of ecological processes and relationships, slowly turning the tide on coral reef degradation.

References

Abesamis, R. A., Stockwell, B. L., Bernardo, L. P. C., Villanoy, C. L., & Russ, G. R. (2016). Predicting reef fish connectivity from biogeographic patterns and larval dispersal modelling to inform the development of marine reserve networks. Ecological Indicators, 66, 534–544. https://doi.org/10.1016/j.ecolind.2016.02.032

Acosta, C., & Robertson, D. (2002). Diversity in coral reef fish communities: The effects of habitat patchiness revisited. Marine Ecology Progress Series, 227, 87–96. https://doi.org/10.3354/meps227087

Adam, T., Burkepile, D., Ruttenberg, B., & Paddack, M. (2015). Herbivory and the resilience of Caribbean coral reefs: Knowledge gaps and implications for management. Marine Ecology Progress Series, 520, 1–20. https://doi.org/10.3354/meps11170

Adjeroud, M., Kayal, M., & Penin, L. (2017). Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages. In Marine Animal Forests (pp. 549–569). Springer, Cham. https://doi.org/10.1007/978-3-319-21012-4_12

Agudo-Adriani, E. A., Cappelletto, J., Cavada-Blanco, F., & Cróquer, A. (2019). Structural Complexity and Benthic Cover Explain Reef-Scale Variability of Fish Assemblages in Los Roques National Park, Venezuela. Frontiers in Marine Science, 6, 690. https://doi.org/10.3389/fmars.2019.00690

Ainsworth C. H., Mumby PJ (2015) Coral–algal phase shifts alter fish communities and reduce fisheries production. Glob Chang Biol 21:165–172. https://doi.org/10.1111/gcb.12667

Albuquerque, T., Loiola, M., Nunes, J. de A. C. C., Reis-Filho, J. A., Sampaio, C. L. S., & Leduc, A. O. H. C. (2015). In situ effects of human disturbances on coral reef-fish assemblage structure: Temporary and persisting changes are reflected as a result of intensive tourism. Marine and Freshwater Research, 66(1), 23. https://doi.org/10.1071/MF13185

Allard, H., Ayling, A. M., & Shears, N. T. (2022). Long-term changes in reef fish assemblages after 40 years of no-take marine reserve protection. Biological Conservation, 265, 109405. https://doi.org/10.1016/j.biocon.2021.109405

Allen, G., Steene, R., Humann, P., & DeLoach, N. (2015). Reef Fish Identification: Tropical Pacific (Edição: 2 New). New World Publications.

Almany, G. R. (2004a). Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. Oecologia, 141(1), 105–113. https://doi.org/10.1007/s00442-004-1617-0

Almany, G. R. (2004b). Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos, 106(2), 275–284. https://doi.org/10.1111/j.0030-1299.2004.13193.x

Almany, G. R., Berumen, M. L., Thorrold, S. R., Planes, S., & Jones, G. P. (2007). Local Replenishment of Coral Reef Fish Populations in a Marine Reserve. Science, 316(5825), 742–744. https://doi.org/10.1126/science.1140597

Alvarez-Filip L., Dulvy NK, Gill J. A., Côté I. M., Watkinson A. R. (2009) Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. Proceedings of the Royal Society B: Biological Sciences 276:3019–3025. https://doi.org/10.1098/rspb.2009.0339

Amorim, M. C. P., Vieira, M., Meireles, G., Novais, S. C., Lemos, M. F. L., Modesto, T., Alves, D., Zuazu, A., Lopes, A. F., Matos, A. B., & Fonseca, P. J. (2022). Boat noise impacts Lusitanian toadfish breeding males and reproductive outcome. Science of The Total Environment, 830, 154735. https://doi.org/10.1016/j.scitotenv.2022.154735

Aoki, N., Weiss, B., Jézéquel, Y., Zhang, W. G., Apprill, A., Mooney, T. A. (2024). Soundscape enrichment increases larval settlement rates for the brooding coral *Porites astreoides*. Royal Society Open Science, 11(3), 231514. https://doi.org/10.1098/rsos.231514

Appeldoorn, R. S., Friedlander, A., Nowlis, J. S., Usseglio, P., & Mitchell-Chui, A. (2003). Habitat Connectivity in Reef Fish Communities and Marine Reserve Design in Old Providence-Santa Catalina, Colombia. Gulf and Caribbean Research, 14. https://doi.org/10.18785/gcr.1402.05

Araújo, M. E. de, Mattos, F. M. G. de, Melo, F. P. L. de, Chaves, L. de C. T., Feitosa, C. V., Lippi, D. L., Félix-Hackradt, F. C., Hackradt, C. W., Nunes, J. L. S., Leão, Z. M. de A. N., Kikuchi, R. K. P. de, Ferreira Junior, A. V., Pereira, P. H. C., Macedo, C. H. R., Sampaio, C. L. S., & Feitosa, J. L. L. (2020). Diversity patterns of reef fish along the Brazilian tropical coast. Marine Environmental Research, 160, 105038. https://doi.org/10.1016/j.marenvres.2020.105038

Armsworth, P. R. (2002). Recruitment Limitation, Population Regulation, and Larval Connectivity in Reef Fish Metapopulations. Ecology, 83(4), 1092–1104. https://doi.org/10.1890/0012-9658(2002)083[1092:RLPRAL]2.0.CO;2

Bachtiar, I., Hadi, T. A., Karnan, K., & Bachtiar, N. T. (2023). Other faunas, coral rubbles, and soft coral covers are important predictors of coral reef fish diversity, abundance, and biomass. Fisheries and Aquatic Sciences, 26(4), 268–281. https://doi.org/10.47853/FAS.2023.e23

Badalamenti, F., Ramos, A. A., Voultsiadou, E., Lizaso, J. L. S., D'anna, G., Pipitone, C., Mas, J., Fernandez, J. a. R., Whitmarsh, D., & Riggio, S. (2000). Cultural and socio-economic impacts of Mediterranean marine protected areas. Environmental Conservation, 27(2), 110–125. https://doi.org/10.1017/S0376892900000163

Beese, C. M., Mumby, P. J., & Rogers, A. (2023). Small-scale habitat complexity preserves ecosystem services on coral reefs. Journal of Applied Ecology, 60(9), 1854–1867. https://doi.org/10.1111/1365-2664.14458

Bell, J., & Galzin, R. (1984). Influence of live coral cover on coral-reef fish communities. Marine Ecology Progress Series, 15, 265–274. https://doi.org/10.3354/meps015265

Bellwood, D. R. (1988). Ontogenetic changes in the diet of early post-settlement Scarus species (Pisces: Scaridae). Journal of Fish Biology, 33(2), 213–219. https://doi.org/10.1111/j.1095-8649.1988.tb05464.x

Bellwood, D. R., & Choat, J. H. (1989). A description of the juvenile phase colour patterns of 24 parrotfish species (family Scaridae) from the Great Barrier Reef, Australia. Records of the Australian Museum, 41(1), 1–41. https://doi.org/10.3853/j.0067-1975.41.1989.134

Bellwood, D. R., Tebbett, S. B., Bellwood, O., Mihalitsis, M., Morais, R. A., Streit, R. P., & Fulton, C. J. (2018). The role of the reef flat in coral reef trophodynamics: Past, present, and future. Ecology and Evolution, 8(8), 4108–4119. https://doi.org/10.1002/ece3.3967

Ben-Tzvi O., Kiflawi M., Polak O., Abelson A. (2009) The Effect of Adult Aggression on Habitat Selection by Settlers of Two Coral-Dwelling Damselfishes. PLOS ONE 4:e5511. https://doi.org/10.1371/journal.pone.0005511

Bittencourt, L., Carvalho, R. R., Lailson-Brito, J., & Azevedo, A. F. (2014). Underwater noise pollution in a coastal tropical environment. Marine Pollution Bulletin, 83(1), 331–336. https://doi.org/10.1016/j.marpolbul.2014.04.026

Bohnsack, J. A., & Bannerot, S. P. (1986). A stationary visual census technique for quantitatively assessing community structure of coral reef fishes (Technical Publication No. 41; NOAA Technical Report NMFS, p. 15). National Oceanic and Atmospheric Administration.

http://aquaticcommons.org/2781/

Bonin, M. C. (2011). Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. Ecology. https://www.academia.edu/22369990/Contrasting_effects_of_habitat_loss_and_fragmentation_on_coral_associated_reef_fishes

Bonin, M. C., Munday, P. L., McCormick, M. I., Srinivasan, M., & Jones, G. P. (2009). Coral-dwelling fishes resistant to bleaching but not to mortality of host corals. Marine Ecology Progress Series, 394, 215–222. https://doi.org/10.3354/meps08294

Booth, D. J., & Beretta, G. A. (1994). Seasonal recruitment, habitat associations and survival of pomacentrid reef fish in the US Virgin Islands. Coral Reefs, 13(2), 81–89. https://doi.org/10.1007/BF00300765

Booth, D. J., & Beretta, G. A. (2002). Changes in a fish assemblage after a coral bleaching event. Marine Ecology Progress Series, 245, 205–212. https://doi.org/10.3354/meps245205

Booth, D. J., & Hixon, M. A. (1999). Food ration and condition affect early survival of the coral reef damselfish, Stegastes partitus. Oecologia, 121(3), 364–368. https://doi.org/10.1007/s004420050940

Booth, D. J., & Wellington, G. (1998). Settlement preferences in coral-reef fishes: Effects on patterns of adult and juvenile distributions, individual fitness and population structure. Australian Journal of Ecology, *23*(3), 274–279. https://doi.org/10.1111/j.1442-9993.1998.tb00731.x

Brander, L. M., Van Beukering, P., & Cesar, H. S. J. (2007). The recreational value of coral reefs: A meta-analysis. Ecological Economics, 63(1), 209–218. https://doi.org/10.1016/j.ecolecon.2006.11.002

Brandl S. J., Johansen J. L., Casey J. M., Tornabene L., Morais R. A., Burt J. A. (2020) Extreme environmental conditions reduce coral reef fish biodiversity and productivity. Nat Commun 11(1):3832. https://doi.org/10.1038/s41467-020-17731-2

Brandl, S. J., Rasher, D. B., Côté, I. M., Casey, J. M., Darling, E. S., Lefcheck, J. S., & Duffy, J. E. (2019). Coral reef ecosystem functioning: Eight core processes and the role of biodiversity. *Frontiers in Ecology and the Environment*, *17*(8), 445–454. https://doi.org/10.1002/fee.2088

Branscomb, E. S., & Rittschof, D. (1984). An investigation of low frequency sound waves as a means of inhibiting barnacle settlement. Journal of Experimental Marine Biology and Ecology, 79(2), 149–154. https://doi.org/10.1016/0022-0981(84)90215-6

Breiman L. (2001) Random Forests. Machine Learning 45:5–32 https://doi.org/10.1023/A:1010933404324

Brogan, M. W. (1994). Two methods of sampling fish larvae over reefs: A comparison from the Gulf of California. Marine Biology, 118(1), 33–44. https://doi.org/10.1007/BF00699217

Brook, B. W., Sodhi, N. S., & Bradshaw, C. J. A. (2008). Synergies among extinction drivers under global change. Trends in Ecology & Evolution, 23(8), 453–460. https://doi.org/10.1016/j.tree.2008.03.011

Bruce, T., Meirelles, P. M., Garcia, G., Paranhos, R., Rezende, C. E., Moura, R. L. de, Filho, R.-F., Coni, E. O. C., Vasconcelos, A. T., Filho, G. A., Hatay, M., Schmieder, R., Edwards, R., Dinsdale, E., & Thompson, F. L. (2012). Abrolhos Bank Reef Health Evaluated by Means of Water Quality, Microbial Diversity, Benthic Cover, and Fish Biomass Data. *PLOS ONE*, *7*(6), e36687. https://doi.org/10.1371/journal.pone.0036687

Bruno, J. F., & Selig, E. R. (2007). Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. PLoS ONE, *2*(8), e711. https://doi.org/10.1371/journal.pone.0000711

Bruno, J. F., Côté, I. M., & Toth, L. T. (2019). Climate Change, Coral Loss, and the Curious Case of the Parrotfish Paradigm: Why Don't Marine Protected Areas Improve Reef Resilience? Annual Review of Marine Science, 11(1), 307–334. https://doi.org/10.1146/annurev-marine-010318-095300

Butler, J., Anderson, E. R., & Butler, M. J. (2022). Habitat Restoration Restores Underwater Soundscapes and Larval Recruitment. Frontiers in Ecology and Evolution, 10. https://doi.org/10.3389/fevo.2022.785986

Cabaitan P. C., Gomez E. D., Aliño P. M. (2008) Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. Journal of Experimental Marine Biology and Ecology 357:85–98. https://doi.org/10.1016/j.jembe.2008.01.001

Caicedo D. F. (2024) Taiwan's Green Island tourism: The green to the sight holds the dark of the past.

Calizza, E., Costantini, M. L., Careddu, G., & Rossi, L. (2017). Effect of habitat degradation on competition, carrying capacity, and species assemblage stability. Ecology and Evolution, 7(15), 5784–5796. https://doi.org/10.1002/ece3.2977

Canan, B., Pessoa, E. K. R., Volpato, G. L. [UNESP, Araújo, A., & Chellappa, S. (2011). Feeding and reproductive dynamics of the damselfish, *Stegastes fuscus* in the coastal reefs of northeastern Brazil. Animal Biology Journal, 113–126.

Canty S. W. J., Nowakowski A. J., Cox C. E., Valdivia A., Holstein D. M., Limer B., Lefcheck J. S., Craig N., Drysdale I., Giro A., Soto M., McField M. (2024) Interplay of management and environmental drivers shifts size structure of reef fish communities. Global Change Biology 30:e17257. https://doi.org/10.1111/gcb.17257

Carlson, R. R., Evans, L. J., Foo, S. A., Grady, B. W., Li, J., Seeley, M., Xu, Y., & Asner, G. P. (2021). Synergistic benefits of conserving land-sea ecosystems. Global Ecology and Conservation, 28, e01684. https://doi.org/10.1016/j.gecco.2021.e01684

Chan, Y., Lo, S., Quan, A., & Blumstein, D. T. (2019). Ontogenetic shifts in perceptions of safety along structural complexity gradients in a territorial damselfish. Current Zoology, *65*(2), 183–188. https://doi.org/10.1093/cz/zoy091

Chang, C.-H., Shih, H.-J., Chen, W.-B., Su, W.-R., Lin, L.-Y., Yu, Y.-C., & Jang, J.-H. (2018). Hazard Assessment of Typhoon-Driven Storm Waves in the Nearshore Waters of Taiwan. Water, 10, 926. https://doi.org/10.3390/w10070926

Chapman, M. R., & Kramer, D. L. (2000). Movements of Fishes Within and Among Fringing Coral Reefs in Barbados. Environmental Biology of Fishes, 57(1), 11–24. https://doi.org/10.1023/A:1004545724503

Cheminée, A., Merigot, B., Vanderklift, M. A., Francour, P. (2016). Does habitat complexity influence fish recruitment? Mediterranean Marine Science, 17, 39–46. https://doi.org/10.12681/mms.1231

Chen, L.-S. (2002). Post-settlement Diet Shift of *Chlorurus sordidus* and *Scarus schlegeli* (Pisces: Scaridae). Zoological Studies.

Cheung, P.-Y., Nozawa, Y., & Miki, T. (2021). Ecosystem engineering structures facilitate ecological resilience: A coral reef model. Ecological Research, 36(4), 673–685. https://doi.org/10.1111/1440-1703.12230

Choat, J. H., & Bellwood, D. R. (1991). Reef fishes: Their history and evolution. In The ecology of fishes on coral reefs (pp. 39–66). Elsevier.

Christensen, V., Coll, M., Piroddi, C., Steenbeek, J., Buszowski, J., & Pauly, D. (2014). A century of fish biomass decline in the ocean. Marine Ecology Progress Series, 512, 155–166. https://doi.org/10.3354/meps10946

Claudet, J. (2018). Six conditions under which MPAs might not appear effective (when they are). ICES Journal of Marine Science, 75(3), 1172–1174. https://doi.org/10.1093/icesjms/fsx074

Coker D. J., Wilson SK, Pratchett MS (2013) Importance of live coral habitat for reef fishes. Reviews in Fish Biology and Fisheries 24:89. https://doi.org/10.1007/s11160-013-9319-5

Coker, D. J., Graham, N. A. J., & Pratchett, M. S. (2012). Interactive effects of live coral and structural complexity on the recruitment of reef fishes. Coral Reefs, 31(4), 919–927. https://doi.org/10.1007/s00338-012-0920-1

Collins, W. P., Bellwood, D. R., & Morais, R. A. (2024). Small coral reef fishes with large ecological footprints. Coral Reefs, 43(2), 233–242. https://doi.org/10.1007/s00338-023-02384-6

Connell SD, Jones GP (1991) The influence of habitat complexity on postrecruitment processes in a temperate reef fish population. Journal of Experimental Marine Biology and Ecology 151:271–294. https://doi.org/10.1016/0022-0981(91)90129-K

Coppock AG, Gardiner NM, Jones GP (2016) Sniffing out the competition? Juvenile coral reef damselfishes use chemical cues to distinguish the presence of conspecific and heterospecific aggregations. Behavioral Processes 125:43–50. https://doi.org/10.1016/j.beproc.2016.02.001

Cox, K., Brennan, L. P., Gerwing, T. G., Dudas, S. E., & Juanes, F. (2018). Sound the alarm: A meta-analysis on the effect of aquatic noise on fish behavior and physiology. Global Change Biology, 24(7), 3105–3116. https://doi.org/10.1111/gcb.14106

Crisp S. K., Tebbett S. B., Bellwood D. R. (2022) A critical evaluation of benthic phase shift studies on coral reefs. Marine Environmental Research 178:105667. https://doi.org/10.1016/j.marenvres.2022.105667

Cruz I. C. S., Loiola M., Albuquerque T., Reis R., Nunes J. de A. C. C., Reimer J. D., Mizuyama M., Kikuchi R. K. P. , Creed J. C. (2015) Effect of Phase Shift from Corals to Zoantharia on Reef Fish Assemblages. PLOS ONE 10:e0116944. https://doi.org/10.1371/journal.pone.0116944

Dahlgren, C. P., & Eggleston, D. B. (2000). Ecological Processes Underlying Ontogenetic Habitat Shifts in a Coral Reef Fish. Ecology. https://www.academia.edu/68548785/Ecological_Processes_Underlying_Ontogenetic_Habitat_Shifts_in_a_Coral_Reef_Fish

Dai C-F., Soong K., Chen C. A., Hwang J-S., Fan T., Hen-yi, Hsieh, Chang J. (2009) The status of coral reefs in Taiwan and the conservation problems. 265–276

Darling E. S., Graham N. A. J., Januchowski-Hartley F. A., Nash K. L., Pratchett M. S., Wilson S. K. (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561–575. https://doi.org/10.1007/s00338-017-1539-z

Davenport, J., & Davenport, J. L. (2006). The impact of tourism and personal leisure transport on coastal environments: A review. Estuarine, Coastal and Shelf Science, 67(1), 280–292. https://doi.org/10.1016/j.ecss.2005.11.026

Davies, H. L., Cox, K. D., Murchy, K. A., Shafer, H. M., Looby, A., & Juanes, F. (2024). Marine and Freshwater Sounds Impact Invertebrate Behavior and Physiology: A Meta-Analysis. Global Change Biology, 30(11), e17593. https://doi.org/10.1111/gcb.17593

de Jong, K., Amorim, M. C. P., Fonseca, P. J., Fox, C. J., & Heubel, K. U. (2018). Noise can affect acoustic communication and subsequent spawning success in fish. Environmental Pollution, 237, 814–823. https://doi.org/10.1016/j.envpol.2017.11.003

De'ath G., Fabricius K. E., Sweatman H., Puotinen M. (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences USA 109:17995–17999. https://doi.org/10.1073/pnas.1208909109

Debusschere, E., Hostens, K., Adriaens, D., Ampe, B., Botteldooren, D., De Boeck, G., De Muynck, A., Sinha, A. K., Vandendriessche, S., Van Hoorebeke, L., Vincx, M., & Degraer, S. (2016). Acoustic stress responses in juvenile sea bass *Dicentrarchus labrax* induced by offshore pile driving. Environmental Pollution, 208, 747–757. https://doi.org/10.1016/j.envpol.2015.10.055

Díaz Pérez, L., Rodriguez Zaragoza, F., Ortiz, M., Cupul-Magaña, A., Carriquiry, J., Rios-Jara, E., Rodríguez-Troncoso, A., & García Rivas, C. (2016). Coral Reef Health Indices versus the Biological, Ecological and Functional Diversity of Fish and Coral Assemblages in the Caribbean Sea. *PloS One*, *11*, e0161812. https://doi.org/10.1371/journal.pone.0161812

Donati, G., Parravicini, V., Leprieur, F., Hagen, O., Gaboriau, T., Heine, C., Kulbicki, M., Rolland, J., Salamin, N., Albouy, C., & Pellissier, L. (2019). A process-based model supports an association between dispersal and the prevalence of species traits in tropical reef fish assemblages. Ecography, 42. https://doi.org/10.1111/ecog.04537

Dunn, R. R., Harris, N. C., Colwell, R. K., Koh, L. P., & Sodhi, N. S. (2009). The sixth mass coextinction: Are most endangered species parasites and mutualists? Proceedings of the Royal Society B: Biological Sciences, 276(1670), 3037–3045. https://doi.org/10.1098/rspb.2009.0413

Dustan, P., Doherty, O., & Pardede, S. (2013). Digital Reef Rugosity Estimates Coral Reef Habitat Complexity. PLOS ONE, 8(2), e57386. https://doi.org/10.1371/journal.pone.0057386

Eddy, T. D., Lam, V. W. Y., Reygondeau, G., Cisneros-Montemayor, A. M., Greer, K., Palomares, M. L. D., Bruno, J. F., Ota, Y., & Cheung, W. W. L. (2021). Global decline in capacity of coral reefs to provide ecosystem services. One Earth, 4(9), 1278–1285. https://doi.org/10.1016/j.oneear.2021.08.016

Egner, S. A., & Mann, D. A. (2005). Auditory sensitivity of sergeant major damselfish Abudefduf saxatilis from post-settlement juvenile to adult. Marine Ecology Progress Series, 285, 213–222. https://doi.org/10.3354/meps285213

El-Dairi, R., Outinen, O., & Kankaanpää, H. (2024). Anthropogenic underwater noise: A review on physiological and molecular responses of marine biota. Marine Pollution Bulletin, 199, 115978. https://doi.org/10.1016/j.marpolbul.2023.115978

Elma E., Gullström M., Yahya S. A. S., Jouffray J-B., East H. K., Nyström M. (2023) Post-bleaching alterations in coral reef communities. Marine Pollution Bulletin 186:114479. https://doi.org/10.1016/j.marpolbul.2022.114479

Emslie, M. J., Cheal, A. J., & Johns, K. A. (2014). Retention of Habitat Complexity Minimizes Disassembly of Reef Fish Communities following Disturbance: A Large-Scale Natural Experiment. PLOS ONE, 9(8), e105384. https://doi.org/10.1371/journal.pone.0105384

Emslie, M. J., Cheal, A. J., Sweatman, H., & Delean, S. (2008). Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. Marine Ecology Progress Series, 371, 177–190. https://doi.org/10.3354/meps07657

Endo, C. A. K., Gherardi, D. F. M., Pezzi, L. P., & Lima, L. N. (2019). Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. Scientific Reports, 9(1), 1–11. https://doi.org/10.1038/s41598-019-45042-0

Engleman, A., Cox, K., Brooke, S. (2023). Dead but not forgotten: complexity of Acropora palmata colonies increases with greater composition of dead coral. PeerJ, 11, e16101.

English, S. A., Wilkinson, C., Baker, V., & Australian Institute of Marine Science (Eds.). (1997). Survey manual for tropical marine resources (2. ed). Australian Institute of Marine Science.

Epstein H. E., Kingsford M. J. (2019) Are soft coral habitats unfavourable? A closer look at the association between reef fishes and their habitat. Environ Biol Fish 102:479–497. https://doi.org/10.1007/s10641-019-0845-4

Erbe, C., Dunlop, R., & Dolman, S. (2018). Effects of Noise on Marine Mammals (pp. 277–309). https://doi.org/10.1007/978-1-4939-8574-6_10

Fabricius, K., De'ath, G., McCook, L., Turak, E., & Williams, D. McB. (2005). Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. Marine Pollution Bulletin, 51(1), 384–398. https://doi.org/10.1016/j.marpolbul.2004.10.041

Fakan, E. P., Dubuc, A., Hemingson, C. R., McCormick, M. I., & Hoey, A. S. (2025). Habitat degradation has species-specific effects on the stress response of coral reef fishes. Journal of Experimental Marine Biology and Ecology, 582, 152070. https://doi.org/10.1016/j.jembe.2024.152070

Fay, R. (2009). Soundscapes and the sense of hearing of fishes. Integrative Zoology, 4(1), 26–32. https://doi.org/10.1111/j.1749-4877.2008.00132.x

Feary, D. A., Almany, G. R., McCormick, M. I., & Jones, G. P. (2007). Habitat choice, recruitment and the response of coral reef fishes to coral degradation. Oecologia, 153(3), 727–737. https://doi.org/10.1007/s00442-007-0773-4

Félix-Hackradt, F. C. (2013). Temporal patterns of settlement, recruitment and post-settlement losses in a rocky reef fish assemblage in the South-Western Mediterranean Sea. Marine Biology. https://www.academia.edu/81227550/Temporal_patterns_of_settlement_recruitment_and_post_settlement_losses_in_a_rocky_reef_fish_assemblage_in_the_South_Western_Mediterranean_Sea

Félix-Hackradt, F. C., Hackradt, C. W., Treviño-Otón, J., Pérez-Ruzafa, A., & García-Charton, J. A. (2014). Habitat use and ontogenetic shifts of fish life stages at rocky reefs in South-western Mediterranean Sea. Journal of Sea Research, 88, 67–77. https://doi.org/10.1016/j.seares.2013.12.018

Ferrari, M. C. O., McCormick, M. I., Meekan, M. G., Simpson, S. D., Nedelec, S. L., & Chivers, D. P. (2018). School is out on noisy reefs: The effect of boat noise on predator learning and survival of juvenile coral reef fishes. Proceedings of the Royal Society B: Biological Sciences, 285(1871), 20180033. https://doi.org/10.1098/rspb.2018.0033

Ferreira, C. E. L., Floeter, S. R., Gasparini, J. L., Ferreira, B. P., & Joyeux, J. C. (2004). Trophic structure patterns of Brazilian reef fishes: A latitudinal comparison. Journal of Biogeography, 31(7), 1093–1106. https://doi.org/10.1111/j.1365-2699.2004.01044.x

Ferreira, C. M., Coni, E. O. C., Medeiros, D. V., Sampaio, C. L. S., Reis-Filho, J. A., Barros, F., Loiola, M., & Nunes, J. de A. C. da C. (2015). Community structure of shallow rocky shore fish in a tropical bay of the southwestern Atlantic. Brazilian Journal of Oceanography, 63(4), 379–396. https://doi.org/10.1590/S1679-87592015074706304

Fisher, R., O'Leary, R. A., Low-Choy, S., Mengersen, K., Knowlton, N., Brainard, R. E., & Caley, M. J. (2015). Species Richness on Coral Reefs and the Pursuit of Convergent Global Estimates. Current Biology, *25*(4), 500–505. https://doi.org/10.1016/j.cub.2014.12.022

Fontoura, L., Zawada, K. J. A., D'agata, S., Álvarez-Noriega, M., Baird, A. H., Boutros, N., Dornelas, M., Luiz, O. J., Madin, J. S., Maina, J. M., Pizarro, O., Torres-Pulliza, D., Woods, R. M., & Madin, E. M. P. (2020). Climate-driven shift in coral morphological structure predicts decline of juvenile reef fishes. Global Change Biology, 26(2), 557–567. https://doi.org/10.1111/gcb.14911

Garpe, K. C., Yahya, S. A. S., Lindahl, U., & Öhman, M. C. (2006). Long-term effects of the 1998 coral bleaching event on reef fish assemblages. Marine Ecology Progress Series, 315, 237–247. https://doi.org/10.3354/meps315237

Glynn, P., Enochs, I., Afflerbach, J., Brandtneris, V., & Serafy, J. (2014). Eastern Pacific reef fish responses to coral recovery following El Niño disturbances. Marine Ecology Progress Series, 495, 233–247. https://doi.org/10.3354/meps10594

Goatley, C. H. R., & Bellwood, D. R. (2016). Body size and mortality rates in coral reef fishes: A three-phase relationship. Proceedings of the Royal Society B: Biological Sciences, 283(1841), 20161858. https://doi.org/10.1098/rspb.2016.1858

Gordon, T. A. C., Harding, H. R., Wong, K. E., Merchant, N. D., Meekan, M. G., McCormick, M. I., Radford, A. N., & Simpson, S. D. (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. Proceedings of the National Academy of Sciences of the United States of America, 115(20), 5193–5198. https://doi.org/10.1073/pnas.1719291115

Gordon, T. A. C., Radford, A. N., Davidson, I. K., Barnes, K., McCloskey, K., Nedelec, S. L., Meekan, M. G., McCormick, M. I., & Simpson, S. D. (2019). Acoustic enrichment can enhance fish community development on degraded coral reef habitat. Nature Communications, *10*(1), 5414. https://doi.org/10.1038/s41467-019-13186-2

Gorospe, K. D., Donahue, M. J., Heenan, A., Gove, J. M., Williams, I. D., & Brainard, R. E. (2018). Local Biomass Baselines and the Recovery Potential for Hawaiian Coral Reef Fish Communities. Frontiers in Marine Science, 5, 162. https://doi.org/10.3389/fmars.2018.00162

Gössling, S. (1999). Ecotourism: A means to safeguard biodiversity and ecosystem functions? Ecological Economics, 29(2), 303–320. https://doi.org/10.1016/S0921-8009(99)00012-9

Gouezo, M., Fabricius, K., Harrison, P., Golbuu, Y., & Doropoulos, C. (2021). Optimizing coral reef recovery with context-specific management actions at prioritized reefs. Journal of Environmental Management, *295*, 113209. https://doi.org/10.1016/j.jenvman.2021.113209

Gouezo, M., Golbuu, Y., Van Woesik, R., Rehm, L., Koshiba, S., & Doropoulos, C. (2015). Impact of two sequential super typhoons on coral-reef communities in Palau. Marine Ecology

Progress Series. https://doi.org/10.3354/meps11518

Graham N.A. J., Nash K. L. (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326. https://doi.org/10.1007/s00338-012-0984-y

Graham, N. A. J., Nash, K. L., & Kool, J. T. (2011). Coral reef recovery dynamics in a changing world. Coral Reefs, 30(2), 283–294. https://doi.org/10.1007/s00338-010-0717-z

Gratwicke, B., & Speight, M. R. (2005). Effects of habitat complexity on Caribbean marine fish assemblages. Marine Ecology Progress Series, 292, 301–310. https://doi.org/10.3354/meps292301

Green, A. L., Bellwood, D. R., & International Union for Conservation of Nature. (2009). Monitoring functional groups of herbivorous reef fishes as indicators of coral reef resilience: A practical guide for coral reef managers in the Asia Pacific region. ftp://ftp.library.noaa.gov/noaa_documents.lib/CoRIS/IUCN_herbivorous_reef-fishes_2009.pdf

Grol, M., Rypel, A., & Nagelkerken, I. (2014). Growth potential and predation risk drive ontogenetic shifts among nursery habitats in a coral reef fish. Marine Ecology Progress Series, 502, 229–244. https://doi.org/10.3354/meps10682

Grorud-Colvert K., Sponaugle S. (2008) Larval supply and juvenile recruitment of coral reef fishes to marine reserves and non-reserves of the upper Florida Keys, USA. Marine Biology 156:277–288. https://doi.org/10.1007/s00227-008-1082-0

Grutter A. S., Blomberg S. P., Fargher B., Kuris A. M., McCormick M. I., Warner R. R. (2017) Size-related mortality due to gnathiid isopod micropredation correlates with settlement size in coral reef fishes. Coral Reefs 36:549–559. https://doi.org/10.1007/s00338-016-1537-6

Hafizt, M., Ministry of Marine Affairs and Fisheries, Indonesia, Munawaroh, M., Geospatial Information Agency, Indonesia, Wouthuyzen, S., Research Center for Oceanography, Indonesian Research and Innovation Agency, Adji, A. S., & Research Center for Oceanography, Indonesian Research and Innovation Agency. (2023). Coral Reef Health Index Calculation From Remote Sensing Data: A Review. International Journal of Conservation Science, 14(1), 247–264. https://doi.org/10.36868/IJCS.2023.01.17

Halford, A., Cheal, A. J., Ryan, D., & Williams, D. McB. (2004). Resilience to Large-Scale Disturbance in Coral and Fish Assemblages on the Great Barrier Reef. Ecology, 85(7), 1892–1905. https://doi.org/10.1890/03-4017

Harrison, P., Babcock, R., BULL, G., Oliver, J., Wallace, C., & Willis, B. (1984). Mass Spawning in Tropical Reef Corals. Science (New York, N.Y.), 223, 1186–1189.

https://doi.org/10.1126/science.223.4641.1186

Hatcher, B. G. (1990). Coral reef primary productivity. A hierarchy of pattern and process. Trends in Ecology and Evolution, 5(5), 149–155.

Hawkins, A. D. (1986). Underwater Sound and Fish Behaviour. In T. J. Pitcher (1st Ed.), The Behaviour of Teleost Fishes (pp. 114–151). Springer US. https://doi.org/10.1007/978-1-4684-8261-4_5

Hawkins, A. D., & Popper, A. N. (2017). A sound approach to assessing the impact of underwater noise on marine fishes and invertebrates. ICES Journal of Marine Science, *74*(3), 635–651. https://doi.org/10.1093/icesjms/fsw205

Heinrichs, J., Bender, D., & Schumaker, N. (2016). Habitat degradation and loss as key drivers of regional population extinction. Ecological Modelling, 335, 64–73. https://doi.org/10.1016/j.ecolmodel.2016.05.009

Helder, N. K., Burns, J. H. R., & Green, S. J. (2022). Intra-habitat structural complexity drives the distribution of fish trait groups on coral reefs. Ecological Indicators, 142, 109266. https://doi.org/10.1016/j.ecolind.2022.109266

Hickford, M. (2003). Comparative dispersal of larvae from demersal versus pelagic spawning fishes. Marine Ecology-Progress Series - Marine Ecology Progresss Series, 252, 255–271. https://doi.org/10.3354/meps252255

Holbrook, S. J., Schmitt, R. J., & Brooks, A. J. (2008). Resistance and resilience of a coral reef fish community to changes in coral cover. Marine Ecology Progress Series, 371, 263–271. https://doi.org/10.3354/meps07690

Horta e Costa, B., Guimarães, M. H., Rangel, M., Ressurreição, A., Monteiro, P., Oliveira, F., Bentes, L., Sales Henriques, N., Sousa, I., Alexandre, S., Pontes, J., Afonso, C. M. L., Belackova, A., Marçalo, A., Cardoso-Andrade, M., Correia, A. J., Lobo, V., Gonçalves, E. J., Pitta e Cunha, T., & Gonçalves, J. M. S. (2022). Co-design of a marine protected area zoning and the lessons learned from it. Frontiers in Marine Science, 9. https://doi.org/10.3389/fmars.2022.969234

Hothorn, T., Winell, H., Hornik, K., Wiel, M. A. van de, & Zeileis, A. (2023). coin: Conditional Inference Procedures in a Permutation Test Framework (Version 1.4-3) [Computer software]. https://cran.r-project.org/web/packages/coin/index.html

Hsiao C., Chen T., Dai C., Jan R. (2003) Colonization of Juveniles of the Damselfish Dascyllus reticulatus (Richardson) on the Southern Coast of Taiwan.

Hughes, T. P. (1994). Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. Science, 265(5178), 1547–1551.

Husson F., Josse J., Le S., Mazet J. (2006) FactoMineR: Multivariate Exploratory Data Analysis and Data Mining. 2.11 https://doi.org/10.32614/CRAN.package.FactoMineR

Igulu, M.M., Nagelkerken, I., Fraaije, R., van Hintum, R., Ligtenberg, H. & Mgaya, Y.D. (2011). The potential role of visual cues for microhabitat selection during the early life phase of a coral reef fish (*Lutjanus fulviflamma*). Journal of Experimental Marine Biology and Ecology, 401, 118–125. https://doi.org/10.1016/j.jembe.2011.01.022

Jenkins S. R., Marshall D., Fraschetti S. (2009) Settlement and Recruitment. In: Wahl M. (eds) Marine Hard Bottom Communities: Patterns, Dynamics, Diversity, and Change. Springer, Berlin, Heidelberg, pp 177–190. https://doi.org/10.1007/b76710_12

Jessen, C., & Wild, C. (2013). Herbivory effects on benthic algal composition and growth on a coral reef flat in the Egyptian Red Sea. Marine Ecology Progress Series, 476. https://doi.org/10.3354/meps10157

Jimenez, L. V., Fakan, E. P., & McCormick, M. I. (2020). Vessel noise affects routine swimming and escape response of a coral reef fish. PLOS ONE, *15*(7), e0235742. https://doi.org/10.1371/journal.pone.0235742

Johnson, D.W. (2007). Habitat Complexity Modifies Post-Settlement Mortality and Recruitment Dynamics of a Marine Fish. Ecology, 88, 1716–1725. https://doi.org/10.1890/06-0591.1

Jones, G. P. (1988). Some interactions between residents and recruits in two coral reef fishes. Journal of Experimental Marine Biology and Ecology, 114(2), 169–182. https://doi.org/10.1016/0022-0981(88)90136-0

Jones, G. P. (1990). The Importance of Recruitment to the Dynamics of a Coral Reef Fish Population. Ecology, 71, 1691–1698. https://doi.org/10.2307/1937578

Jones, G. P. (2015). Mission impossible: Unlocking the secrets of coral reef fish dispersal (pp. 16–27). https://doi.org/10.1017/CBO9781316105412.004

Jones, G. P., McCormick, M. I., Srinivasan, M., & Eagle, J. V. (2004). Coral decline threatens fish biodiversity in marine reserves. Proceedings of the National Academy of Sciences, 101(21), 8251–8253. https://doi.org/10.1073/pnas.0401277101

Juanes, F., Cox, K., Brennan, L., & Dudas, S. (2017). The effect of anthropogenic and biological noise on fish behavior and physiology: A meta-analysis. The Journal of the Acoustical Society of America, 141(5_Supplement), 3862. https://doi.org/10.1121/1.4988626

Juncker M., Wantiez L., Ponton D. (2006) Flexibility in size and age at settlement of coral reef fish:

spatial and temporal variations in Wallis Islands (South Central Pacific). Aquatic Living Resources 19:339–348. https://doi.org/10.1051/alr:2007004

Kaplan M., Mooney T., Partan J., Solow A. (2015) Coral reef species assemblages are associated with ambient soundscapes. Marine Ecology Progress Series 533:93–107. https://doi.org/10.3354/meps11382

Kaplan, M. B., & Mooney, T. A. (2016). Coral reef soundscapes may not be detectable far from the reef. Scientific Reports, *6*(1), 31862. https://doi.org/10.1038/srep31862

Kaplan, M. B., Mooney, T., Partan, J., & Solow, A. (2015). Coral reef species assemblages are associated with ambient soundscapes. Marine Ecology Progress Series, *533*, 93–107. https://doi.org/10.3354/meps11382

Kaufman, L., Sala, E., Sandin, S. A., Obura, D. O., Rohwer, F., & Tschirky, J. (2011). Coral health index (CHI): Measuring coral community health (Science and Knowledge Division, p. 15). Conservation International. https://portals.iucn.org/library/node/28851

Keck, F., Peller, T., Alther, R., Barouillet, C., Blackman, R., Capo, E., Chonova, T., Couton, M., Fehlinger, L., Kirschner, D., Knüsel, M., Muneret, L., Oester, R., Tapolczai, K., Zhang, H., & Altermatt, F. (2025). The global human impact on biodiversity. Nature, 641(8062), 395–400. https://doi.org/10.1038/s41586-025-08752-2

Keough M. J., Downes B. J. (1982) Recruitment of marine invertebrates: the role of active larval choices and early mortality. Oecologia 54:348–352. https://doi.org/10.1007/BF00380003

Keshavmurthy, S., Kuo, Y.-L., Huang, H. L., Carballo-Bolaños, R., Meng, P.-J., Wang, C., & Chen, W. (2019). Coral Reef Resilience in Taiwan: Lessons from Long-Term Ecological Research on the Coral Reefs of Kenting National Park (Taiwan). Journal of Marine Science and Engineering, 7, 388. https://doi.org/10.3390/jmse7110388

Kimirei, I. A., Nagelkerken, I., Trommelen, M., Blankers, P., van Hoytema, N., Hoeijmakers, D., Huijbers, C. M., Mgaya, Y. D., & Rypel, A. L. (2013). What Drives Ontogenetic Niche Shifts of Fishes in Coral Reef Ecosystems? Ecosystems, 16(5), 783–796. https://doi.org/10.1007/s10021-013-9645-4

Komyakova, V. (2018). Strong effects of coral species on the diversity and structure of reef fish communities: A multi-scale analysis. PLOS ONE. https://doi.org/10.1371/journal.pone.0202206

Komyakova, V., Munday, P. L., & Jones, G. P. (2013). Relative Importance of Coral Cover, Habitat Complexity and Diversity in Determining the Structure of Reef Fish Communities. PLOS ONE, 8(12), e83178. https://doi.org/10.1371/journal.pone.0083178

Komyakova, V., Munday, P. L., & Jones, G. P. (2019). Comparative analysis of habitat use and ontogenetic habitat-shifts among coral reef damselfishes. Environmental Biology of Fishes, 102(9), 1201–1218. https://doi.org/10.1007/s10641-019-00903-5

Kramer, M. J., Bellwood, O., Fulton, C. J., & Bellwood, D. R. (2015). Refining the invertivore: Diversity and specialisation in fish predation on coral reef crustaceans. Marine Biology, 162(9), 1779–1786. https://doi.org/10.1007/s00227-015-2710-0

Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R. K., Helm, A., Kuussaari, M., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K. M., Sang, A., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2010). Habitat fragmentation causes immediate and time-delayed biodiversity loss at different trophic levels. Ecology Letters, 13(5), 597–605. https://doi.org/10.1111/j.1461-0248.2010.01457.x

Kuo, C.-Y., Yuen, Y. S., Meng, P.-J., Ho, P.-H., Wang, J.-T., Liu, P.-J., Chang, Y.-C., Dai, C.-F., Fan, T.-Y., Lin, H.-J., Baird, A. H., & Chen, C. A (2012). Recurrent Disturbances and the Degradation of Hard Coral Communities in Taiwan. PLOS ONE, 7, e44364. https://doi.org/10.1371/journal.pone.0044364

Kuznetsova A., Brockhoff P. B., Christensen R. H. B. (2017) lmerTest Package: Tests in Linear Mixed Effects Models. Journal of Statistical Software 82:1–26. https://doi.org/10.18637/jss.v082.i13

La Manna, G., Picciulin, M., Crobu, A., Perretti, F., Ronchetti, F., Manghi, M., Ruiu, A., & Ceccherelli, G. (2021). Marine soundscape and fish biophony of a Mediterranean marine protected area. PeerJ, 9, e12551. https://doi.org/10.7717/peerj.12551

Lamont T. A. C., Williams B., Chapuis L., Prasetya M. E., Seraphim M. J., Harding H. R., May E. B., Janetski N., Jompa J., Smith D. J., Radford A. N., Simpson S. D. (2022) The sound of recovery: Coral reef restoration success is detectable in the soundscape. Journal of Applied Ecology 59:742–756 https://doi.org/10.1111/1365-2664.14089

Lassig, B. R. (1983). The effects of a cyclonic storm on coral reef fish assemblages. Environmental Biology of Fishes, 9(1), 55–63. https://doi.org/10.1007/BF00001058

Leahy S. M., Russ G. R., Abesamis R. A. (2015) Pelagic larval duration and settlement size of a reef fish are spatially consistent, but post-settlement growth varies at the reef scale. Coral Reefs 34:1283–1296. https://doi.org/10.1007/s00338-015-1330-y

Lecchini, D., Planes, S., & Galzin, R. (2005). Experimental assessment of sensory modalities of coral-reef fish larvae in the recognition of their settlement habitat. Behavioral Ecology and Sociobiology, 58(1), 18–26. https://doi.org/10.1007/s00265-004-0905-3

Lecchini, D., Planes, S., & Galzin, R. (2007). The influence of habitat characteristics and conspecifics on attraction and survival of coral reef fish juveniles. Journal of Experimental Marine Biology and Ecology, 341(1), 85–90. https://doi.org/10.1016/j.jembe.2006.10.006

Lecchini, D., Shima, J., Banaigs, B., & Galzin, R. (2005). Larval sensory abilities and mechanisms of habitat selection of a coral reef fish during settlement. Oecologia, 143(2), 326–334. https://doi.org/10.1007/s00442-004-1805-y

Lecchini, D., Waqalevu, V., Parmentier, E., Radford, C., & Banaigs, B. (2013). Fish larvae prefer coral over algal water cues: Implications of coral reef degradation. Marine Ecology Progress Series, 475, 303–307. https://doi.org/10.3354/meps1009

Lecchini, D., Waqalevu, V., Parmentier, E., Radford, C., & Banaigs, B. (2013). Fish larvae prefer coral over algal water cues: Implications of coral reef degradation. Marine Ecology Progress Series, *475*, 303–307. https://doi.org/10.3354/meps10094

Leis J. M. (1984) Larval fish dispersal and the East Pacific Barrier. Oceanog trop 19:181–192

Leis J. M., Hay A. C., Gaither M. R. (2011) Swimming ability and its rapid decrease at settlement in wrasse larvae (Teleostei: Labridae). Marine Biology 158:1239–1246. https://doi.org/10.1007/s00227-011-1644-4

Leis, J. M., Trnski, T., Doherty, P. J., & Dufour, V. (1998). Replenishment of fish populations in the enclosed lagoon of Taiaro Atoll: (Tuamotu Archipelago, French Polynesia) evidence from eggs and larvae. *Coral Reefs*, *17*(1), 1–8. https://doi.org/10.1007/s003380050085

Lessa, A. A., Xavier, F. C., Barroso, V. R., Cordeiro, C. A. M. M., & Ferreira, C. E. L. (2025). Exposure to anthropogenic noise affects feeding but not territory defence in damselfishes. Animal Behaviour, 223, 123130. https://doi.org/10.1016/j.anbehav.2025.123130

Leu M-Y., Meng P-J., Siong Tew K., Kuo J., Hung C-C. (2012) Spawning and Development of Larvae and Juveniles of the Indian Ocean Oriental Sweetlips, *Plectorhinchus vittatus* (Linnaeus, 1758), in the Aquarium. Journal of the World Aquaculture Society 43:595–606. https://doi.org/10.1111/j.1749-7345.2012.00594.x

Levin, P. S. (1993). Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. Oecologia, *94*(2), 176–185. https://doi.org/10.1007/BF00341315

Lewis, A. R. (1997). Recruitment and post-recruit immigration affect the local population size of coral reef fishes. Coral Reefs, *16*(3), 139–149. https://doi.org/10.1007/s003380050068

Lewis, S. M., & Wainwright, P. C. (1985). Herbivore abundance and grazing intensity on a Caribbean coral reef. Journal of Experimental Marine Biology and Ecology, 87(3), 215–228. https://doi.org/10.1016/0022-0981(85)90206-0

Lieske, E., & Myers, R. (2001). Reef Fishes of the World Indo-pacific and Caribbean (Revised Edition). Periplus.

Lillis, A., Apprill, A., Suca, J. J., Becker, C., Llopiz, J. K., & Mooney, T. A. (2018). Soundscapes influence the settlement of the common Caribbean coral *Porites astreoides* irrespective of light conditions. Royal Society Open Science, 5(12), 181358. https://doi.org/10.1098/rsos.181358

Lillis, A., Bohnenstiehl, D., Peters, J. W., & Eggleston, D. (2016). Variation in habitat soundscape characteristics influences settlement of a reef-building coral. PeerJ, 4, e2557. https://doi.org/10.7717/peerj.2557

Lillis, A., Eggleston, D. B., & Bohnenstiehl, D. R. (2013). Oyster Larvae Settle in Response to Habitat-Associated Underwater Sounds. PLOS ONE, 8(10), e79337. https://doi.org/10.1371/journal.pone.0079337

Lin, T.-H., Akamatsu, T., Sinniger, F., & Harii, S. (2021). Exploring coral reef biodiversity via underwater soundscapes. Biological Conservation, 253, 108901. https://doi.org/10.1016/j.biocon.2020.108901

Lin, T.-H., Sinniger, F., Harii, S., & Akamatsu, T. (2023). Using Soundscapes to Assess Changes in Coral Reef Social-Ecological Systems. Oceanography. https://doi.org/10.5670/oceanog.2023.s1.7

Lin, Y. V., Château, P.-A., Nozawa, Y., Wei, C.-L., Wunderlich, R. F., & Denis, V. (2024). Drivers of coastal benthic communities in a complex environmental setting. Marine Pollution Bulletin, 203, 116462. https://doi.org/10.1016/j.marpolbul.2024.116462

Lindahl, U., Ohman, M. C., & Schelten, C. K. (2001). The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. Marine Pollution Bulletin, 42(2), 127–131. https://doi.org/10.1016/s0025-326x(00)00167-3

Lirman, D. (1994). Ontogenetic shifts in habitat preferences in the three-spot damselfish, Stegastes planifrons (Cuvier), in Roatan Island, Honduras. Journal of Experimental Marine Biology and Ecology, 180(1), 71–81. https://doi.org/10.1016/0022-0981(94)90080-9

Liu, C.-H. E., Ribas-Deulofeu, L., Wu, M.-H. M., Chang, Y.-J., & Denis, V. (2024). Contrasting energy flow associated with tropical and subtropical reef fish assemblages. In Review. https://doi.org/10.21203/rs.3.rs-5359712/v1

Liu, P.-J., Meng, P.-J., Liu, L.-L., Wang, J.-T., & Leu, M.-Y. (2012). Impacts of human activities on coral reef ecosystems of southern Taiwan: A long-term study. Marine Pollution Bulletin, 64(6), 1129–1135. https://doi.org/10.1016/j.marpolbul.2012.03.031

Lönnstedt, O. M., McCormick, M. I., Chivers, D. P., & Ferrari, M. C. O. (2014). Habitat degradation is threatening reef replenishment by making fish fearless. Journal of Animal Ecology, 83(5), 1178–1185. https://doi.org/10.1111/1365-2656.12209

Lou D. C. (1993) Growth in juvenile Scarus rivulatus and Ctenochaetus binotatus: a comparison of families Scaridae and Acanthuridae. Journal of Fish Biology 42:15–23. https://doi.org/10.1111/j.1095-8649.1993.tb00302.x

Luiz, O. J., Allen, A. P., Robertson, D. R., Floeter, S. R., Kulbicki, M., Vigliola, L., Becheler, R., & Madin, J. S. (2013). Adult and larval traits as determinants of geographic range size among tropical reef fishes. Proceedings of the National Academy of Sciences, 110(41), 16498–16502. https://doi.org/10.1073/pnas.1304074110

MacNeil, M. A., Graham, N. A. J., Cinner, J. E., Wilson, S. K., Williams, I. D., Maina, J., Newman, S., Friedlander, A. M., Jupiter, S., Polunin, N. V. C., & McClanahan, T. R. (2015). Recovery potential of the world's coral reef fishes. Nature, *520*(7547), 341–344. https://doi.org/10.1038/nature14358

Mann D., Casper B., Boyle K., Tricas T. (2007) On the attraction of larval fishes to reef sounds. Mar Ecol Prog Ser 338:307–310. https://doi.org/10.3354/meps338307

Marcon, E., & Hérault, B. (2015). Entropart: An R package to measure and partition diversity. Journal of Statistical Software, 67(1), 1–26. https://doi.org/10.18637/jss.v067.i08

Martinez Arbizu, P. (2020). pairwiseAdonis: Pairwise multilevel comparison using adonis (Version 0.4) [R]. https://github.com/pmartinezarbizu/pairwiseAdonis (Original work published 2017)

Matte, J.-M. O., Fraser, D. J., & Grant, J. W. A. (2024). Recruitment dynamics of juvenile salmonids: Comparisons among populations and with classic case studies. Journal of Fish Biology, *105*(1), 10–22. https://doi.org/10.1111/jfb.15748

Mattos, F. M. G., Yeemin, T., Sutthacheep, M., & Feitosa, J. L. L. (2023). Biogeographic and environmental drivers of reef fish diversity in coastal islands of the Gulf of Thailand. Marine Ecology Progress Series, 724, 33–46. https://doi.org/10.3354/meps14447

McAfee, D, Williams, BR, McLeod, L, Reuter, A, Wheaton, Z, Connell, SD (2023). Soundscape enrichment enhances recruitment and habitat building on new oyster reef restorations. Journal of Applied Ecology, 60, 111–120. https://doi.org/10.1111/1365-2664.14307

McClanahan, T. R. (2018). Community biomass and life history benchmarks for coral reef fisheries. Fish and Fisheries, 19(3), 471–488. https://doi.org/10.1111/faf.12268

McCloskey, K. P., Radford, A. N., Rose, A., Casiraghi, G., Lubbock, N., Weschke, E., Titus, B. M., Exton, D. A., & Simpson, S. D. (2023). SCUBA noise alters community structure and cooperation at Pederson's cleaner shrimp cleaning stations. Frontiers in Marine Science, 10. https://doi.org/10.3389/fmars.2023.1058414

McCormick, M. I., Allan, B. J. M., Harding, H., & Simpson, S. D. (2018). Boat noise impacts risk assessment in a coral reef fish but effects depend on engine type. Scientific Reports, 8(1), 3847. https://doi.org/10.1038/s41598-018-22104-3

Mccormick, M., & Makey, L. (1997). Post-settlement transition in coral reef fishes: Overlooked complexity in niche shifts. Marine Ecology Progress Series, 153, 247–257. https://doi.org/10.3354/meps153247

Mccormick, M., Fakan, E., Nedelec, S., & Allan, B. (2019). Effects of boat noise on fish fast-start escape response depend on engine type. Scientific Reports, 9, 6554. https://doi.org/10.1038/s41598-019-43099-5

McKenna, M. F., Rowell, T. J., Margolina, T., Baumann-Pickering, S., Solsona-Berga, A., Adams, J. D., Joseph, J., Kim, E. B., Kok, A. C., Kügler, A., Lammers, M. O., Merkens, K., Reeves, L. P., Southall, B. L., Stimpert, A. K., Barkowski, J., Thompson, M. A., Van Parijs, S., Wall, C. C., … Hatch, L. T. (2024). Understanding vessel noise across a network of marine protected areas. Environmental Monitoring and Assessment, 196(4), 369. https://doi.org/10.1007/s10661-024-12497-2

Medeiros, P. R., Grempel, R. G., Souza, A. T., Ilarri, M. I., & Sampaio, C. L. S. (2007). Effects of recreational activities on the fish assemblage structure in a northeastern Brazilian reef. 13.

Mendes, C. (2024). Assessing the Impacts of Overfishing on Coral Reef Ecosystems. Journal of Fisheries Research, 8(6). https://www.alliedacademies.org/abstract/

Mezger S. D., Klinke A., Tilstra A., El-Khaled Y. C., Thobor B., Wild C. (2022) The widely distributed soft coral *Xenia umbellata* exhibits high resistance against phosphate enrichment and temperature increase. Sci Rep 12:22135. https://doi.org/10.1038/s41598-022-26325-5

Milazzo, M., Chemello, R., Badalamenti, F., Camarda, R., & Riggio, S. (2002). The Impact of Human Recreational Activities in Marine Protected Areas: What Lessons Should Be Learnt in the Mediterranean Sea? Marine Ecology, 23(s1), 280–290. https://doi.org/10.1111/j.1439-0485.2002.tb00026.x

Milne, R., Bauch, C., & Anand, M. (2021). Local overfishing patterns have regional effects on health of coral, and economic transitions can promote its recovery. (p. 2021.08.15.456395) https://doi.org/10.1101/2021.08.15.456395

Minier, L., Bertucci, F., Gay, T., Chamot, Z., Turco, T., Schligler, J., Mills, S. C., Vidal, M., Parmentier, E., Sturny, V., Mathevon, N., Beauchaud, M., Lecchini, D., & Médoc, V. (2024). Behavioural response to boat noise weakens the strength of a trophic link in coral reefs. Environmental Pollution, *361*, 124770. https://doi.org/10.1016/j.envpol.2024.124770

Minier, L., Bertucci, F., Gay, T., Chamot, Z., Turco, T., Schligler, J., Mills, S. C., Vidal, M., Parmentier, E., Sturny, V., Mathevon, N., Beauchaud, M., Lecchini, D., & Médoc, V. (2024). Behavioural response to boat noise weakens the strength of a trophic link in coral reefs. Environmental Pollution, 361, 124770. https://doi.org/10.1016/j.envpol.2024.124770

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef ecosystems. Ecological Economics, 29(2), 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9

Mora, C. (2008). A clear human footprint in the coral reefs of the Caribbean. Proceedings. Biological Sciences, *275*(1636), 767–773. https://doi.org/10.1098/rspb.2007.1472

Morais, J., Morais, R., Tebbett, S.B. & Bellwood, D.R. (2022). On the fate of dead coral colonies. Functional Ecology, 36, 3148–3160. https://doi.org/10.1111/1365-2435.14182

Morais, R. A., Depczynski, M., Fulton, C., Marnane, M., Narvaez, P., Huertas, V., Brandl, S. J., & Bellwood, D. R. (2020). Severe coral loss shifts energetic dynamics on a coral reef. Functional Ecology, 34(7), 1507–1518. https://doi.org/10.1111/1365-2435.13568

Morais, R., & Bellwood, D. (2020). Principles for estimating fish productivity on coral reefs. Coral Reefs, 39. https://doi.org/10.1007/s00338-020-01969-9

Mouillot, D., Bellwood, D. R., Baraloto, C., Chave, J., Galzin, R., Harmelin-Vivien, M., Kulbicki, M., Lavergne, S., Lavorel, S., Mouquet, N., Paine, C. E. T., Renaud, J., & Thuiller, W. (2013). Rare Species Support Vulnerable Functions in High-Diversity Ecosystems. PLOS Biology, 11(5), e1001569. https://doi.org/10.1371/journal.pbio.1001569

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution, 28(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Mouillot, D., Villeger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., Chabanet, P., Floeter, S. R., Friedlander, A., Vigliola, L., & Bellwood, D. R. (2014). Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. Proceedings of the National Academy of Sciences, 111(38), 13757–13762. https://doi.org/10.1073/pnas.1317625111

Moulton, J. M. (1963). Acoustic Orientation of Marine Fishes and Invertebrates. In H. Autrum, E. Bünning, K. v. Frisch, E. Hadorn, A. Kühn, E. Mayr, A. Pirson, J. Straub, H. Stubbe, & W.

Weidel (Eds.), Orientierung der Tiere / Animal Orientation: Symposium in Garmisch-Partenkirchen 17.–21. 9. 1962 (pp. 27–39). Springer. https://doi.org/10.1007/978-3-642-99872-0_4

Moynihan J., Hall A., Kingsford M. (2022) Interrelationships between soft corals and reef-associated fishes on inshore-reefs of the Great Barrier Reef. Marine Ecology Progress Series 698:15–28. https://doi.org/10.3354/meps14160

Mumby, P. J. (2006). Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales. Biological Conservation, 128(2), 215–222. https://doi.org/10.1016/j.biocon.2005.09.042

Munday, P. L. (2001). Fitness consequences of habitat use and competition among coral-dwelling fishes. *Oecologia*, *128*(4), 585–593. https://doi.org/10.1007/s004420100690

Munday, P. L. (2004). Habitat loss, resource specialization, and extinction on coral reefs. Global Change Biology, 10(10), 1642–1647. https://doi.org/10.1111/j.1365-2486.2004.00839.x

Myrberg, A. A. (1980). Fish bio-acoustics: Its relevance to the ‘not so silent world.’ Environmental Biology of Fishes, 5(4), 297–304. https://doi.org/10.1007/BF00005184

Myrberg, A. A. (1997). Sound production by a coral reef fish (*Pomacentrus partitus*): Evidence for a vocal, territorial keep-out signal. Bulletin of Marine Science. https://www.semanticscholar.org/paper/Sound-production-by-a-coral-reef-fish-(Pomacentrus-Myrberg/0164dc3605d334baeb46093fd5d068c7573b18cd

Nedelec, S. L., Mills, S. C., Radford, A. N., Beldade, R., Simpson, S. D., Nedelec, B., & Côté, I. M. (2017). Motorboat noise disrupts co-operative interspecific interactions. Scientific Reports, 7(1), 6987. https://doi.org/10.1038/s41598-017-06515-2

Nedelec, S. L., Radford, A. N., Gatenby, P., Davidson, I. K., Velasquez Jimenez, L., Travis, M., Chapman, K. E., McCloskey, K. P., Lamont, T. A. C., Illing, B., McCormick, M. I., & Simpson, S. D. (2022). Limiting motorboat noise on coral reefs boosts fish reproductive success. Nature Communications, 13(1), 2822. https://doi.org/10.1038/s41467-022-30332-5

Nedelec, S., Radford, A., Gatenby, P., Keesje Davidson, I., Velasquez Jimenez, L., Travis, M., Chapman, K., McCloskey, K., Lamont, T., Illing, B., McCormick, M., & Simpson, S. (2023). Coral reef soundscapes and noise. The Journal of the Acoustical Society of America, 153(3_supplement), A61. https://doi.org/10.1121/10.0018162

Nelson, J. S., Grande, T., & Wilson, M. V. H. (2016). Fishes of the world (Fifth edition). John Wiley & Sons.

Nepstad, D. C., Stickler, C. M., Filho, B. S.-, & Merry, F. (2008). Interactions among Amazon land use, forests and climate: Prospects for a near-term forest tipping point. Philosophical Transactions of the Royal Society B: Biological Sciences, 363(1498), 1737–1746. https://doi.org/10.1098/rstb.2007.0036

Nichols, T. A., Anderson, T. W., & Širović, A. (2015). Intermittent Noise Induces Physiological Stress in a Coastal Marine Fish. PLOS ONE, 10(9), e0139157. https://doi.org/10.1371/journal.pone.0139157

Norström A, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral–macroalgal phase shifts. Marine Ecology Progress Series 376:295–306. https://doi.org/10.3354/meps07815

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). vegan: Community Ecology Package (Version 2.5-6) [Computer software]. https://CRAN.R-project.org/package=vegan

Osuka, K. E., Stewart, B. D., Samoilys, M., McClean, C. J., Musembi, P., Yahya, S., Hamad, A. R., & Mbugua, J. (2022). Depth and habitat are important drivers of abundance for predatory reef fish off Pemba Island, Tanzania. Marine Environmental Research, 175, 105587. https://doi.org/10.1016/j.marenvres.2022.105587

Paradis, E., Blomberg, S., Bolker [aut, B., cph, Brown, J., Claramunt, S., Claude, J., Cuong, H. S., Desper, R., Didier, G., Durand, B., Dutheil, J., Ewing, R. J., Gascuel, O., Guillerme, T., Heibl, C., Ives, A., Jones, B., Krah [aut, F., … Vienne, D. de. (2024). ape: Analyses of Phylogenetics and Evolution (Version 5.8-1) [Computer software]. https://cran.r-project.org/web/packages/ape/index.html

Parks, S. E., Miksis-Olds, J. L., & Denes, S. L. (2014). Assessing marine ecosystem acoustic diversity across ocean basins. Ecological Informatics, 21, 81–88. https://doi.org/10.1016/j.ecoinf.2013.11.003

Parmentier E., Berten L., Rigo P., Aubrun F., Nedelec S. L., Simpson S. D., Lecchini D. (2015) The influence of various reef sounds on coral-fish larvae behaviour: reef-sound influence on fish larvae behaviour. J Fish Biol 86:1507–1518. https://doi.org/10.1111/jfb.12651

Parsons, E. C. M. (2017). Impacts of Navy Sonar on Whales and Dolphins: Now beyond a Smoking Gun? Frontiers in Marine Science, 4, 295. https://doi.org/10.3389/fmars.2017.00295

Peng, C., Zhao, X., & Liu, G. (2015). Noise in the Sea and Its Impacts on Marine Organisms. International Journal of Environmental Research and Public Health, 12(10), 12304–12323. https://doi.org/10.3390/ijerph121012304

Petitgas, P., Secor, D. H., McQuinn, I., Huse, G., & Lo, N. (2010). Stock collapses and their recovery: Mechanisms that establish and maintain life-cycle closure in space and time. ICES Journal of Marine Science, 67(9), 1841–1848. https://doi.org/10.1093/icesjms/fsq082

Philip, J., & Mukundi, M. (2024). Community-Based Approaches to Environmental Conservation: Empowering Local Initiatives. Greener Journal of Social Sciences, 14, 289–299. https://doi.org/10.15580/gjss.2024.2.122024211

Pickens C., Smart T., Reichert M., Sedberry G. R., McGlinn D. (2021) No effect of marine protected areas on managed reef fish species in the southeastern United States Atlantic Ocean. Regional Studies in Marine Science 44:101711. https://doi.org/10.1016/j.rsma.2021.101711

Pieniazek, R. H., Beach, R. K., Dycha, G. M., Mickle, M. F., & Higgs, D. M. (2023). Navigating noisy waters: A review of field studies examining anthropogenic noise effects on wild fish. The Journal of the Acoustical Society of America, 154(5), 2828–2842. https://doi.org/10.1121/10.0022254

Pine, M. K., Jeffs, A. G., Wang, D., & Radford, C. A. (2016). The potential for vessel noise to mask biologically important sounds within ecologically significant embayments. Ocean & Coastal Management, 127, 63–73. https://doi.org/10.1016/j.ocecoaman.2016.04.007

Popper, A. N., & Hawkins, A. D. (2019). An overview of fish bioacoustics and the impacts of anthropogenic sounds on fishes. Journal of Fish Biology, 94(5), 692–713. https://doi.org/10.1111/jfb.13948

Popper, A. N., Amorim, C., Fine, M. L., Higgs, D. M., Mensinger, A. F., & Sisneros, J. A. (2024). Introduction to the special issue on fish bioacoustics: Hearing and sound communicationa). The Journal of the Acoustical Society of America, 155(4), 2385–2391. https://doi.org/10.1121/10.0025553

Pratchett, M. S., Hoey, A. S., Wilson, S. K., Messmer, V., & Graham, N. A. J. (2011). Changes in Biodiversity and Functioning of Reef Fish Assemblages following Coral Bleaching and Coral Loss. Diversity, 3(3), 424–452. https://doi.org/10.3390/d3030424

Price, N. W., Liu, Y., Chen, K.-S., Tang, C.-H., Chen, C.-F., Cheng, M.-C., & Wen, C. K.-C. (2023). Acute noise is harmful on the anti-predator behaviour of commercially important juvenile coral reef fishes. Behavioural Processes, 210, 104908. https://doi.org/10.1016/j.beproc.2023.104908

R Core Team. (2024). R: A Language and Environment for Statistical Computing (Version 4.3.3) [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Radford C. A., Stanley J. A., Simpson S. D., Jeffs A. G. (2011) Juvenile coral reef fish use sound to locate habitats. Coral Reefs 30:295–305. https://doi.org/10.1007/s00338-010-0710-6

Rankin, T. L., & Sponaugle, S. (2014). Characteristics of Settling Coral Reef Fish Are Related to Recruitment Timing and Success. PLOS ONE, 9(9), e108871. https://doi.org/10.1371/journal.pone.0108871

Rees, A., Sheehan, E. V., & Attrill, M. J. (2021). Optimal fishing effort benefits fisheries and conservation. Scientific Reports, 11(1), 3784. https://doi.org/10.1038/s41598-021-82847-4

Reverter, M., Helber, S. B., Rohde, S., de Goeij, J. M., & Schupp, P. J. (2022). Coral reef benthic community changes in the Anthropocene: Biogeographic heterogeneity, overlooked configurations, and methodology. Global Change Biology, *28*(6), 1956–1971. https://doi.org/10.1111/gcb.16034

Ribas-Deulofeu L., Château P-A., Denis V., Chen C. A. (2021) Portraying Gradients of Structural Complexity in Coral Reefs Using Fine-Scale Depth Profiles. Front Mar Sci 8. https://doi.org/10.3389/fmars.2021.675853

Ribas-Deulofeu, L., Denis, V., Palmas, S.D., Kuo, C.-Y., Hsieh, H.J. & Chen, C.A. (2016). Structure of Benthic Communities along the Taiwan Latitudinal Gradient. PLOS ONE, 11, e0160601. https://doi.org/10.1371/journal.pone.0160601

Roberts, L., & Rice, A. N. (2023). Vibrational and acoustic communication in fishes: The overlooked overlap between the underwater vibroscape and soundscape. The Journal of the Acoustical Society of America, *154*(4), 2708–2720. https://doi.org/10.1121/10.0021878

Rooney, T. P., Wiegmann, S. M., Rogers, D. A., & Waller, D. M. (2004). Biotic Impoverishment and Homogenization in Unfragmented Forest Understory Communities. Conservation Biology, 18(3), 787–798. https://doi.org/10.1111/j.1523-1739.2004.00515.x

Roth, F., Saalmann, F., Thomson, T., Coker, D. J., Villalobos, R., Jones, B. H., Wild, C., & Carvalho, S. (2018). Coral reef degradation affects the potential for reef recovery after disturbance. Marine Environmental Research, 142, 48–58. https://doi.org/10.1016/j.marenvres.2018.09.022

Roux N, Brooker RM, Lecellier G, Berthe C, Frédérich B, Banaigs B, Lecchini D (2015) Chemical spying in coral reef fish larvae at recruitment. Comptes Rendus Biologies 338:701–707 https://doi.org/10.1016/j.crvi.2015.05.004

Russ, G., Rizzari, J., Abesamis, R., & Alcala, A. (2020). Coral cover a stronger driver of reef fish trophic biomass than fishing. Ecological Applications, 31. https://doi.org/10.1002/eap.2224

Sartori, G., Taylor, M. L., Sebastian, P., & Prasetyo, R. (2021). Coral reef carnivorous fish biomass relates to oceanographic features depending on habitat and prey preference. Marine Environmental Research, 172, 105504. https://doi.org/10.1016/j.marenvres.2021.105504

Schroeder, R. E. (1987). Effects of Patch Reef Size and Isolation on Coral Reef Fish Recruitment. Bulletin Of Marine Science, 41, 11.

Sheppard, C. E., Williams, G. J., Exton, D. A., & Keith, S. A. (2023). Co-occurrence of herbivorous fish functional groups correlates with enhanced coral reef benthic state. Global Ecology and Biogeography, 32(3), 435–449. https://doi.org/10.1111/geb.13638

Shima J. S. (1999) Variability in relative importance of determinants of reef fish recruitment. Ecology Letters 2:304–310 https://doi.org/10.1046/j.1461-0248.1999.00089.x

Shulman M. J. (1984) Resource limitation and recruitment patterns in a coral reef fish assemblage. Journal of Experimental Marine Biology and Ecology 74:85–109 https://doi.org/10.1016/0022-0981(84)90039-X

Simpson, S. D., Meekan, M., McCauley, R., & Jeffs, A. (2004). Attraction of settlement-stage coral reef fishes to reef noise. Marine Ecology Progress Series, 276, 263–268. https://doi.org/10.3354/meps276263

Simpson, S. D., Purser, J., & Radford, A. N. (2015). Anthropogenic noise compromises antipredator behaviour in European eels. Global Change Biology, 21(2), 586–593. https://doi.org/10.1111/gcb.12685

Simpson, S. D., Radford, A. N., Holles, S., Ferarri, M. C. O., Chivers, D. P., McCormick, M. I., & Meekan, M. G. (2016a). Small-Boat Noise Impacts Natural Settlement Behavior of Coral Reef Fish Larvae. In A. N. Popper & A. Hawkins (Eds.), The Effects of Noise on Aquatic Life II (Vol. 875, pp. 1041–1048). Springer New York. https://doi.org/10.1007/978-1-4939-2981-8_129

Simpson, S. D., Radford, A. N., Nedelec, S. L., Ferrari, M. C. O., Chivers, D. P., McCormick, M. I., & Meekan, M. G. (2016b). Anthropogenic noise increases fish mortality by predation. Nature Communications, 7(1), 10544. https://doi.org/10.1038/ncomms10544

Simpson, S. D., Wittenrich, M. L., Meekan, M. G., & Yan, H. Y. (2002). The importance of sound for navigation at settlement in coral reef fishes, with reference to the development of the auditory response. The Journal of the Acoustical Society of America, *112*(5_Supplement), 2204–2205. https://doi.org/10.1121/1.4778677

Siqueira, A. C., Morais, R. A., Bellwood, D. R., & Cowman, P. F. (2021). Planktivores as trophic drivers of global coral reef fish diversity patterns. Proceedings of the National Academy of

Sciences, 118(9). https://doi.org/10.1073/pnas.2019404118

Siriwong, S., True, J. D., & Piromvarakorn, S. (2018). Number of tourists has less impact on coral reef health than the presence of tourism infrastructure. Songklanakarin Journal of Science and Technology, 40, 1437–1445. https://doi.org/10.14456/sjst-psu.2018.175

Soga, M., & Gaston, K. J. (2024). Global synthesis indicates widespread occurrence of shifting baseline syndrome. BioScience, 74(10), 686–694. https://doi.org/10.1093/biosci/biae068

Sponaugle S., Walter K. D., Grorud-Colvert K., Paddack M. J. (2012) Influence of marine reserves on reef fish recruitment in the upper Florida Keys. Coral Reefs 31:641–652. https://doi.org/10.1007/s00338-012-0915-y

Sponaugle, S. (2015). Recruitment of coral reef fishes: Linkages across stages. In C. Mora (Ed.), Ecology of Fishes on Coral Reefs (pp. 28–33). Cambridge University Press. https://doi.org/10.1017/CBO9781316105412.005

Steele, M. A. (1999). Effects of shelter and predators on reef fishes. Journal of Experimental Marine Biology and Ecology, 233(1), 65–79. https://doi.org/10.1016/S0022-0981(98)00127-0

Stier, A., & Leray, M. (2014). Predators alter community organization of coral reef cryptofauna and reduce abundance of coral mutualists. Coral Reefs, 33. https://doi.org/10.1007/s00338-013-1077-2

Streit, R. P., Hemingson, C. R., Cumming, G. S., & Bellwood, D. R. (2021). How flexible are habitat specialists? Short-term space use in obligate coral-dwelling damselfishes. Reviews in Fish Biology and Fisheries, 31(2), 381–398. https://doi.org/10.1007/s11160-021-09646-y

Sun, Y.-J., Yen, S.-C., & Lin, T.-H. (2022). soundscape_IR: A source separation toolbox for exploring acoustic diversity in soundscapes. Methods in Ecology and Evolution, 13(11), 2347–2355. https://doi.org/10.1111/2041-210X.13960

Suzuki, S., Kawai, T., & Sakamaki, T. (2018). Combination of trophic group habitat preferences determines coral reef fish assemblages. Marine Ecology Progress Series, 586, 141–154. https://doi.org/10.3354/meps12378

Sweatman, H. (1988). Field evidence that settling coral reef fish larvae detect resident fishes using dissolved chemical cues. Journal of Experimental Marine Biology and Ecology, 124(3), 163–174. https://doi.org/10.1016/0022-0981(88)90170-0

Syms C., Jones G. P. (2001) Soft corals exert no direct effects on coral reef fish assemblages. Oecologia 127:560–571. https://doi.org/10.1007/s004420000617

Tebbett, S. B., Bellwood, D. R., Gahan, J., Ng, I., & Siqueira, A. C. (2025). Cross-habitat patterns of sediment transport and release by surgeonfishes. *Coral Reefs*, *44*(1), 63–75. https://doi.org/10.1007/s00338-024-02586-6

Tebbett, S. B., Yan, H. F., Lutzenkirchen, L. L., Siqueira, A. C., & Bellwood, D. R. (2024). Global patterns of herbivorous reef fish productivity: The role of *Prionurus laticlavius* in the Galápagos. *Coral Reefs*, *43*(2), 299–305. https://doi.org/10.1007/s00338-024-02473-0

Thobor B., Tilstra A., Bourne D. G., Springer K., Mezger S. D., Struck U., Bockelmann F., Zimmermann L., Yánez Suárez A. B., Klinke A., Wild C. (2022) The pulsating soft coral *Xenia umbellata* shows high resistance to warming when nitrate concentrations are low. Sci Rep 12:16788. https://doi.org/10.1038/s41598-022-21110-w

Tilman, D., Isbell, F., & Cowles, J. M. (2014). Biodiversity and Ecosystem Functioning. Annual Review of Ecology, Evolution, and Systematics, 45(1), 471–493. https://doi.org/10.1146/annurev-ecolsys-120213-091917

Tkachenko, K. S., Dung, V. V., & Ha, V. T. (2022). Phase shift from a stony-coral to a soft-coral community on a coral reef: A case study of an alternative state. Marine Biology Research, 18(9–10), 544–554. https://doi.org/10.1080/17451000.2022.2153869

Tolimieri, N. (1995). Effects of microhabitat characteristics on the settlement and recruitment of a coral reef fish at two spatial scales. Oecologia, 102(1), 52–63. https://doi.org/10.1007/BF00333310

Tseng R-S., Shao H-Ji, Chang Y-C., Centurioni L. (2012) Turbulent Mixing of the Kuroshio Waters Southeast of Taiwan. Kuroshio Science 6:27–34.

Turner, S. J., Thrush, S. F., Hewitt, J. E., Cummings, V. J., & Funnell, G. (2001). Fishing impacts and the degradation or loss of habitat structure. 6(5), 401–420.

Tyack, P. L. (2008). Implications for marine mammals of large-scale changes in the marine acoustic environment. Journal of Mammalogy, 89(3), 549–558. https://doi.org/10.1644/07-MAMM-S-307R.1

Victor, B. (1989). Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology. https://www.academia.edu/5583147/Planktonic_larval_duration_of_one_hundred_species_of_Pacific_and_Atlantic_damselfishes_Pomacentridae_

Victor, B. C. (2015). How many coral reef fish species are there? Cryptic diversity and the new molecular taxonomy. In C. Mora (Ed.), Ecology of Fishes on Coral Reefs (pp. 76–87). Cambridge University Press. https://doi.org/10.1017/CBO9781316105412.010

Webb, A. E., de Bakker, D. M., Soetaert, K., da Costa, T., van Heuven, S. M. A. C., van Duyl, F. C., Reichart, G.-J., & de Nooijer, L. J. (2021). Quantifying functional consequences of habitat degradation on a Caribbean coral reef. Biogeosciences, 18(24), 6501–6516. https://doi.org/10.5194/bg-18-6501-2021

Wellington G.M., Victor BC (1989) Planktonic larval duration of one hundred species of Pacific and Atlantic damselfishes (Pomacentridae). Marine Biology 101:557–567. https://doi.org/10.1007/BF00541659

Wen C.K.C., Almany GR, Williamson DH, Pratchett MS, Mannering TD, Evans RD, Leis JM, Srinivasan M, Jones GP (2013) Recruitment hotspots boost the effectiveness of no-take marine reserves. Biological Conservation 166:124–131. https://doi.org/10.1016/j.biocon.2013.06.017

Wenger, A., Fabricius, K., Jones, G., & Brodie, J. (2015). Effects of sedimentation, eutrophication, and chemical pollution on coral reef fishes (pp. 145–153). https://doi.org/10.1017/CBO9781316105412.017

Wielgus J., Chadwick-Furman N. E., Dubinsky Z. (2004) Coral cover and partial mortality on anthropogenically impacted coral reefs at Eilat, northern Red Sea. Marine Pollution Bulletin 48:248–253. https://doi.org/10.1016/j.marpolbul.2003.08.008

Williams, B. R., McAfee, D., & Connell, S. D. (2024). Anthropogenic noise disrupts acoustic cues for recruitment. *Proceedings B*. https://doi.org/10.1098/rspb.2024.0741

Williams, I. D., Baum, J. K., Heenan, A., Hanson, K. M., Nadon, M. O., & Brainard, R. E. (2015). Human, Oceanographic and Habitat Drivers of Central and Western Pacific Coral Reef Fish Assemblages. PLOS ONE, 10(4), e0120516. https://doi.org/10.1371/journal.pone.0120516

Williams, R., Erbe, C., Ashe, E., & Clark, C. W. (2015). Quiet(er) marine protected areas. Marine Pollution Bulletin, 100(1), 154–161. https://doi.org/10.1016/j.marpolbul.2015.09.012

Wilson, S. K., Burgess, S. C., Cheal, A. J., Emslie, M., Fisher, R., Miller, I., Polunin, N. V. C., & Sweatman, H. P. A. (2008). Habitat utilization by coral reef fish: Implications for specialists vs. generalists in a changing environment. Journal of Animal Ecology, 77(2), 220–228. https://doi.org/10.1111/j.1365-2656.2007.01341.x

Wilson, S. K., Fisher, R., Pratchett, M. S., Graham, N. a. J., Dulvy, N. K., Turner, R. A., Cakacaka, A., & Polunin, N. V. C. (2010). Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecological Applications: A Publication of the Ecological Society of America, 20(2), 442–451. https://doi.org/10.1890/08-2205.1

Wilson, S.K., Graham, N. A. J., Pratchett, M.S., Jones, G.P. & Polunin, N.V.C. (2006). Multiple disturbances and the global degradation of coral reefs: are reef fishes at risk or resilient? Global Change Biology, 12, 2220–2234. https://doi.org/10.1111/j.1365-2486.2006.01252.x

Wismer, S., Tebbett, S. B., Streit, R. P., & Bellwood, D. R. (2019). Young fishes persist despite coral loss on the Great Barrier Reef. Communications Biology, 2(1), Article 1. https://doi.org/10.1038/s42003-019-0703-0

Woodhead, A. J., Hicks, C. C., Norström, A. V., Williams, G. J., & Graham, N. A. J. (2019). Coral reef ecosystem services in the Anthropocene. Functional Ecology, *33*(6), 1023–1034. https://doi.org/10.1111/1365-2435.13331

Wormald C. L., Steele M. A., Forrester G. E. (2013) High population density enhances recruitment and survival of a harvested coral reef fish. Ecol Appl 23:365–373. https://doi.org/10.1890/12-0790.1

Wright, K. J., Higgs, D. M., Cato, D. H. & Leis, J. M. (2010). Auditory sensitivity in settlement-stage larvae of coral reef fishes. Coral Reefs, 29, 235–243. https://doi.org/10.1007/s00338-009-0572-y

Yang, R.-T., Chi, K.-S., Hu, S.-C., & Chen, H.-T. (1975). Yangetal1975-corals_fishs_and_benthic_biota_of_hsiao-liuchiu (No. 7; Special Publication, p. 53). Institute of Oceanography, College of Science, National Taiwan University. https://www.dipintothereef.com/uploads/3/7/3/5/37359245/yangetal1975-corals_fishs_and_benthic_biota_of_hsiao-liuchiu.pdf

Yang, T-L., Lee, S., Tsai, P-Y., Tan, C-J., Fan, T-Y. (2017). Spatial variation in the benthic community structure of coral reefs of Hsiaoliuchiu, Taiwan.

Yen K-W., Pan C-I., Chen C-H., Lien W-H. (2022) Spatiotemporal Characteristics of Fish Larvae and Juveniles in the Waters around Taiwan from 2007 to 2019. Animals 12:1890 https://doi.org/10.3390/ani12151890

Zhou, X.-Y., Lei, K., & Meng, W. (2017). An approach of habitat degradation assessment for characterization on coastal habitat conservation tendency. Science of The Total Environment, 593–594, 618–623. https://doi.org/10.1016/j.scitotenv.2017.03.212

Appendices

Appendix A: Supplementary material for Chapter 2

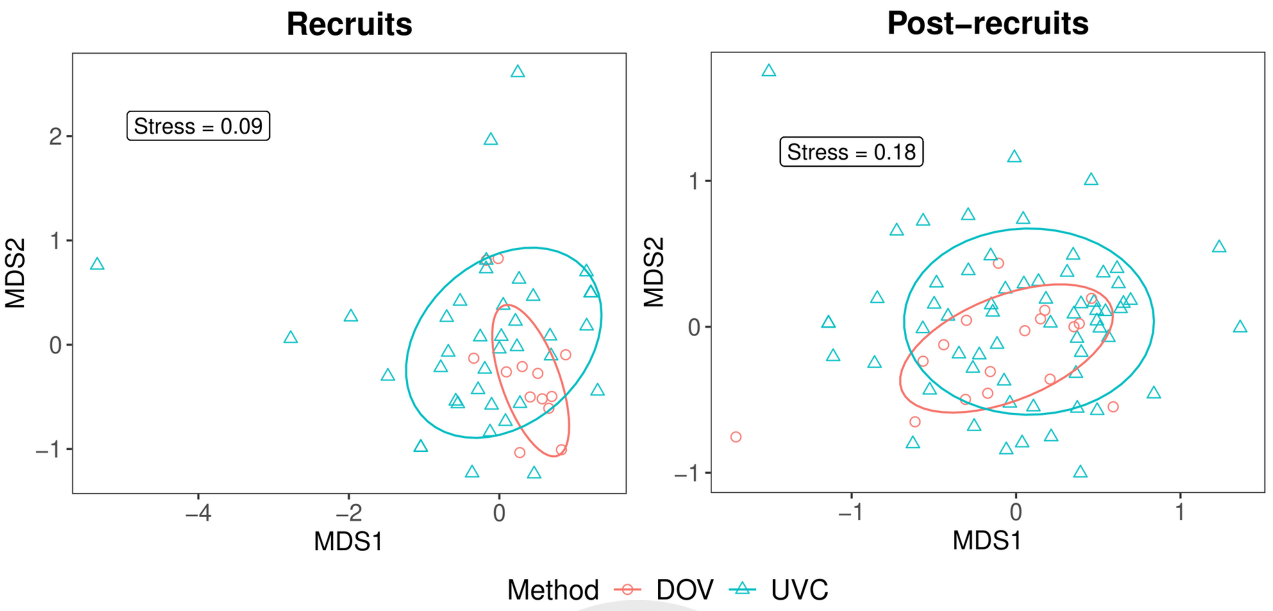

Fig. A1. NMDS results comparing the results from DOV vs UVC methods in the live and the dead coral patch treatments and the control area based on Bray-Curtis distance matrices from the count data.

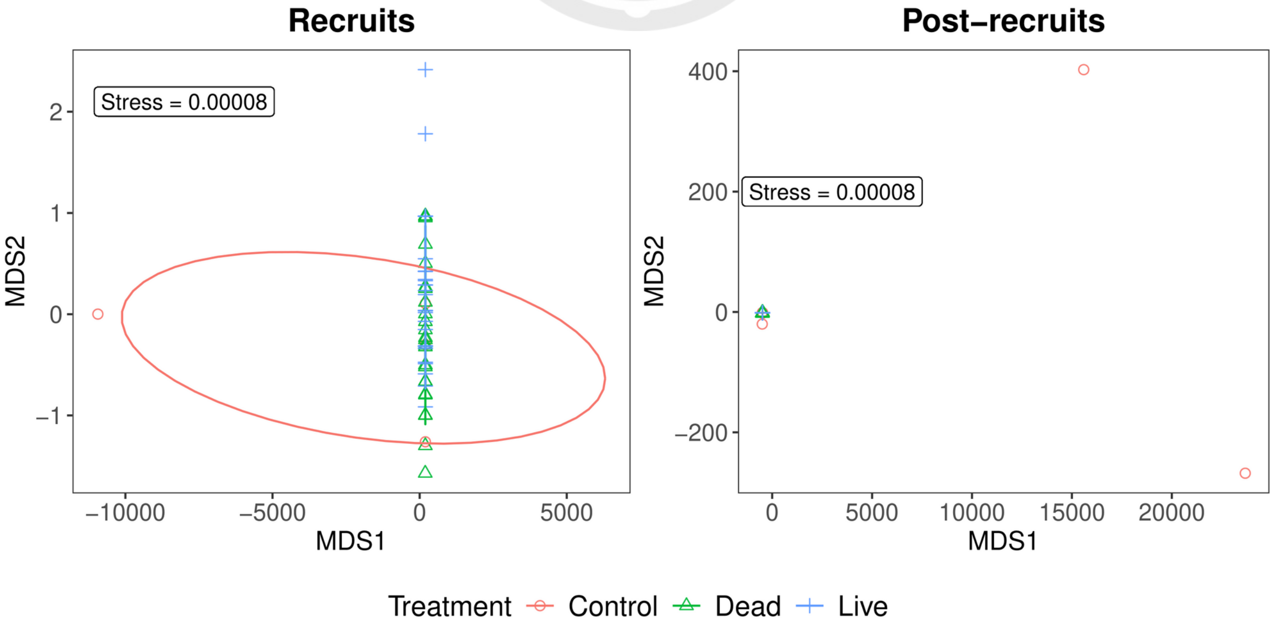

Fig. A2. NMDS results displaying the original Bray-Curtis similarity from raw abundance-count data recruit and adult reef fish assemblages in the live and dead coral treatments and the control area. This figure shows the over-dispersion caused by one sample in recruit and three samples in post-recruit assemblages

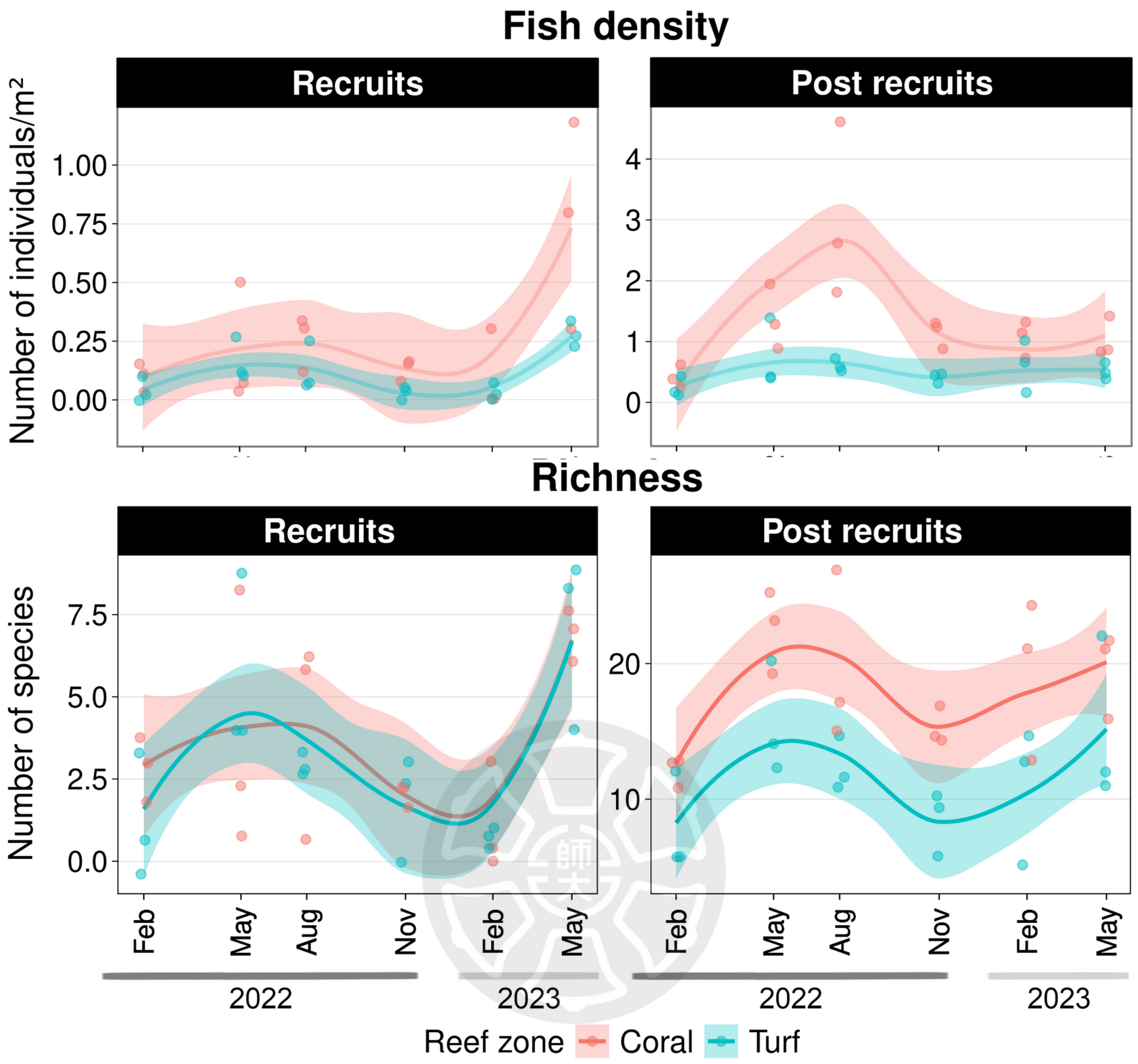

Fig. A3. Abundance and richness of recruits and post-recruits per transect in the turf and the coral zones of Shanfu reef. Points represent individual samples, and lines and the shaded areas represent the smoothed conditional means with the respective 95% confidence intervals.

Table A1. Results of the pairwise Dunn test for the abundance and richness of recruits between months according to DOV and UVC methods. Stars indicate months when DOV was the collection method.

Month pair		**Z**	**P.adj**
Recruit abundance			
2022-03-18	*2022-04-15	-1.74	0.2
2022-03-18	2022-05-30	-2.37	0.07
*2022-04-15	2022-05-30	-0.62	0.66
2022-03-18	*2022-07-20	-0.53	0.67
*2022-04-15	*2022-07-20	1.21	0.39
2022-05-30	*2022-07-20	1.83	0.19
2022-03-18	2022-08-09	-1.15	0.41
2022-04-15	2022-08-09	0.59	0.65
2022-05-30	2022-08-09	1.21	0.43
*2022-07-20	2022-08-09	-0.62	0.64
Recruit richness			
2022-03-18	*2022-04-15	-2.03	0.14
2022-03-18	2022-05-30	-2.39	0.06
*2022-04-15	2022-05-30	-0.36	0.76
2022-03-18	*2022-07-20	-0.58	0.67
*2022-04-15	*2022-07-20	1.45	0.29
2022-05-30	*2022-07-20	1.81	0.18
2022-03-18	2022-08-09	-1.3	0.37
*2022-04-15	2022-08-09	0.73	0.62
2022-05-30	2022-08-09	1.09	0.47
*2022-07-20	2022-08-09	-0.72	0.61

Table A2. Results of the pairwise Dunn test for the abundance and richness of post-recruits between months according to DOV and UVC methods. Stars indicate months when DOV was the collection method.

Month pair		**Z**	**P.adj**
Post-recruit abundance			
2022-03-18	*2022-04-15	-1.48	0.62
2022-03-18	2022-05-30	-2.23	0.92
*2022-04-15	2022-05-30	-0.75	0.86
2022-03-18	*2022-07-20	-0.82	0.83
*2022-04-15	*2022-07-20	0.67	0.91
2022-05-30	*2022-07-20	1.42	0.51
2022-03-18	2022-08-09	-0.65	0.84
*2022-04-15	2022-08-09	0.83	0.86
2022-05-30	2022-08-09	1.58	0.58
*2022-07-20	2022-08-09	0.16	0.92
Post-recruit richness			
2022-03-18	*2022-04-15	-1.81	0.36
2022-03-18	2022-05-30	-2.12	0.41
*2022-04-15	2022-05-30	-0.31	0.94
2022-03-18	*2022-07-20	-0.55	0.88
*2022-04-15	*2022-07-20	1.26	0.53
2022-05-30	*2022-07-20	1.57	0.42
2022-03-18	2022-08-09	-0.36	0.96
*2022-04-15	2022-08-09	1.45	0.48
2022-05-30	2022-08-09	1.76	0.31
*2022-07-20	2022-08-09	0.19	0.96

Table A3. Definitions and explanations of the habitat assessment scores (HAS) adapted from adapted from Gratwicke and Speight (2005).

	HAS Score 1	HAS Score 2	HAS Score 3	HAS Score 4	HAS Score 5
Rugosity (visual topographic estimate of the substratum in each quadrat; see Gratwicke and Speight 2005 for a visual representation)	Mostly flat (e.g. sandy matrix)	Flat with bumps but no holes	Shallow holes and peaks	Mostly vertical but deep holes, gaps and tall peaks	Vertical and horizontal holes, gaps and a maze-like structure
Variety of growth forms (number of growth forms including stalked/lobed/filamentous/ribbon-like/massive/branching/cylindrical/tube/fan/plate/pinnate/encrusting/other)	<2	3-4	5-6	7-8	9-10
Height (average height of habitat architecture in cm)	0-9	10-19	20-39	40-79	>80
Refuge size categories (i.e. how many different sizes the available refuges have). Categories: 1–5, 6–15, 16–30, 31–50 and >50cm).	0-1	2	3	4	5
Hard coral cover (%)	0-19	20-39	40-59	60-79	80-100

Table A4. Results of Kruskall-Wallis test between the live and the dead coral patch treatments. Total abundance and total richness per observation were used. Bold indicates statistical significance ($p < 0.05$).

Life-stage	Variable	Chi-Squared	Df	p-value
Recruits	Richness	40.6	2	**< 0.001**
	Abundance	41.3	2	**< 0.001**
Post-recruits	Richness	68.7	2	**< 0.001**
	Abundance	71.4	2	**< 0.001**

Table A5. Results of the pairwise Dunn's test for the abundance of recruits and post-recruits between patches. Bold indicates statistical significance ($p < 0.05$).

Patch pair			**Z**	**P.adj**
Recruit abundance				
	Live	Dead	-0.18	0.856
	Live	Control	-5.10	**< 0.001**
	Dead	Control	-4.92	**< 0.001**
Post-recruit abundance				
	Live	Dead	-4.46	**< 0.001**
	Live	Control	-8.36	**< 0.001**
	Dead	Control	-3.90	**< 0.001**

Table A6. Results of the pairwise Dunn's test for the richness of recruits and post-recruits between patches. Bold indicates statistical significance ($p < 0.05$).

Patch pair			**Z**	**P.adj**
Recruit richness				
	Live	Dead	0.04	0.968
	Live	Control	-5.01	**< 0.001**
	Dead	Control	-5.05	**< 0.001**
Post-recruit richness				
	Live	Dead	-4.23	**< 0.001**
	Live	Control	-8.44	**< 0.001**
	Dead	Control	-4.21	**< 0.001**

Table A7. Results of PERMANOVA for the Hellinger-transformed abundance count per sample of recruit and post-recruit assemblages. Bold letters in the P-value column indicate significance ($p < 0.05$). We stratified permutations within months and not between months.

Stage	Factor	Df	Sum of Sqs	R^2	F	Pr(>F)
Recruits	Patch	2	1.22	0.05	1.48	**0.006**
	Block	1	0.43	0.02	1.05	0.294
	Residual	53	21.8	0.93		
	Total	56	23.45	1		
Post-recruit	Patch	2	5.38	0.16	7.86	**0.001**
	Block	1	0.68	0.02	1.98	**0.010**
	Residual	79	27.05	0.82		
	Total	82	33.11	1		

Table A8. Results of pairwise PERMANOVA for the Hellinger transformed abundance count per sample of recruit and post-recruit assemblages comparing pairs of conditions in the live and the dead coral treatments and the control area. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Stage	Pair		Df	Sum of Sqs	R^2	F	Pr(>F)
Recruits	Control x Dead		1	0.42	0.03	0.97	0.506
		Residual	28	12	0.97		
		Total	29	12.42	1		
	Control x Live		1	0.52	0.04	1.29	0.178
		Residual	29	11.61	0.96		
		Total	30	12.12	1		
	Dead x Live		1	0.77	0.04	1.88	**0.033**
		Residual	51	20.87	0.96		
		Total	52	21.64	1		
Post-recruits	Control x Dead		1	1.08	0.05	2.59	**0.001**
		Residual	45	18.75	0.95		
		Total	46	19.82	1		
	Control x Live		1	2.89	0.17	9.52	**0.001**
		Residual	48	14.57	0.83		
		Total	49	17.46	1		
	Dead x Live		1	3.65	0.14	11.04	**0.001**
		Residual	67	22.13	0.86		
		Total	68	25.78	1		

Table A9. Results of PERMANOVA for the Hellinger transformed abundance count of recruit assemblages per sample according to functional traits. Three trophic groups were excluded from this analysis due to low abundance counts. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Stage	Functional traits		Df	Sum of Sqs	R^2	F	Pr(>F)
Recruits	Mobility						
	High mobility	Patch	2	1.51	0.08	1.94	**0.002**
		Residual	44	17.08	0.92		
		Total	46	18.59	1.00		
	Low Mobility	Patch	2	0.98	0.07	1.31	0.12
		Residual	34	12.72	0.93		
		Total	36	13.70	1.00		
	Trophic group						
	Mobile-invertebrate feeders	Patch	2	0.91	0.05	1.21	0.19
		Residual	43	16.13	0.95		
		Total	45	17.05	1.00		
	Planktivores	Patch	2	0.73	0.10	1.14	0.19
		Residual	20	6.36	0.90		
		Total	22	7.09	1.00		

Table A10. Results of pairwise PERMANOVA for the Hellinger transformed abundance count of recruit assemblages per sample of high-mobility species. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Recruits – High Mobility	Df	Sum of Sqs	R^2	F	Pr(>F)
Live x Dead	1	1.11	0.07	2.91	**0.001**
Residual	41	15.67	0.93		
Total	42	16.78	1		
Live x Control	1	0.59	0.07	1.69	0.057
Residual	23	8.02	0.93		
Total	24	8.61	1		
Dead x Control	1	0.32	0.03	0.73	0.642
Residual	24	10.48	0.97		
Total	25	10.8	1		

Table A11. Results of PERMANOVA for the Hellinger-transformed abundance count of post-recruit assemblages per sample according to functional traits. The five most abundant trophic groups were examined. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Post-recruits	Functional traits		Df	Sum of Sqs	R^2	F	Pr(>F)
	Mobility						
	High mobility	Patch	2	2.27	0.08	2.98	**0.001**
		Residual	71	27.08	0.92		
		Total	73	29.35	1.00		
	Low Mobility	Patch	2	6.01	0.21	9.31	**0.001**
		Residual	72	23.24	0.79		
		Total	74	29.26	1.00		
	Trophic group						
	Mobile-invertebrate feeders	Patch	2	2.26	0.08	3.17	**0.001**
		Residual	70	24.97	0.92		
		Total	72	27.23	1.00		
	Planktivores	Patch	2	5.15	0.33	11.08	**0.001**
		Residual	46	10.69	0.67		
		Total	48	15.83	1.00		
	Omnivores	Patch	2	5.55	0.30	10.69	**0.001**
		Residual	51	13.23	0.70		
		Total	53	18.78	1.00		
	Carnivores	Patch	2	1.88	0.10	2.78	**0.002**
		Residual	51	17.24	0.90		
		Total	53	19.12	1.00		
	Roving herbivores	Patch	2	0.80	0.08	0.92	0.313
		Residual	20	8.68	0.92		
		Total	22	9.48	1.00		

Table A12. Results of pairwise PERMANOVA for the Hellinger-transformed abundance count of post-recruit assemblages per sample according to mobility traits. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Post-recruits	Mobility traits	Traits	Df	Sum of Sqs	R^2	F	Pr(>F)
	High mobility						
		Live x Dead	1	1.05	0.04	2.78	**0.001**
		Residual	61	23.00	0.96		
		Total	62	24.05	1.00		
		Live x Control	1	1.34	0.08	3.58	**0.001**
		Residual	43	16.12	0.92		
		Total	44	17.46	1.00		
		Dead x Control	1	1.04	0.06	2.63	**0.001**
		Residual	38	15.04	0.94		
		Total	39	16.08	1.00		
	Low Mobility						
		Live x Dead	1	4.60	0.18	14.41	**0.001**
		Residual	66	21.07	0.82		
		Total	67	25.67	1.00		
		Live x Control	1	2.42	0.19	9.82	**0.001**
		Residual	41	10.09	0.81		
		Total	42	12.51	1.00		
		Dead x Control	1	0.88	0.05	2.12	0.025
		Residual	37	15.33	0.95		
		Total	38	16.21	1.00		

Table A13. Results of pairwise PERMANOVA for the Hellinger-transformed abundance count of post-recruit assemblages per sample according to trophic traits. Bold letters in the P-value column indicate statistical significance ($p < 0.05$). We stratified permutations within months and not between months.

Post-recruits	Trophic traits	Traits	Df	Sum of Sqs	R^2	F	Pr(>F)
	Mobile-invertebrate feeders						
		Live x Dead	1	0.94	0.04	2.65	**0.001**
		Residual	62	22.14	0.96		
		Total	63	23.08	1.00		
		Live x Control	1	1.44	0.09	4.24	**0.001**
		Residual	41	13.89	0.91		
		Total	42	15.33	1.00		
		Dead x Control	1	1.10	0.07	2.92	**0.001**
		Residual	37	13.92	0.93		
		Total	38	15.02	1.00		
	Planktivores						
		Live x Dead	1	4.38	0.31	19.89	**0.001**
		Residual	44	9.69	0.69		
		Total	45	14.06	1.00		
		Live x Control	1	1.28	0.17	6.91	0.051
		Residual	33	6.11	0.83		
		Total	34	7.39	1.00		
		Dead x Control	1	0.35	0.06	0.94	0.491
		Residual	15	5.57	0.94		
		Total	16	5.92	1.00		
	Omnivores						
		Live x Dead	1	4.01	0.24	15.17	**0.001**
		Residual	47	12.43	0.76		
		Total	48	16.44	1.00		
		Live x Control	1	2.27	0.24	10.63	**0.002**
		Residual	33	7.06	0.76		
		Total	34	9.34	1.00		
		Dead x Control	1	4.01	0.24	15.17	**0.001**
		Residual	47	12.43	0.76		
		Total	48	16.44	1.00		
	Carnivores						
		Live x Dead	1	1.15	0.07	3.47	**0.004**
		Residual	49	16.24	0.93		
		Total	50	17.39	1.00		

	Live x Control	1	0.84	0.07	2.87	**0.036**
	Residual	37	10.90	0.93		
	Total	38	11.74	1.00		
	Dead x Control	1	0.55	0.07	1.21	0.427
	Residual	16	7.34	0.93		
	Total	17	7.89	1.00		

Appendix B: Supplementary material for Chapter 3

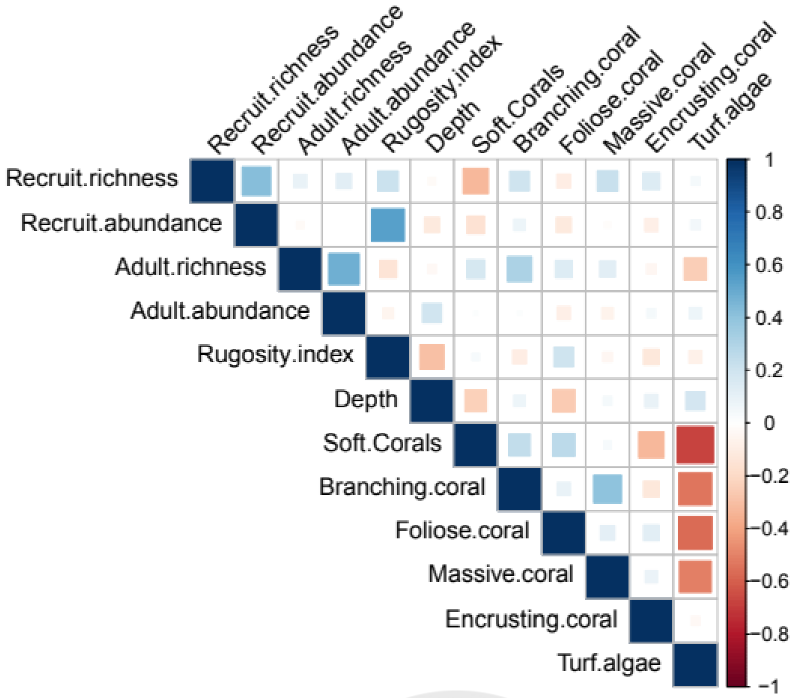

Fig. B1. Correlation plot between all the environmental variables, excluding soundscape, comprising all 17 study sites from both islands

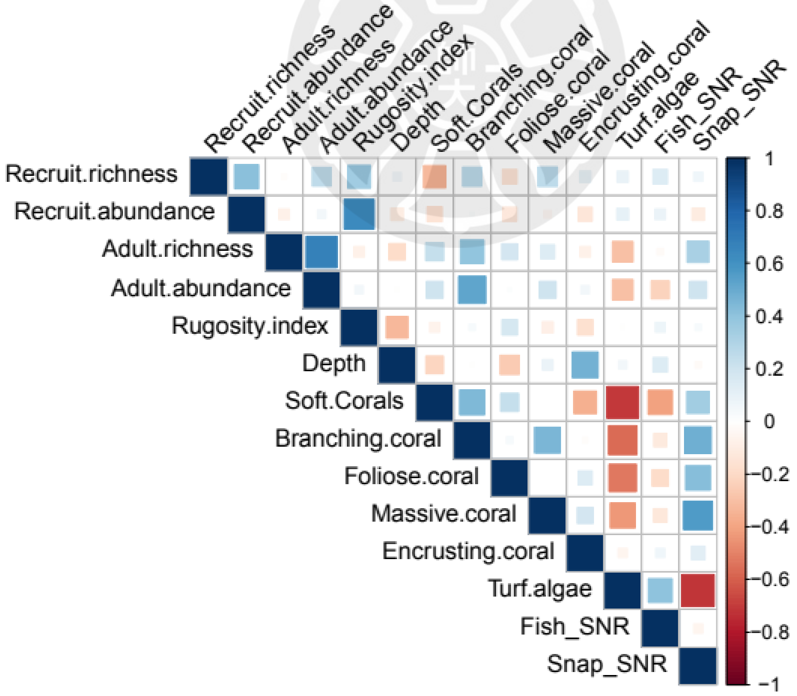

Fig. B2. Correlation plot between all the environmental variables, including soundscape, comprising 13 study sites from both islands.

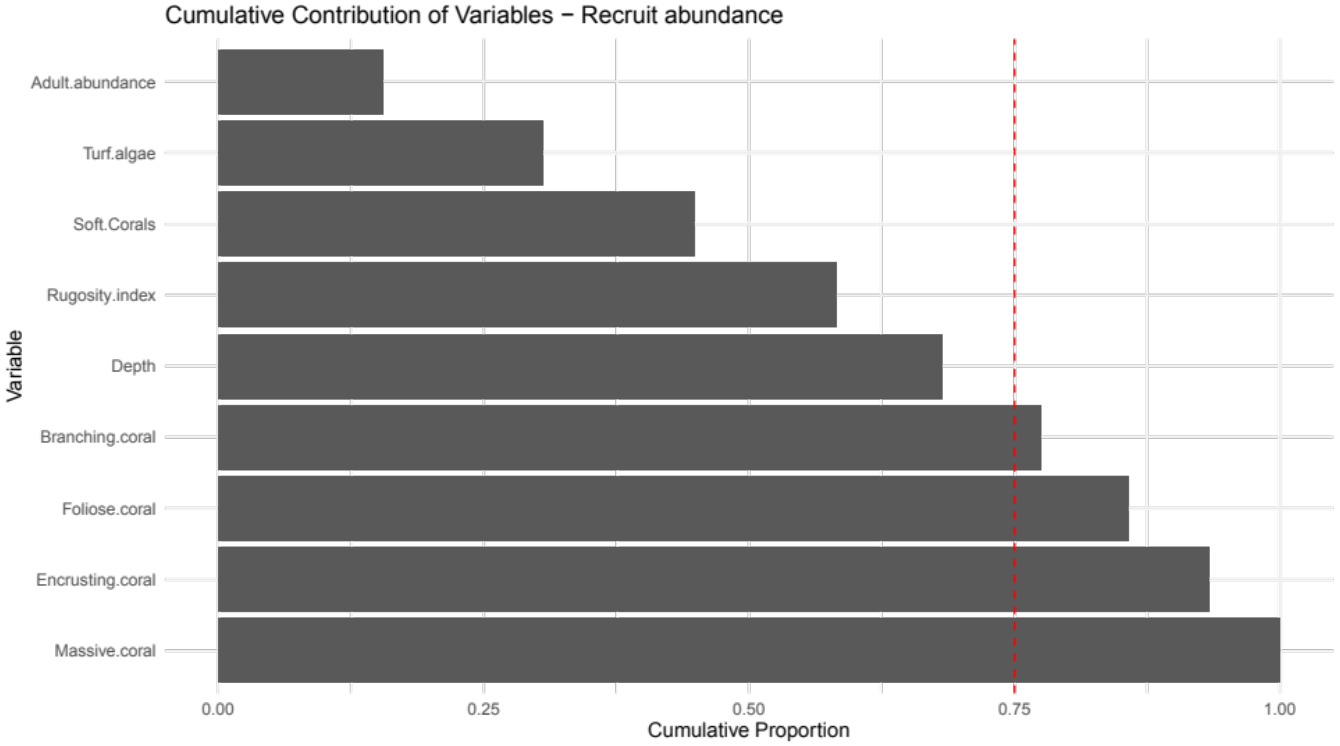

Fig. B3. Random forest model showing the relative importance of the explanatory variables in decreasing order, excluding acoustic variables. The x-axis shows the cumulative proportion of contribution from 0% to 100%. The red dashed line represents the point where variables contribute to at least 75% of the model's explanatory power. This model explains 34% and the first six variables together explain 26% of the variance in recruit abundance.

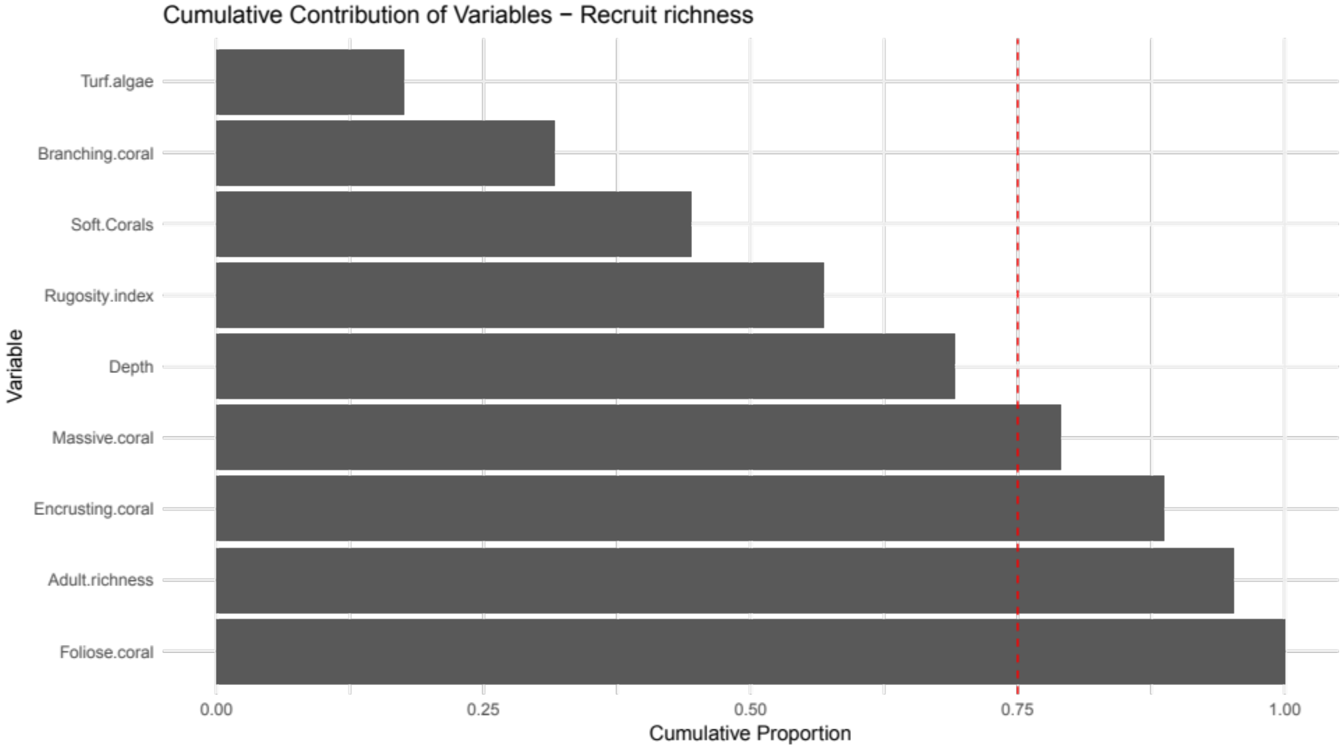

Fig. B4. Random forest model showing the relative importance of the explanatory variables in decreasing order excluding acoustic variables. The x-axis shows the cumulative proportion of contribution from 0% to 100%. The red dashed line represents the point where variables contribute to at least 75% of the model's explanatory power. This model explains 25%, and the first six variables explain 19% of the variance in recruit richness.

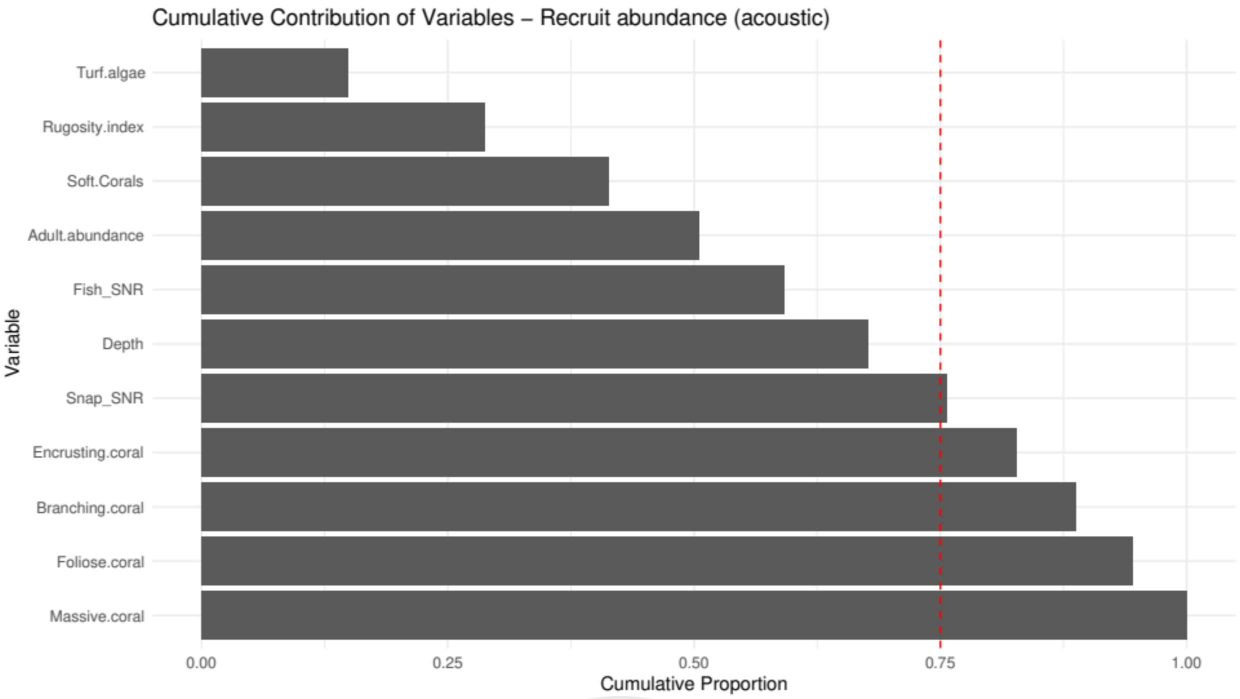

Fig. B5. Random forest model showing the relative importance of the explanatory variables in decreasing order including acoustic variables. The x-axis shows the cumulative proportion of contribution from 0% to 100%. The red dashed line represents the point where variables contribute to at least 75% of the model's explanatory power. This model explains 46%, and the first seven variables explain 36% of the variance in recruit abundance.

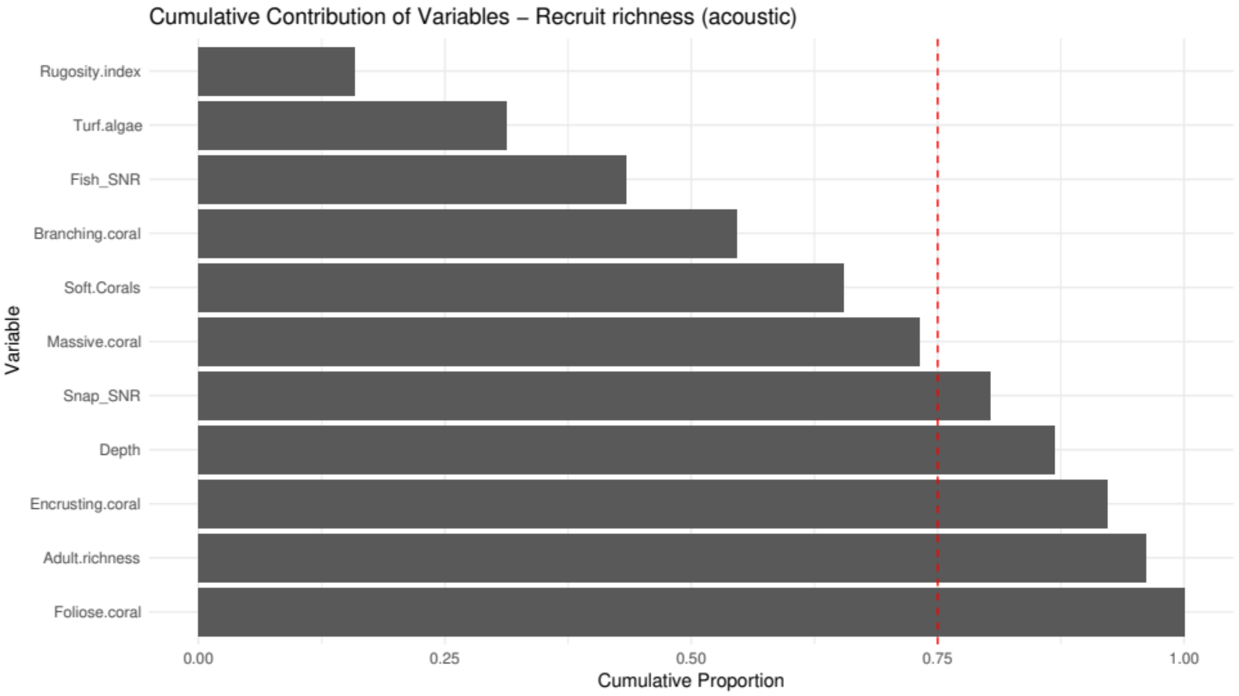

Fig. B6. Random forest model showing the relative importance of the explanatory variables in decreasing order including acoustic variables. The x-axis shows the cumulative proportion of contribution from 0% to 100%. The red dashed line represents the point where variables contribute to at least 75% of the model's explanatory power. This model explains 39%, and the seven first variables explain 31% of the variance in recruit richness.

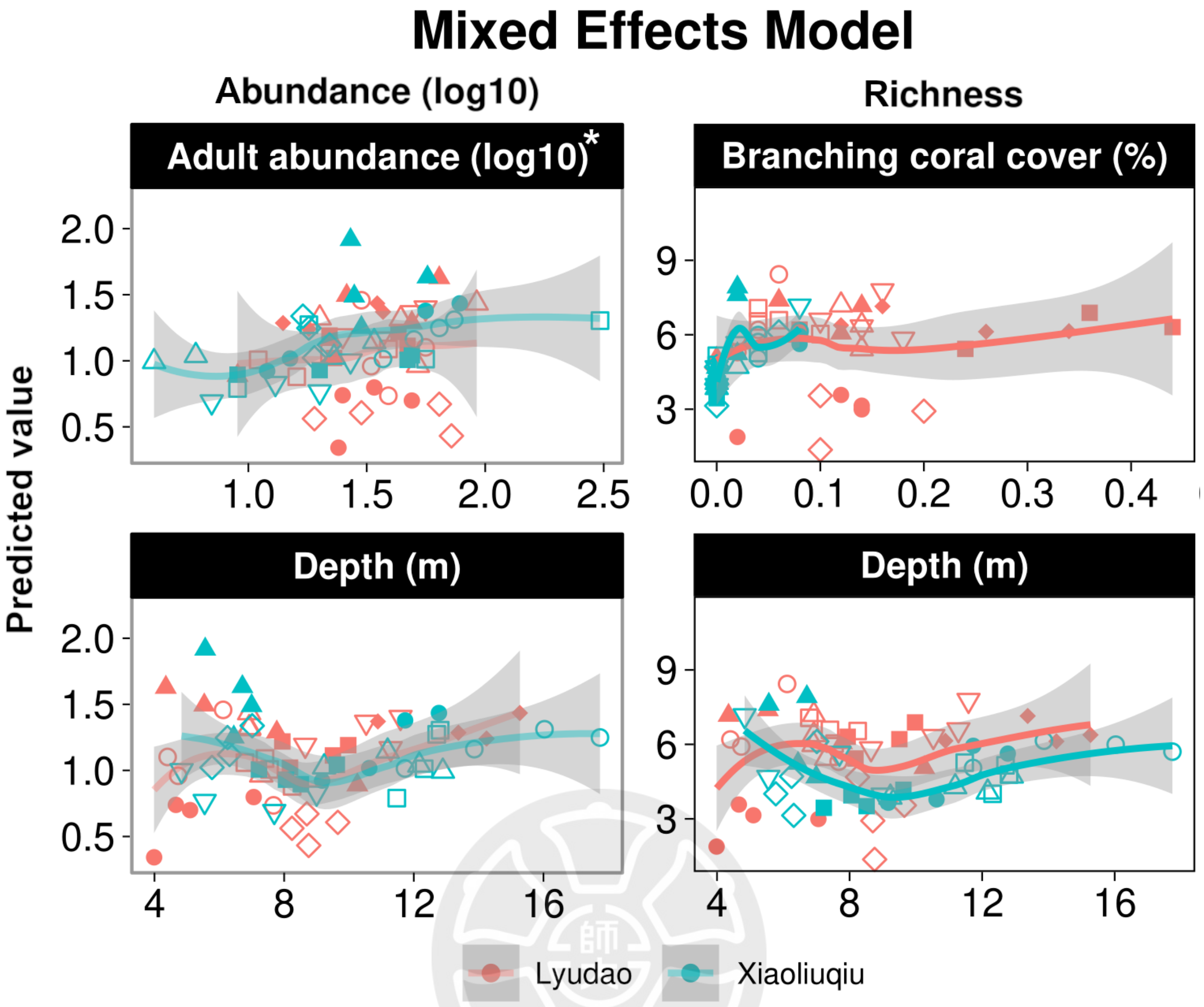

Fig. B7. Plots showing the effect of the environmental factors on the abundance and richness of recruits. This figure shows the factors with lower estimate values based on the MEMs (See table B7 & B9). Asterisks indicate that the factor was significant in the model. Each point represents a transect, lines indicate conditional means, and shaded areas indicate the confidence intervals.

Table B1. Details of the soundscape data collection dates per site.

Island	Site	Census Date	Soundscape recording date
Lyudao	Gueywan	17/May/2022	17/May/2022
Lyudao	Zuping	17/May/2022	-
Lyudao	Shilan	19/May/2022	19/May/2022
Lyudao	Dabaisha	21/May/2022	06/Jun/2023
Lyudao	Zhongliao	11/Jun/2022	11/Jun/2022
Lyudao	Chaikou	12/Jun/2022	12/Jun/2022
Lyudao	Gongguan	13/Jun/2022	13/Jun/2022
Lyudao	Wenquan yugang	16/Jun/2022	22/May/2022
Lyudao	Shuimeiren yan	16/Jun/2022	-
Xiaoliuqiu	Dafu	07/Aug/2022	14/Aug/2022
Xiaoliuqiu	Duzaiping	08/Aug/2022	-
Xiaoliuqiu	Wugueidong	08/Aug/2022	-
Xiaoliuqiu	Shanfu	09/Aug/2022	09/Aug/2022
Xiaoliuqiu	Longxiadong	10/Aug/2022	11/Aug/2022
Xiaoliuqiu	Meirendong	10/Aug/2022	10/Aug/2022
Xiaoliuqiu	Huapingyan	13/Aug/2022	12/Aug/2022
Xiaoliuqiu	Houshi	14/Aug/2022	13/Aug/2022

Table B2. Models tested for best fit based on the interaction of fixed-effect explanatory environmental variables, with islands based on recruit abundance as the response variable. An “X” in the table indicates that the variable was modeled to interact with islands. Models are ordered by AIC (Akaike Information Criterion) value in ascending order, with lower values indicating a better trade-off between model complexity and goodness of fit.

Recruit abundance	Adult abundance (log 10)	Rugosity index	Depth (m)	Soft coral cover	Turf algae cover	Branching coral cover	AIC
Model 1					X		62.7
Model 2					X	X	64.5
Model 3				X	X		64.7
Model 4							65.1
Model 5				X	X	X	66.5
Model 6						X	68.5
Model 7				X			69
Model 8				X		X	70.5

Table B3. Models tested for best fit based on the interaction of fixed-effect explanatory environmental and acoustic variables with islands, based on recruit abundance as the response variable. An "X" in the table indicates that the variable was modeled to interact with islands. Models are ordered by AIC (Akaike Information Criterion) value in ascending order, with lower values indicating a better trade-off between model complexity and goodness of fit.

Recruit abundance	Adult abundance (log 10)	Rugosity index	Depth (m)	Soft coral cover	Turf algae cover	Fish chorus (SNR)	Crustacean snaps (SNR)	AIC
Model 1					X	X		44.6
Model 2					X			45.4
Model 3				X	X	X		46.6
Model 4						X		46.9
Model 5				X	X			47.3
Model 6				X	X	X	X	48.5
Model 7						X	X	48.6
Model 8								48.7
Model 9				X				50.8
Model 10							X	51

Table B4. Models tested for best fit based on the interaction of fixed-effect explanatory environmental variables with islands, based on recruit richness as the response variable. An "X" in the table indicates that the variable was modeled to interact with islands. Models are ordered by AIC (Akaike Information Criterion) value in ascending order, with lower values indicating a better trade-off between model complexity and goodness of fit.

Recruit richness	Depth (m)	Rugosity index	Turf algae cover	Branching coral cover	Soft coral cover	Massive coral cover	AIC
Model 1				X			340.8
Model 2			X	X			341
Model 3			X				341.7
Model 4							342.2
Model 5			X	X	X		343
Model 6			X		X		343.6
Model 7						X	343.8
Model 8					X		343.9
Model 9			X	X	X	X	344.6

Table B5. Models tested for best fit based on the interaction of fixed-effect explanatory environmental and acoustic variables with islands, based on recruit richness as the response variable. An "X" in the table indicates that the variable was modeled to interact with islands. Models are ordered by AIC (Akaike Information Criterion) value in ascending order, with lower values indicating a better trade-off between model complexity and goodness of fit.

Recruit richness	Rugosity index	Turf algae cover	Branching coral cover	Soft coral cover	Massive coral cover	Fish chorus (SNR)	Crustacean snaps (SNR)	AIC
Model 1						X		258.8
Model 2						X	X	258.8
Model 3		X				X		263.9
Model 4		X						264.2
Model 5							X	266.4
Model 6					X			268.1
Model 7			X					268.3
Model 8					X			268.6

Table B6. Results of the variance and standard deviation of the random effects (study site) from the mixed effect model, using recruit abundance as the response variable.

Random effects for abundance			
Model excluding acoustic variables			
	Groups Name	Variance	Std.Dev.
	Site (Intercept)	0.09	0.3
	Residual	0.07	0.26
	Number of obs: 68		groups: Site = 17
Model including acoustic variables			
	Groups Name	Variance	Std.Dev.
	Site (Intercept)	0.04	0.2
	Residual	0.06	0.25
	Number of obs: 52		groups: Site = 13

Appendix C: Supplementary material for Chapter 4

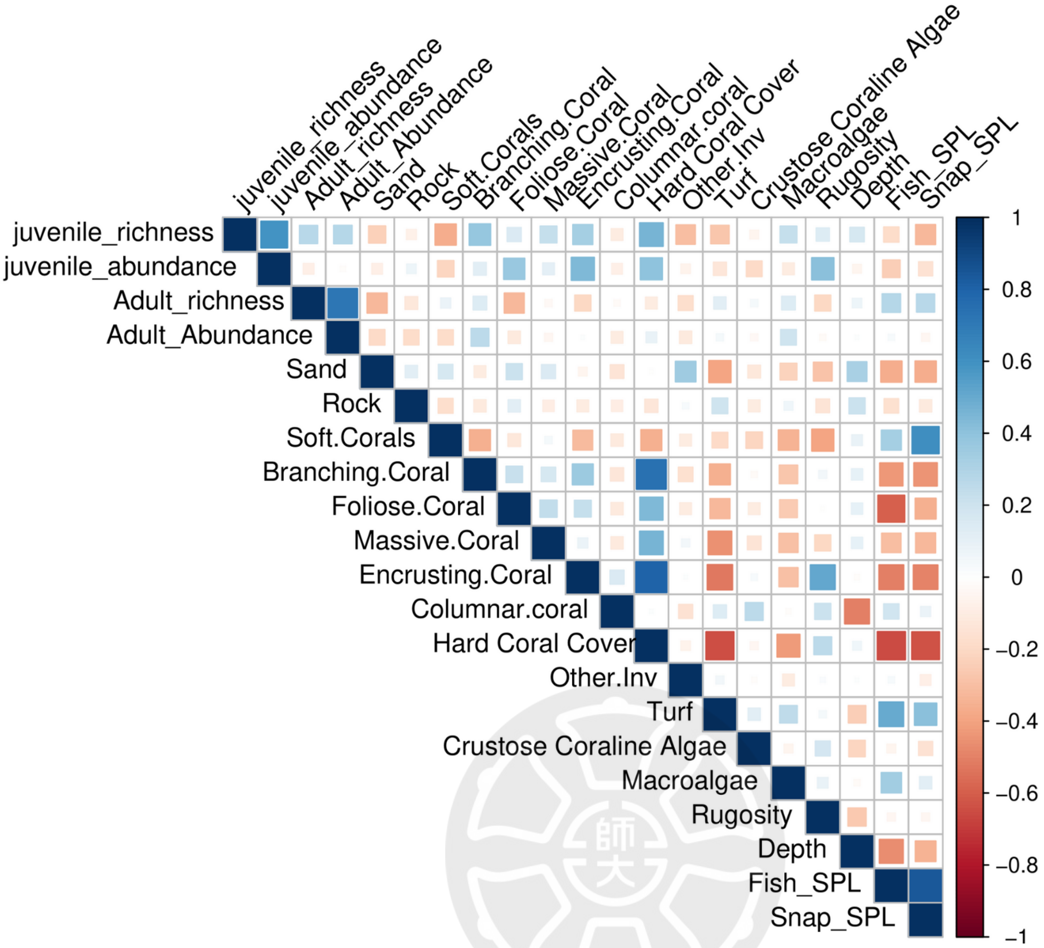

Fig. C1. Pearson correlation matrix portraying the correlations between fish assemblages, substrate characteristics, and vessel noise.

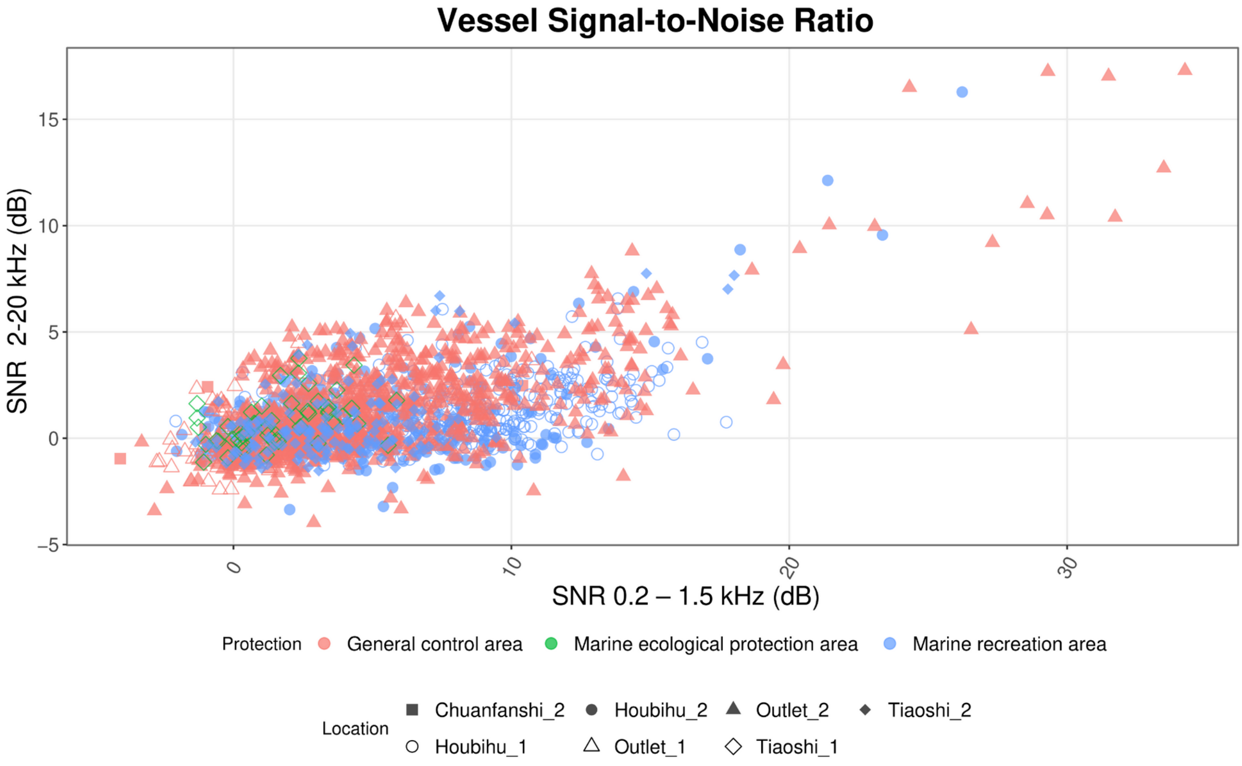

Fig. C2. Scatter plot of vessel signal-to-noise ratio per second per site in two different frequency bands: Fish bands (0.2-1.5 kHz) and crustacean bands (2-20 kHz). Each point represents a one-second sample.

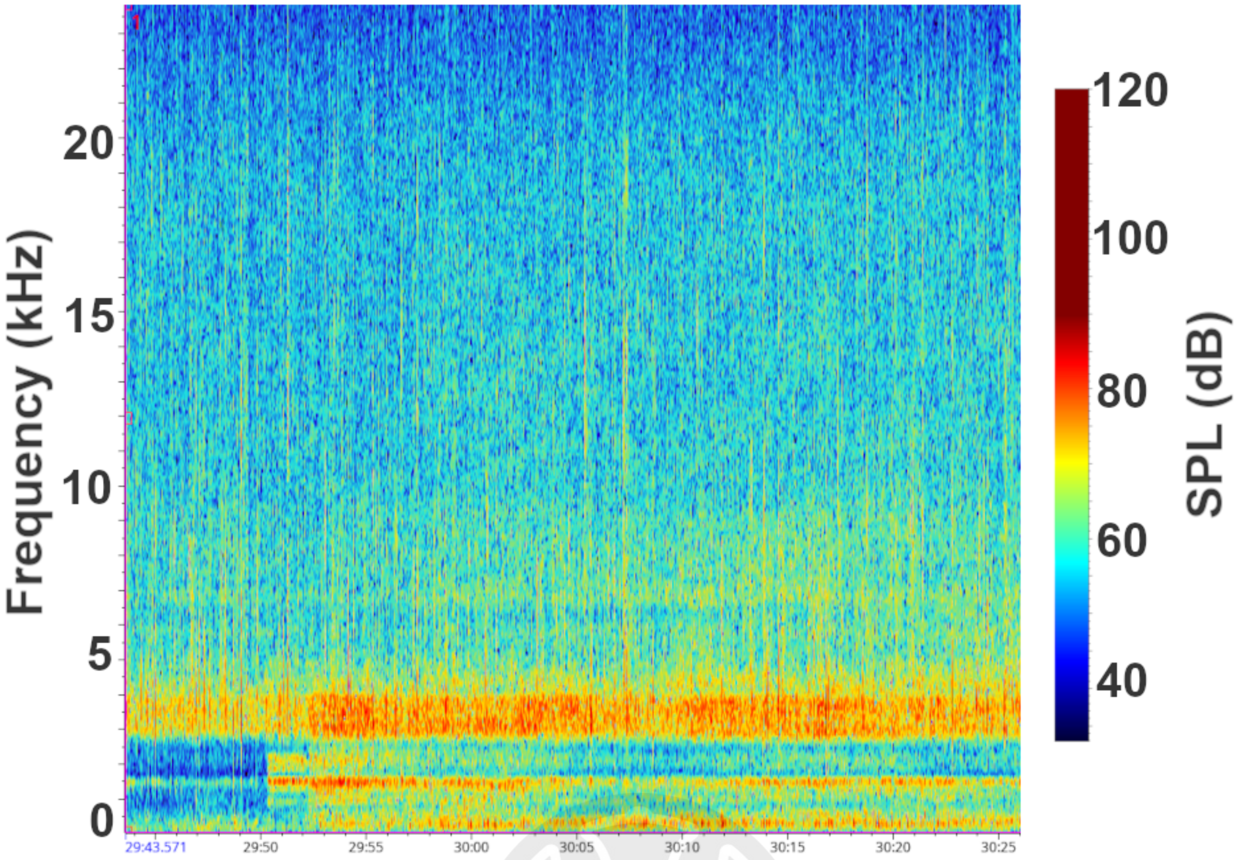

Fig. C3. Spectrogram showing acoustic disruption from a diving boat. SPL: sound pressure level. The x-axis represents time.

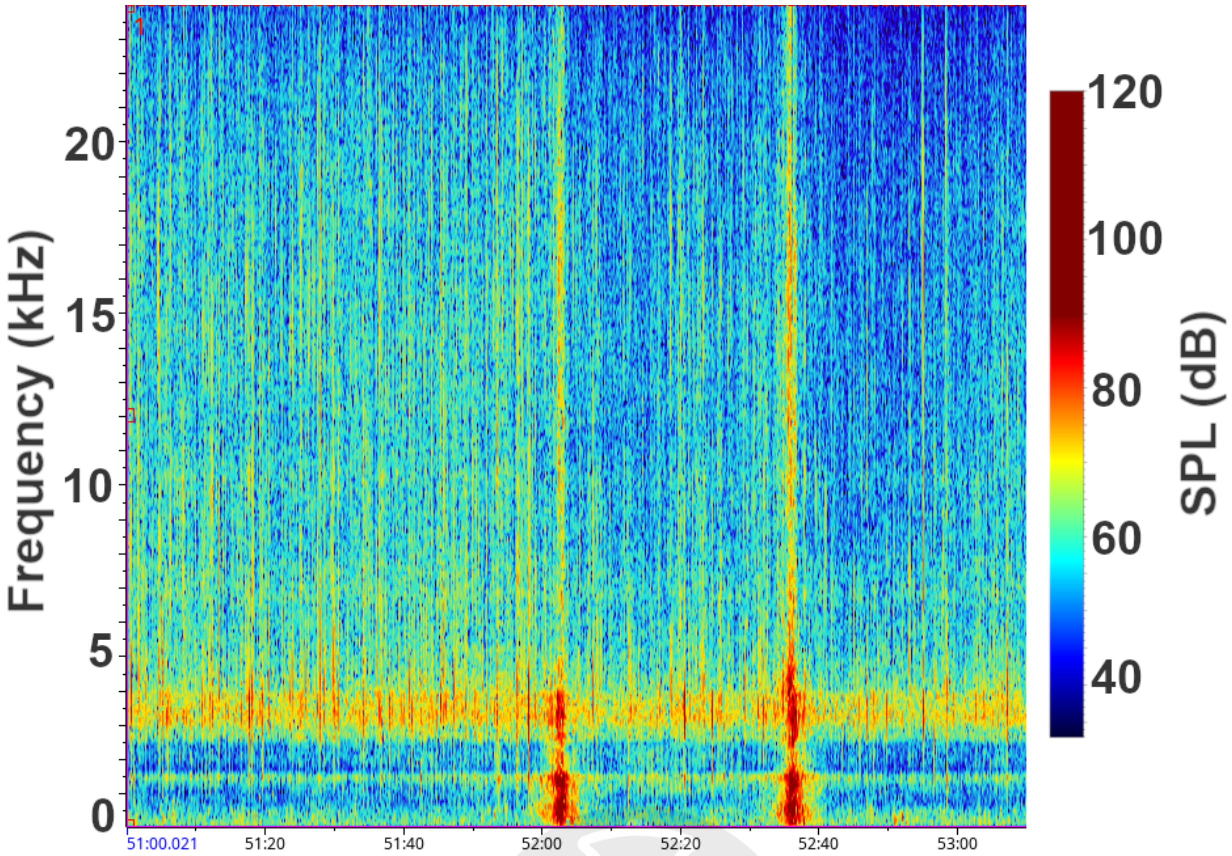

Fig. C4. Spectrogram showing acoustic disruption from a jet ski. SPL: sound pressure level. The x-axis represents time.

Table C1. Principal Component Analysis loadings from the first two components from juvenile abundance count data per trophic group.

Juvenile Abundance	Comp.1 (48%)	Comp.2 (22%)
Carnivore	0.1860321	0.2742169
Herbivore	0.4913093	0.13648851
Invertivore	0.4299541	0.73363436
Omnivore	0.1980553	-0.02512098
Planktivore	0.7070508	-0.60607387

Table C2. Principal Component Analysis loadings from the first two components from adult abundance count data per trophic group.

Adult Abundance	Comp.1 (39%)	Comp.2 (27%)
Carnivore	0.2083927	0.2100401
Herbivore	-0.2018163	0.8719525
Invertivore	-0.1531465	0.2757231
Omnivore	0.3442181	-0.2049619
Planktivore	0.8797174	0.278477

Table C3. Principal Component Analysis loadings from the first two components of substrate cover and rugosity.

Substrate	Comp.1 (25%)	Comp.2 (21%)
Soft.Corals	0.09271009	0.5605472
Branching.Coral	-0.40836749	-0.1365565
Foliose.Coral	-0.35891589	0.0584942
Massive.Coral	-0.33496422	0.304007
Encrusting.Coral	-0.46175991	-0.3167764
Turf	0.485148	-0.178683
CCA	0.05705857	-0.2871542
Macroalgae	0.34717118	-0.2470213
Rugosity	-0.10604189	-0.5436409