

The Relationship Between Reef Fish and Coverage of Coral and Turf Algae in Coral Reef Ecosystems of Biak Island, Papua

Ludi Parwadani Aji^{1,2,3*}, Risandi Dwirama Putra⁴, Muhammad Abrar⁵,
Rikoh Manogar Siringoringo⁵, and Giyanto⁵

1. Research Center for Ecology, National Research and Innovation Agency, Bogor 16911, Indonesia
2. Marine Evolution and Ecology Group, Naturalis Biodiversity Center, Leiden 2300 RA, The Netherlands
3. Aquaculture and Fisheries Group, Wageningen University, Wageningen 6700 AH, The Netherlands
4. Marine Science Department, Faculty of Fisheries and Marine Sciences, Institut Pertanian Bogor, Bogor 16680, Indonesia
5. Research Center for Biotic System, National Research and Innovation Agency, Bogor 16911, Indonesia

*E-mail: ludi.aji.biak@gmail.com

Received March 17, 2025 | Accepted October 23, 2025

Abstract

In this study, we examine the influence of benthic coverage on fish diversity in coral reef ecosystems. Benthic and reef fish community surveys were conducted at 14 sites using underwater photographic transect and underwater visual census methods, respectively. Coral cover (26.1%) was found to be lower than turf algae cover (42.1%). A total of 56 fish species, comprised of 14 carnivores, 21 corallivores, and 21 herbivores, were recorded. The most widely distributed carnivore and herbivore species were *Lethrinus harak* and *Ctenochaetus striatus*, respectively. Two species of butterflyfish, *Chaetodon citrinellus* and *Chaetodon trifasciatus*, were the most widely distributed species among corallivores. The number of herbivorous fish species was correlated with coral cover, but not turf algae cover. In contrast, no correlation was observed between the diversity of corallivorous and carnivorous fish and the coverage values of the two benthic groups (coral and turf algae). Despite this, a pattern was observed in which areas with higher coral cover had more corallivorous and carnivorous fish species, while sites with higher turf algae cover had fewer of these fish species. Reef fish distribution depends on live coral, which are the primary habitat-forming organisms on coral reefs. Coral and reef fish are essential in maintaining ecological functions and shaping reef ecosystems.

Keywords: carnivore, coral, corallivore, herbivore, turf algae

Introduction

Indonesia serves as a habitat for 76% of global coral species and 37% of the world's reef fish species [1]. Despite this remarkable biodiversity, Indonesian coral reefs face significant threats due to climate change and human activities such as destructive fishing and unsustainable tourism [2]. Moreover, phenomena such as El Niño are predicted to trigger mass coral-bleaching events, greatly impacting reef community structures and the survival of the species that depend on them [3]. Coral bleaching, caused by environmental stress, creates substrates for algae turf growth on recently dead corals, which have a crucial effect on reef ecosystem structures. Turf algae are an opportunist benthic group that can use the available substrate space because of coral mortality [4]. Turf algae are characterized by their short, densely branched structure, forming low-lying layers (up to around 1 cm tall), and they are part of a larger community (a heterogenous consortium of algae and cyanobacteria) [5]. Thus, the

shift from coral-dominated reefs to reefs dominated by other benthic groups, such as algae, will impact the ecosystem structure and function of coral reefs.

High turf algae coverage in some locations may indicate environmental pressures, such as increasing nutrient input and low water quality [6, 7]. These algae compete with corals for space and prevent coral recruitment, but can also serve as a food source for reef biota. This relationship highlights the dual role of turf algae in supporting or hindering coral reef ecosystem sustainability, particularly in terms of supporting the associated biota that live in the reefs, such as fish [8–10]. Reef fish rely on corals for habitat and food because the reef structures created by corals offer essential resources and shelters [11, 12]. Coral and reef fish play a crucial role in ecological function and shaping reef ecosystems. The variations in coral community structures reflect the complex interactions between reef fish and environmental conditions [13]. Reef fish serve as indicators of healthy or degraded

coral reef ecosystems, as the presence or absence of specific groups reflects particular environmental and reef conditions. A healthy coral reef with high coral cover is suggested to have a more diverse range of reef fish species than a degraded reef with low coral cover. Reef fish in coral reefs can be classified as herbivores, corallivores, or carnivores [14, 15]. Herbivorous fish can maintain ecosystem balance by controlling algae growth [16, 17]; corallivorous or coral-eating fish may act as indicators of live coral health [18, 19]; and carnivores, or predatory fish, may control the lower trophic level of the reef biota community in coral reef ecosystems [8, 20].

Biak Numfor Regency is located in the northern part of Papua Island, covering a total area of 2.602 km², with a coordinate location between 0° 55'–1° 27' South Latitude and 134° 47'–136° East Longitude [21]. The regency consists of two large islands, Biak and Numfor, along with 42 small islands. To the west, Biak Numfor Regency is bordered by Manokwari Regency. To the east, it is bordered by the Pacific Ocean. To the south, it is bordered by the Yapen Strait. To the north, it is bordered by the Pacific Ocean and Supiori Regency. Most of the local community in Biak depends on fisheries for their livelihood. For example, people rely on reef fish for their food as a protein source [21]. Understanding the dynamics of the reef fish community is critical due to their central role in maintaining coral reef ecosystem balance as well as their economic value. Reef fish may control algal populations that could harm or compete with corals, and can indirectly contribute to coral recruitment processes in coral reef ecosystems [10, 12]. However, research addressing how coral and turf algae cover affects reef fish's presence and distribution in Biak waters remains limited.

In this study, we examine the influence of the benthic dominance of coral and turf algae on reef fish diversity and assemblages in the coral reef ecosystem. This research is expected to provide insights into coral reef ecosystem management, particularly in the context of conservation and restoration.

Materials and Methods

Study areas. The study was conducted on the coral reef ecosystems surrounding Biak Island, which is located in Biak Numfor Regency, Papua, Indonesia. Biak Island lies in the northern part of Papua, directly facing the Pacific Ocean, and it is characterized by fringing and patch reefs with varying exposure and substrate conditions. Fourteen observation stations were established around the island to capture the spatial variation in coral reef conditions (Figure 1). The reef sites are close to the mainland areas, and the reefs typically support a combination of corals and algae. The site selection was based on the monitoring sites established by the local government. Biak Island is one of the regions in the Eastern part of Indonesia chosen as a site for Coral Reef Rehabilitation and Management

Program-Coral Triangle Initiative (Coremap-CTI) activities, which are funded by the World Bank [2, 14, 22]. The Coremap-CTI program is intended to promote community-based management, focusing on sub-components such as community empowerment and the sustainable management of coral reefs [2].

Field data collection. A benthic and reef fish community survey was conducted via SCUBA diving at depths around 3–5 m. The sampling took place in September 2016. Benthic community structure data were collected using underwater photographic transect (UPT) [14, 15]. Data collection was arranged at each site by fixing a 50-m plastic tape along the transect. Each transect was further partitioned into three sub-transects to observe the variation in benthic groups at each site. Photo quadrats of 58 cm x 44 cm (total area 2,552 cm²) [14] were taken every 1 m along the transect with a *Canon PowerShot G16* digital camera with an underwater housing. Furthermore, reef fish richness was counted using an underwater visual census (UVC) methodology along 70-m transects at the same site at which the benthic community survey was performed [23]. Individuals observed within 5 m on either side of the transect line were identified at the species level. For this survey, three groups of reef fish based on feeding type (herbivore, carnivore, and corallivore) were selected for the study. These three reef fish groups are regularly surveyed across Indonesian waters, following the Coremap-CTI monitoring guidelines [2].

Data analysis. The photos of the benthic groups (50 photos per station) were processed with the assistance of Coral Point Count with Excel extensions (CPCe) software [24]. The underwater photographic transect pictures were analyzed to calculate each benthic group's coverage. The program was set to generate 30 random points on each photo, and the benthic organisms below these points per photo were identified. Thirty random points were selected as a statistically appropriate number with which to accurately represent benthic composition while keeping analysis time manageable. For each point, we identified the benthic groups belonging to hard coral, soft coral, crustose coralline algae (CCA), turf algae (dead coral algae), sponge, macroalgae, dead coral, other invertebrates, rubble, and sand. The CPCe files were then prepared for analysis by combining them into one dataset. All analyses were performed in R software Version 4.0.2 [25]. The data were transformed into percentages of cover per benthic group for each transect. None of the data was normally distributed. A stacked bar graph was created to display the average percentage of coverage per benthic group for each station. In addition, boxplots of the percentage of coverage for coral and turf algae from the 14 stations were made. This provided a visual assessment of the benthic community composition across stations. A Pearson correlation (*r*) test was conducted to examine the relationship between coral cover and turf algae cover.

Fish species occurrence was calculated based on the presence of species at all the stations. Furthermore, a species accumulation curve with 999 permutations was created to evaluate whether most reef fish species had been collected. Pearson correlation (r) tests were performed to examine the relationship between the cover percentage of the benthic groups (coral and turf algae) and both the number of fish species according to feeding type (carnivore, herbivore, or corallivore) and the total number of fish species. Lastly, the composition of the benthic group and reef fish communities among stations was visualized using non-metric multidimensional scaling (NMDS) [26]. The metaMDS function in the vegan package [27] was implemented with the Jaccard dissimilarity [28] and Bray–Curtis dissimilarity [29] matrix as input based on the presence or absence of fish species and the total number of fish of each feeding type, respectively. Furthermore, an envfit analysis was performed to analyze the influence of the explanatory variables (benthic group composition) on fish community assemblage across stations.

Results and Discussion

Benthic reef assemblages. The benthic community in the Biak Island reefs was dominated by turf algae, followed by hard coral, rubble, and other groups. Mean turf algae cover reached 42.1%, while hard coral cover averaged 26.1% across the 14 stations (Figure 2). The highest turf algae cover was observed at Station 7, at 58.4%, and the lowest was at Station 12, at 23.9%. The highest coral cover was observed at Station 1 (53.7%), and the lowest was observed at Station 6 (5.4%). Overall, the percentage of cover for hard coral was lower than that for turf algae. On the other hand, the mean coverage for soft coral was 2.5%, and it was found at only eight stations. The mean crustose coralline algae (CCA) cover was 2.1%, and it was observed in only nine stations. Similarly, sponge coverage was observed at only 11 stations, with a mean coverage percentage of 1.5%. Macroalgae coverage was found at eight stations, with a mean coverage of 1.18%. Additionally, the mean coverage values for other invertebrates and recently dead coral were 4.0% and 2.3%, respectively. Lastly, for abiotic benthic groups, such as rubble and sand, coverage values were 7.6% and 10.6%, respectively.

The coverage for coral (Figure 3A) and turf algae (Figure 3B) varied between the stations. There were seven stations with coral coverage below 25%: Station 3 (14%), Station 4 (19%), Station 6 (5%), Station 7 (7%), Station 8 (11%), Station 9 (24%), and Station 11 (24%). These stations also had higher turf algae coverage compared to the other stations. As can be seen from Figure 3D, there was a negative correlation between coral and turf algae coverage. The lower the coral cover, the higher the turf algae coverage ($r = -0.8$, $p = 0.0006$). Coral reef monitoring has been conducted in Biak Numfor by the Research

Center for Oceanography at the Indonesian Institute of Science, but this was done in different years and at different locations as compared to our study. The hard coral coverage was 12% in 2015 [14], 13% in 2017 [22], and 35% in 2019 [15]. Overall, the coral cover in Biak waters can be classified as poor (< 25%) to fair (25–50%) [2]. As a comparison, according to the coral reef monitoring program conducted under Coremap-CTI in 2019, most surveyed areas had fair coral coverage (37%), and just around 6% of reef sites had excellent coral coverage (> 75%) [2]. Spatially, coral cover tended to be higher on western and northern sites, which are more exposed to oceanic currents and have lower sediment input, whereas southern and eastern sites, with their greater exposure to anthropogenic effects, showed elevated turf algae cover [2]. Coral cover is declining due to increasing sea surface temperatures, eutrophication, and overfishing [2, 30]. Subsequently, healthy coral reefs with high coral cover may shift from coral-dominated reefs to algae-dominated reefs [4, 31]. Numerous studies on reef benthic community structure have highlighted algae as an opportunistic group that thrives under elevated nutrient input, representing an intense source of competition for hard corals [4]. A decline in coral cover may lead to the proliferation of turf algae, which can become the dominant benthic group in reef ecosystems. This shift may reduce coral diversity in coral reef ecosystems, which are critical habitats for diverse marine organisms, including invertebrates (e.g., molluscs, crustaceans, holothurians, and polychaetes) and fish. Consequently, reducing habitat complexity may decrease biodiversity and disrupt ecological interactions within the reef ecosystem [30, 31]. Thus, changes in the benthic conditions of the coral reef ecosystem are likely to influence the diversity and composition of reef biota.

Turf algae dominance indicates a potential phase shift from a coral-dominated regime to an algal-dominated regime. The prevalence of turf algae suggests reduced substrate competition for corals and the potential suppression of coral recruitment. The existence and sustainability of coral communities and benthic reef assemblages are largely determined by the recruitment process that produces new individuals, which appear at an early life stage [32]. In addition, coral recruitment also shows an increase in coral reef resilience and encourages recovery after damage [33, 34]. The early life stage is a vulnerable period for coral recruits to grow and develop into adult coral colonies, including competition for space to grow and survive, especially with the rapid growth of the turf algae community [35, 36]. The results of the study show that the direct control of algae growth or natural grazing by various herbivorous biota, including herbivorous fish, can increase the growth and survival of coral recruits to adulthood [37, 38].

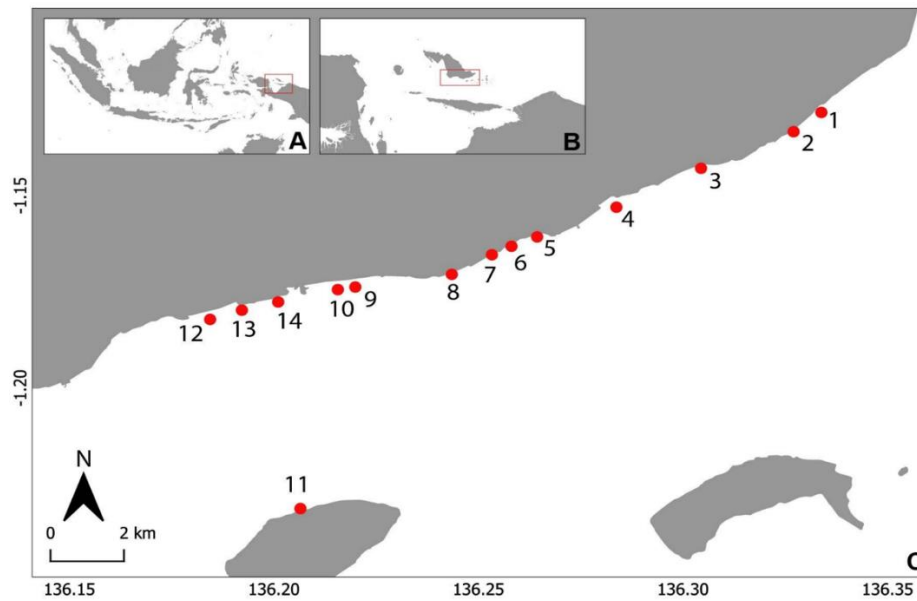


Figure 1. Map of the Sampling Location, Biak Island, Biak Numfor Regency, Papua; (A) Indonesian maps, (B) Papua Regions, (C) 14 Sampling Sites in the Study Area

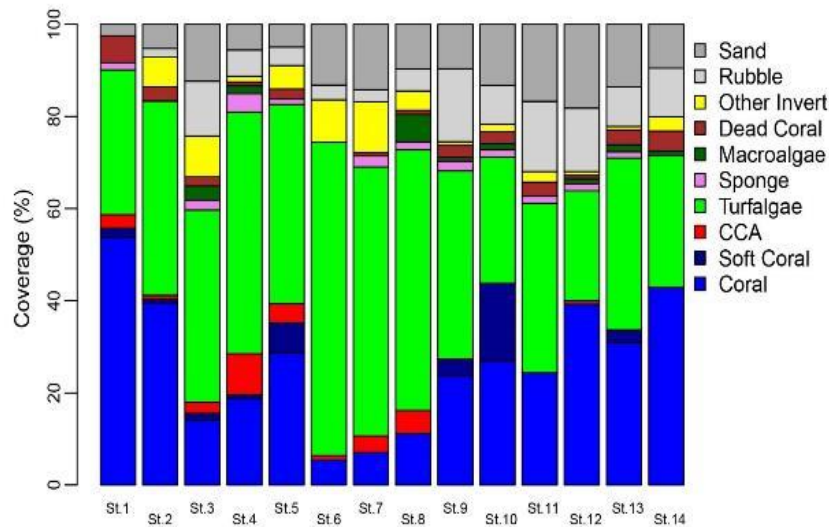


Figure 2. Cover Percentage for the Benthic Groups at 14 Stations in Biak, Papua; Note: CCA = Crustose Coralline Algae

Measurements of juvenile coral abundance showed a negative correlation with turf algae, and juvenile coral abundance was relatively low in the early stages after the 2016 coral-bleaching event in the waters of the Pieh Island Marine National Park, West Sumatra, Indonesia [34]. Turf algae communities were also found to be associated with sediments, providing space closure and preventing coral larvae from settling on the substrate [35].

Fish community assemblage. Across the 14 studied reef sites, a total of 56 fish species, comprised of 14 carnivores, 21 corallivores, and 21 herbivores, were recorded (Table 1, Figure 4). The carnivores consisted of four fam-

ilies (Haemulidae, Lethrinidae, Lutjanidae, and Seranidae); the corallivores consisted of only one family, Chaetodontidae (four genera), and the herbivores consisted of three families (Acanthuridae, Scaridae, and Siganidae). The most widely distributed carnivore species was *Lethrinus harak*, which was found at five stations, followed by *Monotaxis grandoculis*, which was found at three stations. The Thumbprint Emperor *L. harak*, a common species in the Indo-Pacific, utilizes seagrass and mangrove habitats as nursery grounds, transitioning to reef habitats as they mature into larger adults [39]. Most of the reef areas in our present study are adjacent to seagrass and mangrove habitats, which likely support *L.*

harak in its juvenile stages before they migrate to reef ecosystems.

The most widely distributed species of corallivore were the butterflyfishes *Chaetodon citrinellus* and *Chaetodon trifasciatus*, which were found in 13 stations. Corallivores are often considered reliable indicators of a healthy reef [40]. Their species abundance can lead to coral loss or increase corals' vulnerability to other stressors, such as thermal stress or disease outbreaks, as the corals may already be weakened. The presence or absence of *Chaetodon* species suggests that coral reef ecosystems have experienced habitat degradation and changes in the availability of food sources, such as coral polyps and other benthic invertebrates. The melon butterflyfish *C. trifasciatus* and *C. citrinellus* belong to the obligate and facultative corallivores, respectively [18]. *Chaetodon*-tidae can be classified as facultative or obligate corallivores, which differ significantly in their dependence on coral resources [18, 41]. Facultative coral feeders opportunistically feed on corals but can survive without including corals in their diet. In contrast, obligate corallivores rely heavily on corals for their diet, often feeding exclusively on specific coral species and displaying strong preferences for particular types of coral [19, 42].

Lastly, the most widely distributed herbivore species were *Ctenochaetus striatus*, found at 14 stations, followed by *Acanthurus pyroferus*, which was observed at 11 stations. The diet of *C. striatus* includes filamentous algae, macroalgae, microalgae, and detritus/ sediments [12]. The presence of Acanthuridae *C. striatus* is influenced by the characteristics of the reef substrate, with this species commonly being found on various disturbed reefs. Their diet might change in response to shifts in substrate conditions due to environmental disturbances [12]. Reef sites in our study area are predominantly covered by turf algae or dead coral algae, which is likely a feeding ground for *C. striatus*. The impacts of fish on reef ecosystems vary spatially and depend on reef fish diversity and species identity [10]. Herbivorous fish play a vital role in shaping the benthic communities on coral reefs by regulating the abundance of the primary producers of algae. Without herbivores to keep turf algae closely cropped and remove the early stages of macroalgae, the benthic community can shift to one dominated by algae [17]. This transition is often accompanied by a significant increase in algal cover when herbivores fail to control algal proliferation, further exacerbating coral loss.

Regarding species richness across stations, the highest richness was observed at Station 1, with 26 species, followed by Station 3, with 21 species. The lowest richness was observed at Stations 2, 6, and 12, which each had only ten species. The species accumulation curve did not reach an asymptote (Figure 5), indicating that the sampling effort, which involved 14 stations, was insufficient to

capture most species. As the number of samples influences species richness [43], increasing the number of sampling locations on Biak Island would likely reveal more species. Reef fish surveys conducted in the Biak region under the Coremap-CTI program have reported that the reef fish diversity (carnivores, corallivores, and herbivores) was 113 species in 2015 [14], 108 species in 2017 [22], and 128 species in 2019 [15]. In comparison, the present study recorded lower fish diversity (56 species) at our sampling stations because our transect was mainly at shallow depths of up to 5 m. Moreover, our stations is established along coastal areas and spatially closer to one another, which likely caused us to miss other reef fish species from the reefs that are further away from our sites on Biak Island. Expanding the sampling locations to include more reefs could increase the likelihood of observing a greater diversity of fish species.

Relationship between reef fish diversity and benthic group (coral and turf algae) coverage. We found that there was no correlation between the number of carnivore species and coral coverage ($r = 0.47, p = 0.09$) and turf algae coverage ($r = -0.41, p = 0.15$; Figure 6A). Similarly, there was no correlation between the number of corallivore species and the percentages of coral coverage ($r = 0.42, p = 0.14$) and turf algae coverage ($r = -0.2, p = 0.5$) (Figure 6C). Even though we detected no correlation based on the analysis, some patterns were observed: With higher coral cover and lower turf algae cover, the numbers of carnivore and corallivore species increased (Figure 6A and 6C). On the other hand, there was a negative correlation between the number of herbivore species and coral coverage ($r = -0.56, p = 0.037$), but no correlation between herbivore species and turf algae coverage ($r = 0.28, p = 0.32$; Figure 6B). Overall, there was no correlation between the total number of fish species and coral cover ($r = 0.053, p = 0.86$) or turf algae cover ($r = -0.069, p = 0.81$; Figure 6D).

Consistent with [44], our correlation analysis reveals a positive correlation between coral reef cover and the abundance of corallivorous fish, suggesting that various corallivore groups (the Chaetodontidae family) in Biak waters rely on scleractinian corals for sustenance. This correlation underscores the fact that the condition of certain coral reefs in Biak still impacts the composition of corallivores. This dependence is attributed to corallivores' inherent reliance on live coral for food, which makes them vulnerable to significant and widespread reductions in live coral cover [19, 42]. Previous studies show that corallivores play a crucial role in enhancing our understanding of behavioral ecology within coral ecosystems, as their feeding behavior and diet composition are directly reliant on coral [9, 45], thus making corallivores closely associated with coral reefs and an indicator of coral health [40]. The presence of corallivores signifies that the coral reef ecosystem has undergone various modifications, such as habitat degradation, changes

in the availability of preferred food sources (e.g., coral polyps, invertebrates, and small crustaceans), and changes in the marine conditions that support the habitat [40–42].

No correlation was found between herbivores and turf algae; however, the trend line suggests that higher algal availability may increase herbivores presence. Previous

studies indicate that herbivorous fish populations often increase with greater food availability [16, 46], typically following coral loss, during which algal abundance increases [10]. Herbivores play a key role in maintaining coral reef resilience and preventing coral–algal phase shifts [17].

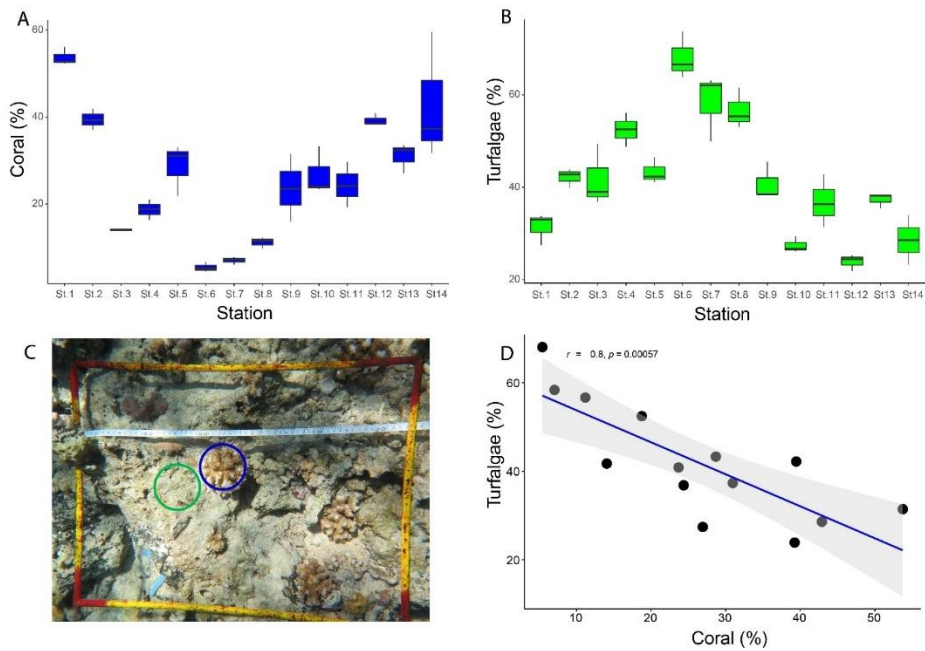


Figure 3. Boxplot of (A) Coral and (B) Turf Algae Cover Across All Stations, (C) The Field Data Collection Photo Shows the Appearance of Coral (Blue Open Circle) and Turf Algae (Green Open Circle), (D) Correlation between Coral and Turf Algae Coverage at the 14 Reef Locations



Figure 4. Representative Pictures of Reef Fish that are Herbivores (A. *Acanthurus lineatus* (Linnaeus, 1758), B. *Chlorurus microrhinos* (Bleeker, 1854)), Corallivores (C. *Chaetodon trifascialis* Quoy & Gaimard, 1825), and Carnivores (D. *Cephalopholis* sp.; Photos: Risandi)

Through grazing, they suppress algal growth, promote coral survival and growth, and maintain suitable substrates for coral recruitment [16]. A transition from coral to algal dominance reflects reef degradation caused by anthropogenic and natural disturbances. Inadequate herbivore populations allow excessive algal growth, increasing the risk of long-term phase shifts [47]. A well-functioning herbivorous fish assemblage helps sustain reef health by reducing algal dominance and regulating competition between algae and reef-building corals [16], [46], whereas carnivorous or predatory fish influence the abundance and composition of other reef fish species [8],

[20]. A decline in their species richness and abundance can alter the structure of lower trophic levels and prey communities, leading to shifts in biotic interactions and overall reef community structure.

Non-metric multidimensional scaling (NMDS) ordination plots illustrate the variation in fish assemblage composition across sampling areas, reflecting differences in species presence. Some clustering of stations can be seen between those with coral coverage below 25% and those with more than 25% coverage.

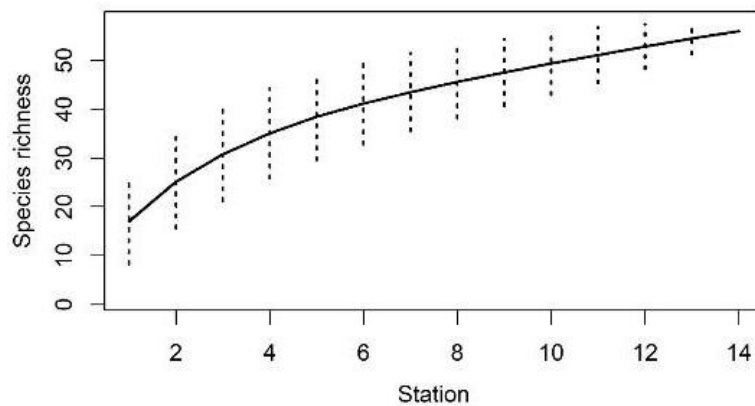


Figure 5. Species Accumulation Curve for Reef Fish from the 14 Stations Near Biak Island, Papua

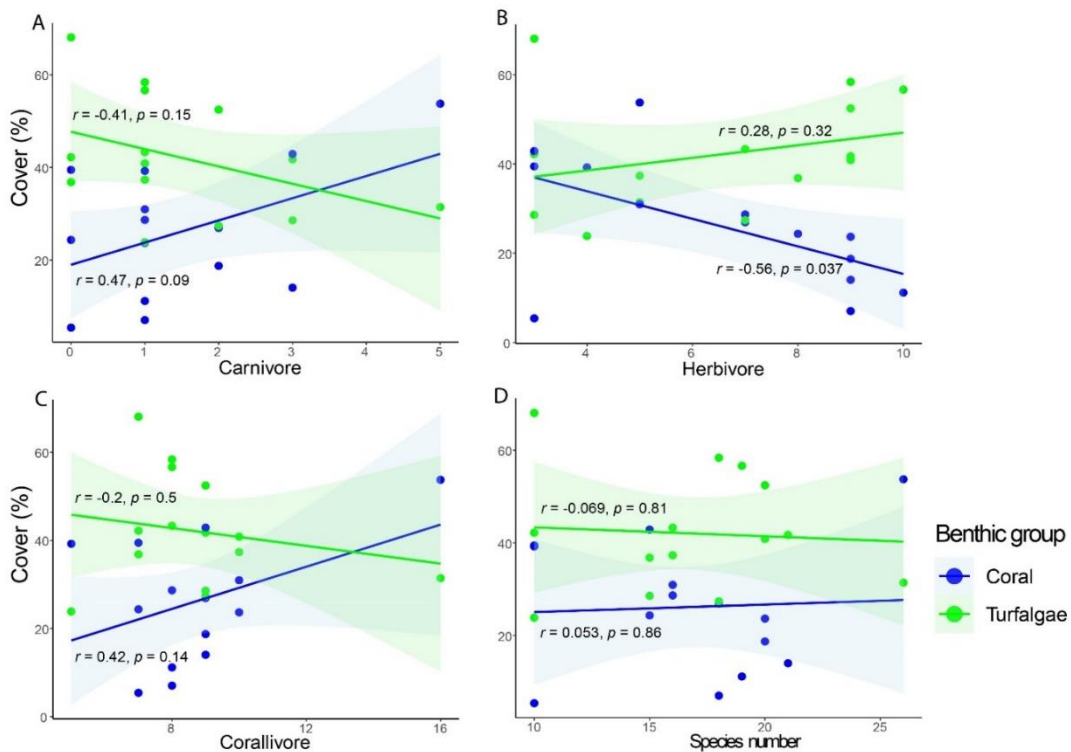


Figure 6. Correlation between Benthic Group Coverage (Coral and Turf Algae) and Species Number for (A) Carnivores, (B) Herbivores, (C) Corallivores, and (D) Total Reef Fish; Note: Blue Represents Benthic Coral, and Green Represents Benthic Turf Algae

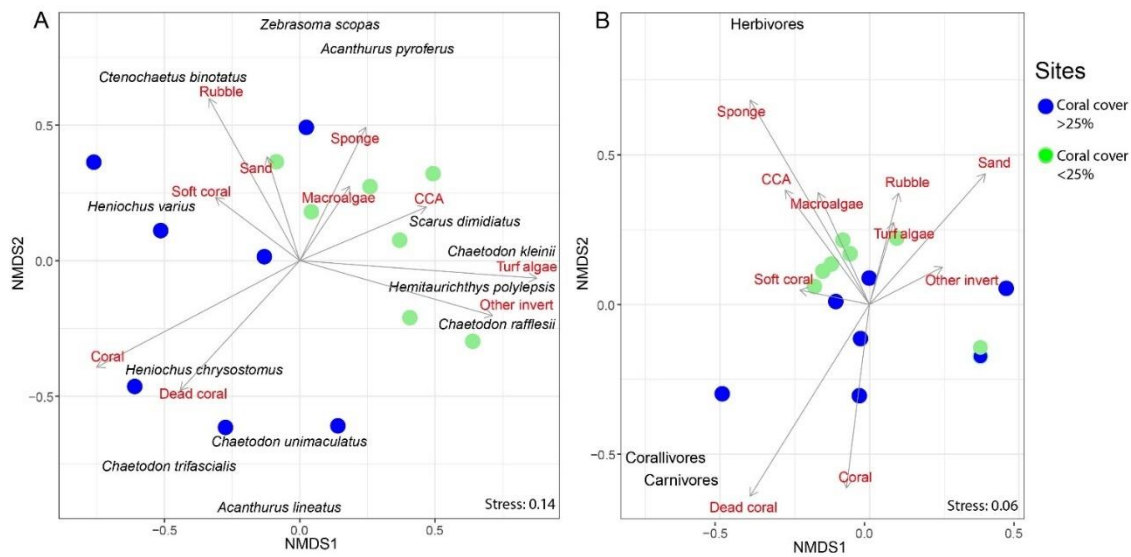


Figure 7. Non-Metric Multidimensional Scaling (NMDS) Ordination Plot based on the Jaccard Distances between Sites with Fish Species that Significantly ($p < 0.001$) Influenced the Community Assemblage are Shown in the Graph (A), as are the Bray–Curtis Distances for the Fish Feeding Types (B) from all 14 Stations in Biak, Papua; Fish Feeding Type ($p < 0.001$) Significantly Influenced the Community Assemblage Across Stations; The Stations are Classified Into Two Categories: Sites with Coral Cover $> 25\%$, Consisting of Seven Stations (Blue Bullet Points), and those with Coral Cover $< 25\%$, also Consisting of Seven Stations (Green Bullet Points); The Arrows Represent Benthic Groups (Coral, Soft Coral, CCA, Turf Algae, Sponge, Macroalgae, Dead Coral, other Invertebrates, Rubble, and Sand)

The fish species *Scarus dimidiatus* ($r^2 = 0.63$, $p = 0.007$), *Acanthurus lineatus* ($r^2 = 0.75$, $p = 0.006$), *Acanthurus pyroferus* ($r^2 = 0.76$, $p = 0.005$), *Ctenochaetus binotatus* ($r^2 = 0.60$, $p = 0.016$), *Zebrasoma scopas* ($r^2 = 0.71$, $p = 0.005$), *Chaetodon kleinii* ($r^2 = 0.64$, $p = 0.005$), *Chaetodon rafflesii* ($r^2 = 0.56$, $p = 0.010$), *Chaetodon trifascialis* ($r^2 = 0.71$, $p = 0.003$), *Chaetodon unimaculatus* ($r^2 = 0.45$, $p = 0.037$), *Hemitaurchthys polylepis* ($r^2 = 0.54$, $p = 0.012$), *Heniochus chrysostomus* ($r^2 = 0.70$, $p = 0.001$), and *Heniochus varius* ($r^2 = 0.69$, $p = 0.003$) significantly influenced the composition of fish community assemblages across sites. Furthermore, based on Figure 7B, the NMDS ordination plot shows that carnivores ($r^2 = 0.77$, $p = 0.001$), herbivores ($r^2 = 0.96$, $p = 0.001$), and corallivores ($r^2 = 0.90$, $p = 0.001$) significantly influenced fish community assemblages across locations. Additionally, the envfit analysis indicated that benthic coral ($r^2 = 0.72$, $p = 0.001$), turf algae ($r^2 = 0.77$, $p = 0.001$), dead coral ($r^2 = 0.42$, $p = 0.048$), other invertebrates ($r^2 = 0.55$, $p = 0.023$), and rubble ($r^2 = 0.47$, $p = 0.032$) significantly influenced fish species composition across the sampling locations (Figure 7A), suggesting that these benthic substrate types play a key role in structuring fish assemblages.

The reef fish community assemblage is not solely influenced by coral and turf algae coverage. The reef fish community is also affected by the presence and richness of other benthic groups [48, 49]. We found that other invertebrates and rubble also influence the composition of reef fish assemblage. Benthic invertebrates in coral reef

ecosystems, such as molluscs, crustaceans, polychaetes, and echinoderms, are food sources for some carnivorous fish. A greater diversity of benthic groups can support a wider variety of organisms living within the reef ecosystem, which, in turn, provides a more abundant and varied food supply for reef fish [11, 48].

Additionally, a more complex and structurally diverse reef habitat can support a higher diversity of reef fish by offering more niches and feeding opportunities [10, 11]. Thus, high rubble coverage reduces structural complexity and limits the shelter available in which prey can hide from their predators, resulting in lower reef fish diversity.

Environmental disturbances drive changes in benthic habitats, leading to shifts in the composition of the reef fish assemblages associated with these habitats [6, 48]. The composition of benthic habitats is crucial in determining the distribution of coral reef fish species [12]. Most coral reef fish rely on specific benthic habitats for food, shelter, and nursery areas. Hard corals often serve one or more of these essential functions. Some species also depend on other benthic groups, such as turf algae, benthic cyanobacterial mats, sponges, rubble, or sand [48]. The composition of the benthic substrata, which reef fish species depend on, is strongly influenced by the composition of benthic groups [6, 48]. Another important factor regarding the distribution of reef fish on coral reefs is human activity [50, 51]. However, our study did not

include the impact of human activities, such as overfishing, on reef fish richness. Overfishing, especially that targeting herbivorous coral reef fish, reduces grazing pressure and can shift benthic dominance from coral to algae [50]. Subsequently, a lack of herbivorous fish may influence the composition of carnivorous fish species assemblage due to the depletion of their diverse food sources, subsequently influencing the ecosystem structure and function [8, 52].

Conclusion

The coral cover in Biak Island, Biak Numfor Regency, is considered fair, with an average coverage of approximately 26%. However, this area is at risk of shifting from a coral-dominated reef to an algae-dominated reef, as some locations exhibit high turf algae or dead coral algae coverage. Changing the benthic cover and composition may affect the trophic structure of reef fish assemblages [18, 48]. The diversity of herbivorous fish species correlated with the percentage of coral cover, but not with turf algae cover. In contrast, no correlation was observed between the diversity of corallivorous and carnivorous fish and the benthic groups' (coral and turf algae) coverage. Nonetheless, a clear pattern emerged: Areas with higher coral cover tended to support greater numbers of corallivorous and carnivorous fish species. Conversely, higher turf algae cover was associated with fewer corallivorous and carnivorous fish species in the ecosystem. Future studies should include data on the abundance and biomass of reef fish to better understand their ecological roles within the coral reef ecosystem. Such data would provide valuable insights into the contributions of reef fish to coral reef health and resilience. Moreover, the impact of overfishing on reef fish and benthic community structure could be studied. This research provides critical information for local government authorities attempting to manage their coral reefs effectively, as these ecosystems play a vital role in supporting the livelihoods of local communities. The sustainable management of coral reefs is essential for maintaining both biodiversity and their socioeconomic benefits.

Acknowledgements

The authors would like to thank Dinas Kelautan dan Perikanan, Kabupaten Biak Numfor, Papua, for their support and cooperation. We also thank the staff of the Technical Implementation Unit for Marine Life Conservation Biak, Papua-Lembaga Ilmu Pengetahuan Indonesia: Latanda for reef fish data collection, Jonas, Alvi, Pattahalang, Lodwyk, Andriani, Albertus, Habel, Demianus, Paul, and Yohana.

References

- [1] Ceccarelli, D.M., Lestari, A.P., Rudyanto, R., White, A.T. 2022. Emerging marine protected areas of eastern Indonesia: Coral reef trends and priorities for management. *Mar. Policy*. 141: 105091, <https://doi.org/10.1016/j.marpol.2022.105091>.
- [2] Hadi, T.A., Abrar, M., Giyanto, G., Prayudha, B., Johan, O., Budiyanto, A., *et al.* 2020. The status of Indonesian coral reefs 2019. Research Center for Oceanography. Indonesia. pp. 86.
- [3] Venegas, R.M., Acevedo, J., Treml, E.A. 2023. Three decades of ocean warming impacts on marine ecosystems: A review and perspective. *Deep Sea Res. Part II Top. Stud. Oceanogr.* 212: 105318, <https://doi.org/10.1016/j.dsr2.2023.105318>.
- [4] Tebbett, S.B., Bellwood, D.R. 2019. Algal turf sediments on coral reefs: what's known and what's next. *Mar. Pollut. Bull.* 149: 110542, <https://doi.org/10.1016/j.marpolbul.2019.110542>.
- [5] Harris, J.L. Lewis, L.S., Smith, J.E. 2015. Quantifying scales of spatial variability in algal turf assemblages on coral reefs. *Mar. Ecol. Prog. Ser.* 532: 41–57, <https://doi.org/10.3354/meps11344>.
- [6] Teichberg, M., Wild, C., Bednarz, V.N., Kegler, H.K., Lukman, M., Gardes, A.A., *et al.* 2018. Spatio-temporal patterns in coral reef communities of the Spermonde Archipelago, 2012-2014, I: Comprehensive reef monitoring of water and benthic indicators reflect changes in reef health. *Front. Mar. Sci.* 5: 33, <https://doi.org/10.3389/fmars.2018.00033>.
- [7] Zamani, N.P., Januar, H.I. 2020. Coral mortality and bioerosion index for assessing environmental stress effects: A study case of the Indonesian Tropical Reef in Banda-Neira Conservation Park. *AACL Bioflux.* 13(2): 1027–1037.
- [8] Mihalitsis, M., Morais, R.A., Bellwood, D.R. 2022. Small predators dominate fish predation in coral reef communities. *PLoS Biol.* 20(11): e3001898, <https://doi.org/10.1371/journal.pbio.3001898>.
- [9] MacDonald, C., Pinheiro, H.T., Shepherd, B., Phelps, T.A.Y., Rocha, L.A. 2021. Disturbance and distribution gradients influence resource availability and feeding behaviours in corallivore fishes following a warm-water anomaly. *Sci. Rep.* 11(1): 23656, <https://doi.org/10.1038/s41598-021-03061-w>.
- [10] Adam, T., Burkepile, D., Ruttenberg, B., Paddock, M. 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar. Ecol. Prog. Ser.* 520: 1–20, <https://doi.org/10.3354/meps11170>.
- [11] Plass-Johnson, J.G., Bednarz, V.N., Hill, J.M., Jompa, J., Ferse, S.C.A., Teichberg, M. 2018. Contrasting responses in the niches of two coral reef herbivores along a gradient of habitat disturbance in the Spermonde Archipelago, Indonesia. *Front. Mar. Sci.* 5: 32, <https://doi.org/10.3389/fmars.2018.00032>.

- [12] Lin, X., Hu, S., Liu, Y., Zhang, L., Huang, H., Liu, S. 2021. Disturbance-Mediated changes in coral reef habitat provoke a positive feeding response in a major coral reef detritivore, *Ctenochaetus striatus*. *Front. Mar. Sci.* 8: 1–14, <https://doi.org/10.3389/fmars.2021.682697>.
- [13] Pranata B., Sala, R., Kusuma A.B, Toha, A.H.A, Purbani, D.C., Mokodongan, D.F., et al. 2024. Genetic diversity and connectivity of red snapper *Lutjanus gibbus* in the Papua waters, Indonesia. *Biodiversitas.* 25(1): 276–286, <https://doi.org/10.13057/biodiv/d250132>.
- [14] Giyanto, G., Supriyadi, I.H, Iswari, M.Y., Widodo, W., Djuwariah, D., Aji, L.P, et al. 2015. Monitoring Kesehatan Terumbu Karang dan Ekosistem Terkait di Kabupaten Biak Numfor. Indonesia. pp. 69.
- [15] Dharmawan, I.W.E., Utama, R.S., Giyanto, G., Aji, L.P., Makatipu, P.C., Irawan, A. 2019. Monitoring Kondisi Kesehatan Terumbu Karang dan Ekosistem Pesisir Terkait di TWP. Padaido, Biak-Numfor 2019. Indonesia. pp. 133.
- [16] Puk, L.D., Ferse, S.C.A., Wild, C. 2016. Patterns and trends in coral reef macroalgae browsing: a review of browsing herbivorous fishes of the Indo-Pacific. *Rev. Fish Biol. Fish.* 26(1): 53–70, <https://doi.org/10.1007/s11160-015-9412-z>.
- [17] Holbrook, S.J., Schmitt, R.J., Adam, T.C., Brooks, A.J. 2016. Coral reef resilience, tipping points and the strength of herbivory. *Sci. Rep.* 6(1): 35817, <https://doi.org/10.1038/srep35817>.
- [18] Pratchett, M.S., Graham, N.A.J., Cole, A.J. 2013. Specialist corallivores dominate butterflyfish assemblages in coral-dominated reef habitats. *J. Fish Biol.* 82(4): 1177–1191, <https://doi.org/10.1111/jfb.12056>.
- [19] Feary, D., Bauman, A., Guest, J., Hoey, A. 2018. Trophic plasticity in an obligate corallivorous butterflyfish. *Mar. Ecol. Prog. Ser.* 605: 165–171, <https://doi.org/10.3354/meps12771>.
- [20] Bradley, D., Conklin, E., Papastamatiou, Y.P., McCauley, D.J., Pollock, K., Pollock, A., et al. 2017. Resetting predator baselines in coral reef ecosystems. *Sci. Rep.* 7(1): 43131, <https://doi.org/10.1038/srep43131>.
- [21] Badan Pusat Statistik Kabupaten Biak Numfor. 2024. Biak Numfor Regency in Figures 2024. Badan Pusat Statistik Kabupaten Biak Numfor. Indonesia.
- [22] Dharmawan, I.W.E., Giyanto, Aji, L.P., Widyastuti, A., Tanda, L., Budiyananto, A., Utama, R.S., Et Al. 2019. Pemantauan Kondisi Kesehatan Terumbu Karang dan Ekosistem Terkait di Kabupaten Biak-Numfor 2019. Indonesia. pp. 91.
- [23] Wilson, S.K., Graham, N.A.J., Holmes, T.H., MacNeil, M.A., Ryan, N.M. 2018. Visual versus video methods for estimating reef fish biomass. *Ecol. Indic.* 85: 146–152, <https://doi.org/10.1016/j.ecolind.2017.10.038>.
- [24] Kohler, K.E., Gill, S.M. 2006. Coral point count with Excel extensions (CPCe): A visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput. Geosci.* 32(9): 1259–1269, <https://doi.org/10.1016/j.cageo.2005.11.009>.
- [25] R Core Team. 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna. Austria.
- [26] Legendre, P., Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia.* 129(2): 271–280, <https://doi.org/10.1007/s004420100716>.
- [27] Oksanen, J.F., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., Minchin, P.R., et al. 2019. Vegan: community ecology package (version 2.5-6).
- [28] Jaccard, P. 1908. Nouvelles recherches sur la distribution florale. *Bull. Soc. Vaud. Sci. Nat.* 44(163): 223–270, <https://doi.org/10.5169/seals-268384>.
- [29] Bray, J.R., Curtis, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecol. Monogr.* 27(4): 325–349, <https://doi.org/10.2307/1942268>.
- [30] Aji, L.P., Maas, D.L., Capriati, A., Ahmad, A., de Leeuw, C., Becking, L.E. 2024. Shifts in dominance of benthic communities along a gradient of water temperature and turbidity in tropical coastal ecosystems. *PeerJ.* 12: e17132, <https://doi.org/10.7717/peerj.17132>.
- [31] Crisp, S.K., Tebbett, S.B., Bellwood, D.R. 2022. A critical evaluation of benthic phase shift studies on coral reefs. *Mar. Environ. Res.* 178: 105667, <https://doi.org/10.1016/j.marenvres.2022.105667>.
- [32] Adjeroud, M., Kayal, M., Penin, L. 2017. Importance of Recruitment Processes in the Dynamics and Resilience of Coral Reef Assemblages. In Rossi, S., Bramanti, L., Gori, A., del Valle, C.O.S. (eds.). *Marine Animal Forests*. Springer. Cham. 549–569, https://doi.org/10.1007/978-3-319-21012-4_12.
- [33] Dajka, J.C., Wilson, S.K., Robinson, J.P.W., Chong-Seng, K.M., Harris, A., Graham, N.A.J. 2019. Uncovering drivers of juvenile coral density following mass bleaching. *Coral Reefs.* 38(4): 637–649, <https://doi.org/10.1007/s00338-019-01785-w>.
- [34] Abrar, M., Bengen, D.G., Zamani, N.P., Suharsono, S., Putra, D.P., Sari, N.W.P., et al. 2024. Spatio-temporal juvenile corals (Scleractinia) following the 2016 coral bleaching event at the *Pieh Islands Marine Tourism Park* (PIMTP), West Sumatra Province, Indonesia. *Reg. Stud. Mar. Sci.* 75: 103533, <https://doi.org/10.1016/j.rsma.2024.103533>.
- [35] Speare, K.E., Duran, A., Miller, M.W., Burkepille, D.E. 2019. Sediment associated with algal turfs inhibits the settlement of two endangered coral species. *Mar. Pollut. Bull.* 144: 189–195, <https://doi.org/10.1016/j.marpolbul.2019.04.066>.
- [36] Schmitt, R.J., Holbrook, S.J., Brooks, A.J., Adam, T.C. 2022. Evaluating the precariousness of coral recovery when coral and macroalgae are alternative basins of attraction. *Limnol. Oceanogr.* 67: S285–

- S297, <https://doi.org/10.1016/j.marpolbul.2019.04.066>.
- [37] Hylkema, A., Debrot, A.O., Cammenga, R.A.R., van der Laan, P.M., Pistor, M., Murk, A.J., *et al.* 2023. The effect of artificial reef design on the attraction of herbivorous fish and on coral recruitment, survival and growth. *Ecol. Eng.* 188: 106882, <https://doi.org/10.1016/j.ecoleng.2022.106882>.
- [38] McDevitt-Irwin, J.M., McCauley, D.J., Brumbaugh, D.R., Elmer, F., Ferretti, F., White, T.D., *et al.* 2023. Dynamic interplay: disentangling the temporal variability of fish effects on coral recruitment. *Sci. Rep.* 13(1): 20971, <https://doi.org/10.1038/s41598-023-47758-6>.
- [39] Hernandez, M.F., Midway, S., West, L., Tillya, H., Polito, M. 2021. Stable isotopes track the ontogenetic movement of three commercially important fishes along a coastal Tanzanian seascape. *Mar. Ecol. Prog. Ser.* 670: 139–154, <https://doi.org/10.3354/meps13754>.
- [40] Hamuna, B. Kalor, J.D., Rachmadani, A.I. 2019. Assessing the condition of coral reefs and the indicator fish (Family: Chaetodontidae) in Coastal Waters of Jayapura City, Papua Province, Indonesia. *Eur. J. Ecol.* 5(2): 126–132, <https://doi.org/10.2478/eje-2019-0020>.
- [41] Grupstra, C.G.B., Rabbitt, K.M., Howe-Kerr, L.I., Correa, A.M.S. 2021. Fish predation on corals promotes the dispersal of coral symbionts. *Anim. Microbiome.* 3(1): 25, <https://doi.org/10.1186/s42523-021-00086-4>.
- [42] Zambre A.M., Arthur, R. 2018. Foraging plasticity in obligate corallivorous Melon butterflyfish across three recently bleached reefs. *Ethology.* 124(5): 302–310, <https://doi.org/10.1111/eth.12733>.
- [43] Azovsky, A.I. 2011. Species-area and species-sampling effort relationships: disentangling the effects. *Ecography.* 34(1): 18–30, <https://doi.org/10.1111/j.1600-0587.2010.06288.x>.
- [44] Coker, D.J., Wilson, S.K., Pratchett, M.S. 2014. Importance of live coral habitat for reef fishes. *Rev. Fish Biol. Fish.* 24(1): 89–126, <https://doi.org/10.1007/s11160-013-9319-5>.
- [45] Tiddy, I.C., Kaullysing, D., Bailey, D.M., Killen, S.S., Le Vin, A., Bhagooli, R. 2023. Effects of territorial damselfish on corallivorous fish assemblage composition and coral predation in the Mauritian lagoon. *J. Exp. Mar. Bio. Ecol.* 569: 151960, <https://doi.org/10.1016/j.jembe.2023.151960>.
- [46] Fong, C.R., Frias, M., Goody, N., Bittick, S.J., Clausing, R.J., Fong, P. 2018. Empirical data demonstrates risk-tradeoffs between landscapes for herbivorous fish may promote reef resilience. *Mar. Environ. Res.* 133: 1–5, <https://doi.org/10.1016/j.marenvres.2017.11.001>.
- [47] Rogers, A., Blanchard, J.L., Newman, S.P., Dryden, C.S., Mumby, P.J. 2018. High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. *Ecology.* 99(2): 450–463, <https://doi.org/10.1002/ecy.2103>.
- [48] Plass-Johnson J.G., Teichberg, M., Bednarz, V., Gardes, A., Heiden, J.P., Lukman, M., *et al.* 2018. Spatio-Temporal patterns in the coral reef communities of the Spermonde Archipelago, 2012–2014, II: Fish assemblages display structured variation related to benthic condition. *Front. Mar. Sci.* 5: 36, <https://doi.org/10.3389/fmars.2018.00036>.
- [49] Rizqi, M.P., Souhoka, J., Makatipu, P.C., Aji, L.P., Kusnadi, A., Nurdiansah, D., *et al.* 2019. Monitoring Kesehatan Terumbu Karang dan Ekosistem Terkait Suaka Alam Perairan (SAP) Raja Ampat Provinsi Papua Barat Tahun 2019. Coral Reef Rehabilitation And Management Program, Coral Triangle Initiative, Pusat Penelitian Oseanografi, Lembaga Ilmu Pengetahuan Indonesia. Indonesia.
- [50] Akita, Y., Kurihara, T., Uehara, M., Shiwa, T., Iwai, K. 2022. Impacts of overfishing and sedimentation on the feeding behavior and ecological function of herbivorous fishes in coral reefs. *Mar. Ecol. Prog. Ser.* 686: 141–157, <https://doi.org/10.3354/meps13996>.
- [51] McClanahan, T.R. 2022. Fisheries yields and species declines in coral reefs. *Environ. Res. Lett.* 17: 044023, <https://doi.org/10.1088/1748-9326/ac5b64>.
- [52] Aji, L.P., de Leeuw, C.A., Riekenberg, P., Capriati, A., Maas, D.L., Christianen M.J.A., *et al.* 2025. Marine ecosystems with elevated temperature and terrestrial input support simplified food webs. *Mar. Ecol. Prog. Ser.* 771: 15–32, <https://doi.org/10.3354/meps14958>.