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Effects of Coral Reef Habitat Complexity on the Community Composition and Trophic Structure of Marine Fish Assemblages in Indonesia's Wakatobi Marine National Park

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EFFECTS OF CORAL REEF HABITAT COMPLEXITY ON THE COMMUNITY
COMPOSITION AND TROPHIC STRUCTURE OF MARINE FISH ASSEMBLAGES
IN INDONESIA'S WAKATOBI MARINE NATIONAL PARK

A Thesis submitted in partial fulfillment of the
requirements for the degree of
Master of Science

by

KUYER JOSIAH FAZEKAS JR.
B.A., Wright State University, 2013

2019

Wright State University

Wright State University

GRADUATE SCHOOL

MAY 02, 2019

I HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER MY SUPERVISION BY KUYER JOSIAH FAZEKAS JR. ENTITLED EFFECTS OF CORAL REEF HABITAT COMPLEXITY ON THE COMMUNITY COMPOSITION AND TROPHIC STRUCTURE OF MARINE FISH ASSEMBLAGES IN INDONESIA'S WAKATOBI MARINE NATIONAL PARK TO BE ACCEPTED IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT

Fazekas Jr., Kuyer Josiah. M.S., Department of Biological Sciences, Wright State University, 2019. Effects of Coral Reef Habitat Complexity on the Community Composition and Trophic Structure of Marine Fish Assemblages in Indonesia's Wakatobi Marine National Park.

The coral reefs within Indonesia's Wakatobi Marine National Park support a high diversity of reef-building hard corals and associated marine fish. Climate change threatens to dramatically affect coral reef ecosystems by altering the interactions between reef fish and the specific microhabitats they depend on for survival. To examine the spatially varied effects of habitat complexity on the community composition and trophic structure of marine fish assemblages, I analyzed fish community and habitat complexity data across reef zones. Habitat complexity metrics were: structural complexity, the percentage of hard coral (HC) cover, HC genera richness, HC genera diversity (Shannon index), and HC growth form diversity (Shannon index). The community composition of fish assemblages was significantly positively related to habitat complexity, reef zones, and reef systems. This study found that the overall direction and strength of relationships between the fish community and coral reef habitat complexity data varies spatially between reef zones. Marine conservation and restoration efforts need to include specific management plans that vary among reef zones based on how varied habitat complexity and fish communities are at local scales.

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1 Introduction

1.1 Background

Coral reefs are biologically diverse ecosystems, largely due to their complex three-dimensional structure that provides habitat and resources for a wide range of organisms (Graham & Nash 2013; Holbrook et al. 2012). As a foundation species, scleractinian reef-building hard corals secrete calcium carbonate skeletons that form the architectural structure for coral reefs (Dikou 2010). Climate change threatens to dramatically alter coral reef ecosystems through warming oceans, sea level rise, changes in storm patterns, changes in precipitation, altered ocean currents, and ocean acidification (NOAA 2017).

It is particularly important to understand how benthic community composition of reefs influences the community composition and trophic structure of local fish assemblages (Richardson et al. 2017). Benthic habitats with greater habitat complexity support a greater number and different composition of species than less complex habitats in marine ecosystems (Gratwicke & Speight 2005). The substrate of benthic habitats plays an important role in the survivorship of existing marine organisms and the recruitment of juveniles along coral reefs, as many juvenile organisms have specific dietary restrictions (i.e. coral, sponges, algae, etc.) that determine their settlement sites (Coker et al. 2012; Feary et al. 2007).

Structural complexity, defined as the three-dimensional architectural structure of a habitat, in coral reefs has long been recognized as being positively correlated with marine fish species richness and abundance (Bruno & Selig 2007; Gratwicke & Speight 2005; Risk 1972). Structural complexity of coral reefs is determined by the identity and coverage of local sessile benthic organisms such as corals, sponges, and algae (Alvarez-Filip et al. 2009). Reef structural complexity influences ecosystems services by providing marine organisms refuge space from predation and food supplies that further mediate interactions such as reproduction, predation, and competition (Coker et al. 2009). Previous studies have shown that preferential habitat selection by reef fish is primarily based on structural complexity and refuge characteristics (Brooker et al. 2013; Underwood et al. 2004).

Structural complexity of coral reefs is in significant decline because of the varied effects of climate change and human activities, which result in the collapse of coral reef ecosystems (Newman et al. 2015; Alvarez-Filip et al. 2011a). Reef flattening and changes in coral community composition have direct and indirect bottom-up effects that will alter community composition of marine fish assemblages and the function of coral reef ecosystems (Richardson et al. 2017). Hard corals are particularly vulnerable to rising sea surface temperatures, ocean acidification, and changes in storm patterns, which result in coral bleaching, increased sedimentation and turbidity, decreased growth rates and structural integrity, destruction of three dimensional reef structure, and increased susceptibility to disease (NOAA 2017; Inoue et al. 2013). Destructive fishing practices,

such as blast fishing, degrades reefs by killing reef fish and physically altering the reef structure by decreasing structural complexity and killing hard corals (Fox et al. 2006). The destruction of hard coral's limestone skeleton produces unstable rubble that further reduces the survivorship of hard coral recruits (Fox et al. 2006 and 2003). Obligate corallivores that depend on hard coral polyps as a food source will no longer be able to survive along the reef (Pratchett et al. 2006; Edinger et al. 1998). Previous research has shown that coral reefs with trophically diverse marine fish communities have less hard coral disease than degraded reefs which in turn increases ecosystem resilience (Raymundo et al. 2009).

While it is widely acknowledged that structural complexity is an important habitat complexity indicator for marine ecosystems, structural complexity does not discriminate benthic substrate type and doesn't differentiate between living and non-living substrate (Gratwicke and Speight 2005, Fuad 2010). Structurally complex soft corals and sponges do not have the same ecological function as reef-building hard corals (Alvarez-Filip et al. 2011a). These corallimorphs do not have structurally complex limestone skeletons and do not provide the same range of habitat complexity that is associated with higher levels of compositional and functional diversity of associated marine fish (Brooker et al. 2013; Pratchett et al. 2006). Certain trophic groups of fish, such as obligate corallivores, require certain hard coral species for shelter, food resources, and recruitment sites (Pratchett et al. 2006; Jones et al. 2004; Holbrook et al. 2002).

Sponges, soft coral, and corallimorphs, such as *Millepora*, will often outcompete hard coral for available substrate in times of increased stress and anthropogenic disturbance (Inoue et al. 2013; Fox et al. 2003). Hard coral is subject to frequent and often fatal natural and anthropogenic disturbances, such as predation by the crown-of-thorns starfish (*Acanthaster planci*) and ocean acidification (Pratchett et al. 2006). Reefs dominated by less structurally complex hard coral growth forms, soft corals, sponges, and algae have markedly different community structures in fish assemblages, such as species diversity and abundance, trophic diversity, and biomass (Richardson et al. 2017).

The percentage of hard coral cover is a representative metric to characterize available habitat on a coral reef (Dikou 2010). Many studies have found a positive relationship between the community composition and structure of marine organisms and the percentage of live hard coral cover (Komyakova et al. 2013; Chong-Seng et al. 2012; Bell and Galzin, 1984). Hard coral cover has been shown to mediate high biodiversity on coral reefs around the world, with regional losses of live hard coral cover resulting in sharp declines in structural complexity, hard coral diversity, and diversity of associated marine organisms (Graham and Nash, 2013; Chong-Seng 2012; Chabanet et al. 1997).

Variety of growth forms has been positively correlated with observed species richness of marine fish in a range of shallow tropical marine habitats (Gratwicke and Speight, 2005b). Growth form variety is an indication of different types of microhabitats and a greater diversity of growth forms presents a larger number of potential resources, such as refuge from predation, breeding sites, food type, camouflage, and cleaning

stations. The use of growth form diversity as a habitat complexity metric is useful to assess the diversity of structural attributes of available habitat that may provide resources for different fish species (Gratwicke and Speight, 2005a).

The ability to quantify structural complexity and distinguish between genera of hard coral and their growth forms is critical to understanding the interactions corals have with associated marine fish (Alvarez-Filip et al. 2011b; Gratwicke and Speight, 2005a). However, most research only examines one or two variables out of six recognized components of habitat complexity: (1) topographic complexity or the rugosity of substratum, (2) substratum diversity, (3) variety of refuge hole sizes, (4) vertical relief or height of substratum architecture, (5) percentage of live cover, and (6) percentage hard substratum (Gratwicke & Speight 2005). Research that examines several components of habitat complexity simultaneously will provide a more comprehensive examination of the effects of habitat complexity structuring marine fish communities.

Many studies consider the effects of habitat complexity on the community composition of fish assemblages across multiple sites without including a spatial gradient of reef zone (Komyakova 2018; Richardson et al. 2017; Gratwicke and Speight, 2005; Green 1996). Few studies examine the fine-scale varied effects of habitat complexity on the structuring fish communities across multiple major recognized zones of a coral reef (moving seaward from the shore, the reef flat, reef crest, and slope (Unsworth et al. 2008; Friedlander and Parrish, 1998; Chabanet et al. 1997; Green 1996; McGehee, 1994).

The main goal of my research was to examine whether the overall direction and strength of relationships between the fish community and coral reef habitat complexity data varied spatially between reef zones and reef systems. This study expanded on previous research by considering several habitat complexity factors simultaneously and further examining their spatial variation across reef zones and reef systems. From a marine conservation perspective, it is important to understand how the distribution of hard coral and fish communities across zones will affect the rest of the ecosystem (Green 1996). This will enable future conservation and restoration plans to develop more targeted programs that may protect vulnerable microhabitats that play a key role in major ecosystem processes and services. By examining habitat complexity of coral reefs across this reef zone spatial gradient, I determined that patterns of abundance, diversity, and distribution of fish assemblages across the reef were not the result of random processes but reflected the outcomes of fine-scale interactions between reef-building corals and associated reef fish.

2 Methods

2.1 Study Area

I collected data for this study from different three fringing reef systems located in the Indonesia's Wakatobi Marine National Park (WMNP). Fringing reefs grow seaward directly from the shoreline where they form borders along the contour of the shoreline and surrounding islands. Operation Wallacea (Opwall) established and currently

maintains six permanent research sites along three major reef systems (Hoga, Kaledupa, and Sampela) around Hoga and Kaledupa Island. These three reef systems are suitable locations to examine changes in coral reef habitat complexity and its impact on marine fish community composition because they are representative of both pristine reefs and reefs heavily degraded by human activities in the region (Powell et al. 2010). I collected data during the months of June through August 2018 at the Hoga Marine Research facility.

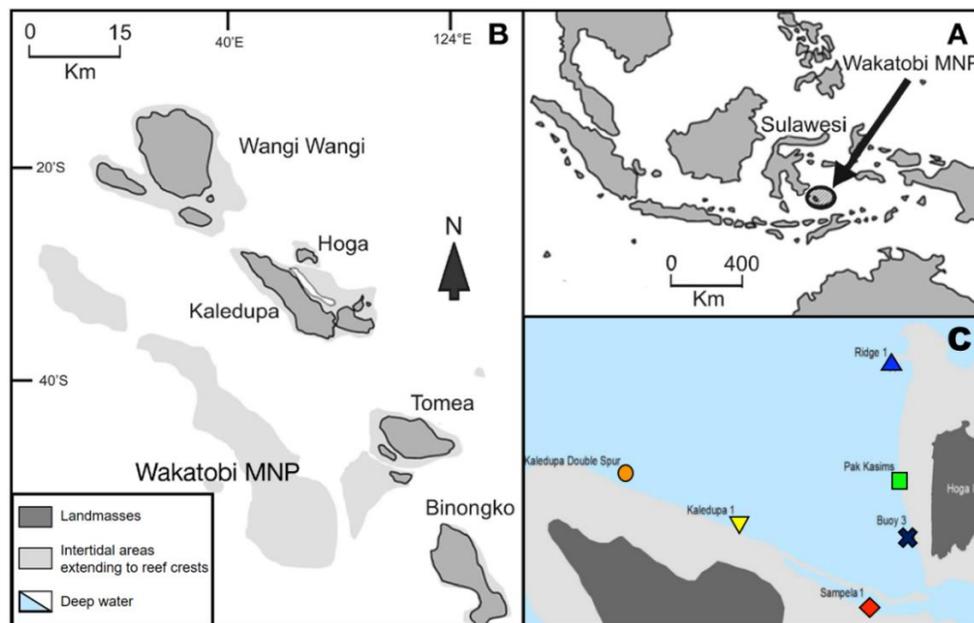


Figure 1. Map of study site (modified from Ahmadia et al. 2012). Study site is located in Indonesia (panel A), within the Wakatobi Marine National Park (MNP) between $05^{\circ}12'$ - $06^{\circ}10'S$ and $123^{\circ}20'$ - $124^{\circ}39'E$ (panel B), on the coral reefs located around Hoga and Kaledupa Island (panel C).

I chose the following six sites: Buoy 3 [S 05°28.40; E 123°45.45], Pak Kasims [S 05°27.569; E 123°45.179], Ridge 1 [S 05°26.565; E 123°45.138], Kaledupa 1 [S 05°28.22; E 133°43.47], Kaledupa Double Spur [S 05°27.432; E 123°42.412], and Sampela 1 [S 05°28.975; E 123°44.95] so that existing monitoring efforts of coral reef habitat complexity and biodiversity could continue (Table 1).

Table 1. Sample sites within each of the three reef systems. Three transects were collected in each of the reef zones (flat/crest/slope). N = 50. The bold number in parentheses denotes the number of transect collected at each site.

Hoga Reef	Kaledupa Reef	Sampela Reef
Buoy 3 (9)	Kaledupa 1 (9)	Sampela 1 (9)
Pak Kasims (9)	Kaledupa Double Spur (9)	
Ridge 1 (6)		

2.2 Sampling Design

The sites within each of their respective reef systems can be divided into 3 distinct habitat zones, which differ in their position along the shoreline and depth (Figure 2). At each dive site, I surveyed three primary types of coral reef sections: (1) reef flat (2) crest and (3) slope (Figure 2). The reef flat is located closest to the shore of the island and ranged from 0 – 4 meters in depth. The reef crest, defined as the seaward edge of the reef where the reef edge drops off into deeper water, is the highest point of the reef that separates the reef flat and the slope. The reef crest's depth ranged from 2 – 5 meters across the three studied reef systems. The reef slope descends from the crest to the sea floor and ranged from 9 – 12 meters in depth across reef systems. Within each zone, I collected data along three separate 50m transects that were parallel to the shore, with

sampling effort being consistent throughout each component ($n = 3$ transects/zone, $n = 9$ transects/site, $N = 51$ transects total). Due to topographical characteristics, Ridge 1 does not have a reef flat and has three less transects (Appendix A: Figure 3c). I unrolled a 50 m tape measure and then tucked it along the reef between the two permanently fixed transect pins within each zone. A detailed map of the sampling regime for each site is included in Appendix A.

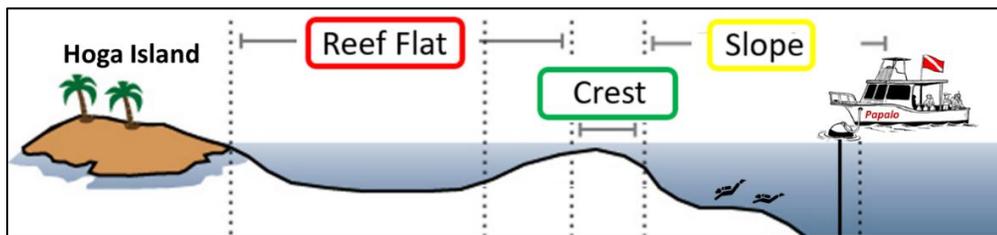


Figure 2. Breakdown of reef zones for a dive site. Dotted lines denote where one reef zone starts and ends. Modified from NOAA 2018.

2.3 Data Collection

2.3.1 Coral Reef Habitat Complexity Data

Structural Complexity Measurements

The most standard method of assessing structural complexity of coral reefs is the chain-and-tape method that estimates complexity using a rugosity index (Caldwell et al. 2016). I used the standard chain-and-tape method to collect rugosity measurements. I placed a 1.49 m link chain (link length = 1 cm) underneath each transect tape, every 5 m along each transect ($n = 11$ /transect, $n = 33$ /zone, $n = 99$ /site), and directly against the

substrate as closely as possible to all the contours and crevices without damaging the reef. I then recorded the horizontal distance that the 1.49 m chain extended along the contour of the reef.

Benthic Cover

I collected the coral biodiversity data using video-line point intercept (LPI) surveys of benthic substrate along each 50 m transect. I recorded LPI data every 25 cm along each transect (n = 201/transect, = 603/zone, n=1809/site) to characterize the community composition of benthic substrate over a large scale (Table 2). If the benthic substrate type category was hard coral, I identified the genus for each individual hard coral point using Coral Finder 3.0 (Kelley, 2016),

Table 2. Benthic substrate type

Benthic Type

Algae
Ascidian
Dead Coral
Hard Coral
Rock
Rubble
Sand
Silt
Soft Coral
Sponge
Water
Zoanthid
Unknown

2.3.2 Fish Community Composition

I collected the fish diversity data using diver-operated stereo-video (stereo-DOV) surveys along each 50 m transect using the methods standardized by Opwall (Andradi-Brown et al. 2016). The stereo-DOV system consists of two video cameras (GoPro Hero 5) in underwater housings mounted 0.7 m apart on a bar. I analyzed the footage from the stereo-DOV survey transects in SEAGIS EventMeasure v3.51 software to identify each individual fish encountered along transect in each site (n = 9 transects/site) down to its lowest taxonomic unit.

2.4 Data Analysis

2.4.1 Coral Reef Habitat Complexity Data

Coral reef habitat complexity metrics were analyzed for each transect: (1) rugosity index score, (2) percent coverage of hard coral, (3) hard coral genera richness, (4) hard coral Shannon diversity index score using the hard coral genera data, and (5) hard coral functional Shannon diversity index score using the hard coral growth form data.

The rugosity index score is expressed as the ratio of the total length of a chain and the length of the same chain molded to a surface, with a perfectly flat surface having a rugosity score of 0 and larger numbers indicating a greater degree of structural complexity (Knudby and LeDrew 2007). I calculated rugosity [R], as $R = (l/d)$, where l

is the total length of the chain when fully extended and d is the horizontal distance the 1.49 m chain extended along the contour of the reef (Figure 3).

I calculated an average rugosity index score for each transect and then an average rugosity index score for every reef zone within each reef system. The percentage of hard coral cover was calculated by identifying the frequency of hard coral points under benthic type. I calculated the percentage of hard coral cover for each reef zone by taking the average percent cover across transects located in the same reef zone.

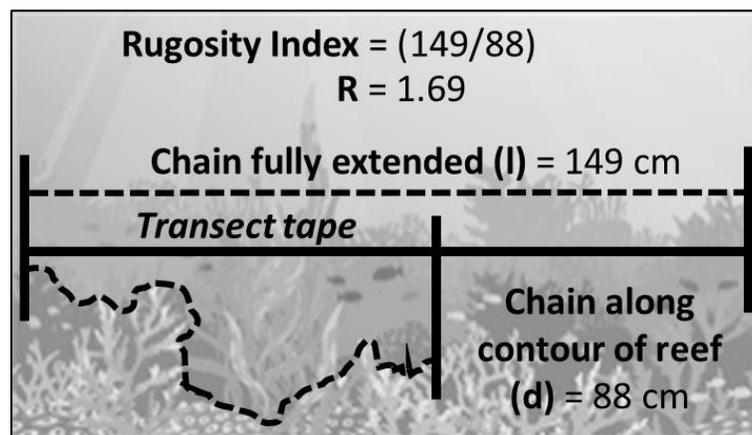


Figure 3. Method for calculating rugosity index scores. Dotted lines represent the chain.

I calculated hard coral genera richness (G) by counting the total number of each reef-building hard coral genus that was recorded in each transect. Hard coral genera diversity was determined by calculating the Shannon diversity index score for each transect based on the abundance of each hard coral genus recorded in each transect. The Shannon diversity index measures alpha (within-community) diversity and it takes into

consideration both the genera richness and the evenness in the distribution of the individuals encountered among the species recorded in each transect. I selected the Shannon diversity index because it captures both genera richness and evenness across transects and is widely used in coral reef ecology (Meixia et al. 2008). I calculated Shannon diversity as $H = -\sum p_i \times \ln p_i$, where p_i is the proportion cover of the i^{th} hard coral genera across the transect.

I further grouped hard coral into growth forms based on their morphotypes to investigate changes in hard coral functional diversity among reef zones and reef systems (Table 3). I recorded the total abundance for each hard coral genus within each recognized growth form for each transect (McMellor et al. 2010). Hard coral growth form diversity was determined by calculating the Shannon diversity index score based on the abundance for each hard coral genus within each recognized growth form for each transect.

Table 3. Hard coral growth form categories

Hard Coral Growth Forms
Branching
Digitate
Encrusting
Foliose
Massive
Mushroom
Submassive
Tabular

Due to the potential for co-variation among habitat complexity characteristics, I examined the relationships between structural complexity, the percentage of hard coral cover, hard coral genera richness, hard coral diversity, and hard coral functional diversity using Pearson's correlation analysis. I visualized variation in all the measured habitat complexity variables among reef zones and reef systems with principal components analysis (PCA) based on a correlation matrix to determine if habitat complexity varied along a spatial gradient. I performed two-way fixed analysis of variance to test the effects of reef zone, reef system, and the interaction between reef and zone on each habitat complexity variable. Significant effects were further tested using *post hoc* Tukey's HSD to determine if the variation in the means of habitat complexity variables among reef zone and reef systems gradient were statistically significant. I performed these statistical analyses JMP Pro 14.

2.4.2 Fish Community Data

I analyzed the community composition of fish assemblages using (1) log fish abundance, (2) species richness, (3) fish diversity (Shannon diversity index), and (4) trophic group functional diversity of fish (Shannon diversity index) for each transect. I calculated total abundance by identifying all diurnally active fish observed along each transect using stereo-DOV surveys. I identified and counted each individual fish in SEAGIS EventMeasure software. I log transformed total abundance of fish data to

normalize extreme values of fish abundance and meet basic assumptions for statistical analysis.

Fish species richness (S) was calculated by counting the total number of species that were represented in each transect (alpha diversity). Fish diversity was determined at the transect level by examining the fish community data for the presence and abundance of each species. I calculated Shannon diversity index scores using the fish community data for each transect. I grouped fish into trophic groups based on functional feeding strategies to investigate changes in functional fish diversity among reef zones and reef systems. I calculated relative abundance of each fish species and trophic group in the reef flat, crest, and slope of each reef system. I then calculated Shannon diversity index scores for functional fish diversity using the trophic group abundance and distribution data.

I visualized the variation in the community composition and trophic group structure of fish assemblages between reef zones and reef systems with non-metric multi-dimensional scaling (nMDS) based on Bray-Curtis similarities distance matrices of fish community data in R (version 3.5.1). I fourth root transformed the species-level fish abundance data before running the nMDS.

I performed two-way fixed analysis of variance to test the effects of reef zone, reef system, and the interaction between reef and zone on each fish community response variable (log fish abundance, fish species richness, fish diversity, and fish functional diversity). Significant effects were further tested using *post hoc* Tukey's HSD to determine if the variation in the means of fish community data across a reef zone and reef

system spatial gradient were statistically significant. I performed these statistical analyses using JMP Pro 14.

2.4.3 Relationships Between Habitat Complexity and Fish Community Data

I used multiple linear regression analysis to examine the relationships between the coral reef habitat complexity characteristics (explanatory variables) and the community composition and structure of fish assemblages (fish abundance, species richness, and fish diversity, and fish functional diversity as response variables). Models of fish abundance, species richness, and fish diversity (Shannon index) regression included reef zone, reef system, and the interaction of zone*reef system as explanatory variables to determine whether the effect of reef zone and reef system influenced the overall direction and strength of relationships between the fish community and habitat complexity data.

3 Results

3.1 Coral reef habitat complexity data

The reefs within the Wakatobi Marine National Park (WMNP) supported a high diversity of structurally complex reef-building hard corals. Previous research had catalogued over 390 species of hard coral belonging to 68 genera within the WMNP. In total, this study captured 62% of all hard coral genera richness previously recorded in the WMNP, with 42 hard coral genera recorded across 6 sites during the two-month field data collection period. The detailed data containing the list of each genus recorded in

each growth form are in Appendix B. These recorded levels of genera richness in hard coral are among the highest recorded within coral reef ecosystems (McMellor et al. 2010).

3.1.1 Variation in coral reef habitat complexity among reef zones and reef systems

Coral reef habitat complexity varied spatially across reefs zones and reef systems. The first two axes of the PCA (PC1 and PC2) covered 64.7 % of the variation in coral reef habitat complexity characteristics (Table 4). Structural complexity, hard coral genera richness, hard coral genera diversity, and hard coral growth form diversity loaded significantly and positively on PC1 (Table 4). The percentage of hard coral cover loaded significantly and positively on PC2 (Table 4).

The results of the PCA found that coral reef habitat complexity varied across reefs zones and reef systems (Figure 4). Transects within the same reef zone grouped together, indicating their similarity across combinations of coral reef habitat complexity variables (Figure 4a, PERMANOVA, $p < 0.001$). Adjacent reef zones (flat to crest and crest to slope) grouped together away from the shore, indicating that they shared the most similarity in habitat complexity (Figure 4a). Transects also grouped together within the same reef system, which further suggested that habitat complexity varied across a reef system gradient (Figure 4b, PERMANOVA, $p < 0.001$).

Table 4. Results for principal component analysis (PCA) of coral reef habitat complexity predictor variables using data from 50 transects. The eigenvalues for the first two principal components (PC) are shown in parentheses. The loading scores for coral reef habitat complexity variables are shown for the first two PC axes. Bold faced loading scores reflect significant correlations ($\alpha = 0.05$).

	% Variance Explained	Cumulative % Variance Explained
Principal component 1 (2.22)	44.5	44.5
Principal component 2 (1.0)	20.2	64.7
<i>Habitat Complexity Variables</i>	<i>PC 1 Loading Score</i>	<i>PC 2 Loading Score</i>
Structural Complexity	0.38	-0.08
Hard Coral Cover	0.12	0.97
Hard Coral Genera Richness	0.61	0.08
Hard Coral Diversity (Shannon index)	0.57	-0.15
Hard Coral Growth Form Diversity (Shannon index)	0.39	0.11

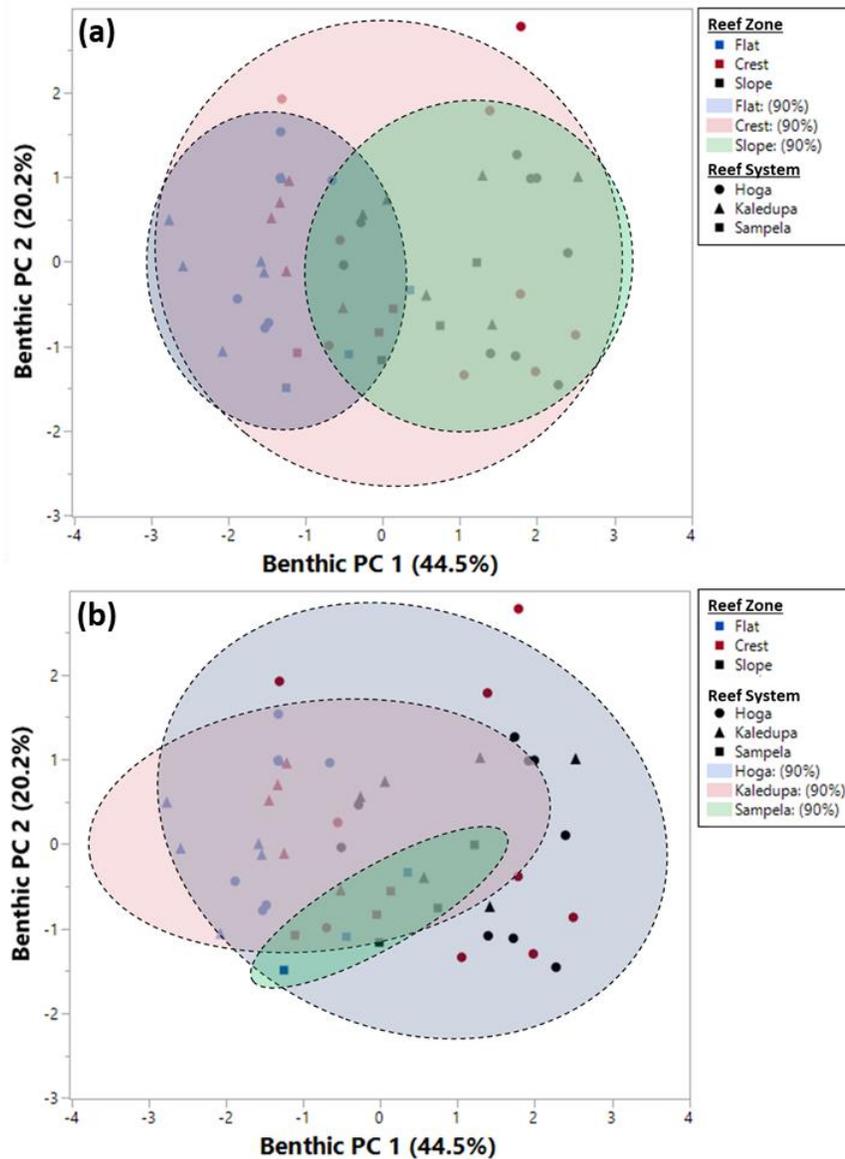


Figure 4. Principal components analysis showing spatial variation in habitat complexity variables: structural complexity, percentage of hard coral cover, hard coral genera richness, hard coral diversity, and hard coral growth form diversity for 50 transects across (a) reef zones and (b) reef systems. Spatial variation of habitat complexity was assessed using correlations matrix. Each symbol represents an individual transect. Confidence ellipses encompass 90% of transects clustering within each spatial gradient based on the similarities across combinations of coral reef habitat complexity variables.

Structural complexity, measured as rugosity index scores, marginally significantly varied among reef zone and reef systems (Table 5). In contrast, there was no significant interaction among reef zone and reef system for structural complexity. Rugosity index scores increased across reef zones away from the shore (no interaction, Figure 6a). There was a weak increasing trend in structural complexity across reef zones away from the shore within each reef system; however, this difference was not in itself statistically significant (Table 5 and Figure 5a). Although not statistically significant, the Hoga reef system had the highest range (1.29 to 2.66) and mean \pm SE (1.62 ± 0.05) rugosity index scores among the reef systems.

Hard coral was the most abundant benthic substrate type observed in this study (Table 6). The percentage of hard coral cover did not significantly vary across reef zones or reef systems (Table 5 and Figure 5b). The Hoga reef system had the highest percentage of hard coral cover across all reef zones (Table 6). After hard coral, rock and rubble were the two most abundant benthic substrate types in the Hoga reef system. The substrate in the Kaledupa reef system was dominated by soft corals (Table 6).

The Kaledupa reef system had the lowest percentage of hard coral cover among all reef systems. Rock, rubble, and sand had higher percentages of cover compared to hard coral in the Kaledupa reef system (Table 6). The percentage of hard coral cover increased across reef zones away from the shore in the Kaledupa and Sampela reef systems (Figure 5a). The substrate in the Sampela reef system was dominated by rubble,

rock, and sand. Hard coral was the fourth most prevalent benthic substrate type recorded in the Sampela reef system (Table 6).

Hard coral genera richness varied significantly across reef zones and reef systems (Table 5). Hard coral genera richness increased across reef zones away from the shore when all reef systems were considered (Figure 5c). Hard coral genera richness was significantly higher in the Hoga reef system than in the Kaledupa reef system (Figure 5h). Hard coral Shannon diversity index scores significantly increased across reef zones away from the shore (Figure 5d). Hard coral Shannon diversity index scores in the Sampela reef system were significantly higher than the Hoga and Kaledupa reef systems (Figure 5h).

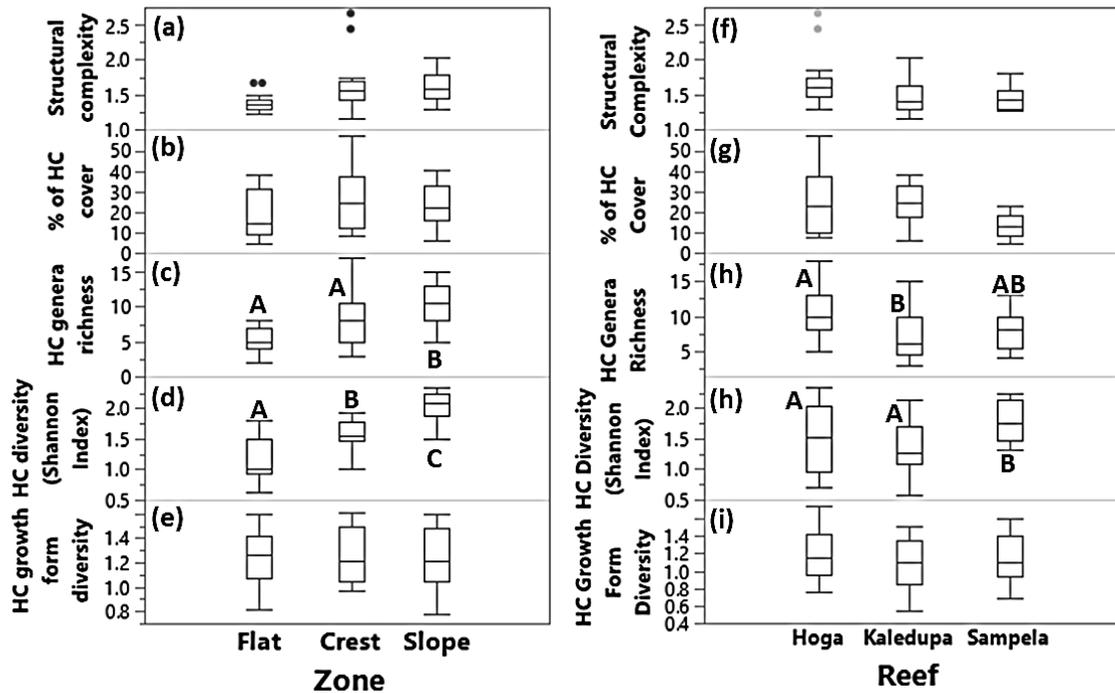


Figure 5. Variation in structural complexity, percentage of hard coral cover, hard coral genera richness, hard coral diversity (Shannon index), and hard coral growth form diversity (lower case a-e) by reef zone (left panel) and reef system (right panel). Different capital letters symbolize significant differences between reef zones and reef systems as determined by *post hoc* Tukey pair-wise comparisons that were ran on significant main effects (A-C, Tukey, all $P < 0.05$). Total number of transects across study site: $N = 50$.

Hard coral growth form diversity (Shannon index) significantly increased across zones away from the shore in the Kaledupa reef system (Figures 6e). Hard coral growth form diversity in the Sampela reef system did not follow the same pattern as the rest of the habitat complexity variables and decreased across reef zones away from the shore (Figure 6e) leading to a significant interaction among reef zone and system for this variable (Table 5 and Figure 6e). Growth form diversity in reef flats in the Sampela reef

system was significantly higher than in the reef flats in the Kaledupa reef system (Figure 6e). Overall, coral reef habitat complexity increased across reef zones away from the shore in each of the three sampled reef systems (Figure 6).

Table 5. Results from two-way ANOVA testing the main effects of zone and reef on each habitat complexity variable for 50 transects collected across study sites. Models included the interaction of zone*reef. Bold numbers indicate statistically significant effects on habitat complexity variables. Main effects that did not reveal statistically significant pair-wise comparison in post hoc Tukey tests are not bold. Alpha was set at 0.05 for all tests.

Habitat complexity variables	Main effects		Interaction	Combined Effect			
	Zone (<i>p</i>)	Reef (<i>p</i>)	Zone*Reef (<i>p</i>)	R ²	<i>df</i>	<i>F</i>	<i>p</i>
Structural Complexity	0.05	0.06	0.21	0.35	(8,41)	2.76	0.02
% of Hard Coral Cover	0.58	0.05	0.93	0.17	(8,41)	1.07	0.41
Hard Coral Genera Richness	< 0.001	< 0.001	0.77	0.56	(8,41)	6.54	< 0.0001
Hard Coral Genera Diversity (Shannon index)	< 0.0001	< 0.001	0.22	0.78	(8,41)	17.70	< 0.0001
Hard Coral Growth Form Diversity (Shannon index)	0.75	0.55	< 0.001	0.42	(8,41)	3.64	< 0.01

Table 6. Percentage of cover for each benthic type across reef zones within each reef system. Individual numbers represent overall mean density (No. of individuals/50 m transect) of each benthic type recorded in each transect across each reef zone and reef system. Calculations were based on untransformed benthic count data. Bold numbers indicate the largest percentage of benthic cover across reef zones within each reef system relative to the other benthic substrate categories.

Benthic Type	Hoga					Kaledupa					Sampela 1					Grand Total	% Cover
	Flat	Crest	Slope	Total	% Cover	Flat	Crest	Slope	Total	% Cover	Flat	Crest	Slope	Total	% Cover		
Algae	0.33	2.89	25.89	10.88	5.4%	5.67	10.80	12.33	9.53	4.5%	0	0.67	2.33	48	0.5%	9	4.2%
Ascidian	0.17	0.89	0.56	0.58	0.3%	1.83	2.60	0.67	1.65	0.8%	0	0	0	4.67	0.0%	1	0.4%
Cnidarian	0	0.56	1.89	0.92	0.5%	0	0	0.17	0.06	0.0%	0	0.67	0.33	2.89	0.2%	1	0.3%
Dead Coral	6.67	8.22	2.44	5.67	2.8%	4.83	7.20	4.00	5.24	2.5%	0.67	3	1.33	26.67	0.8%	5	2.3%
Hard Coral	56.50	71.89	53.11	61	30.4%	19.33	26.40	35.50	27.12	12.8%	24.00	25	31	240.56	13.3%	43	21.1%
Rock	38.33	35.89	24.11	32.08	16.0%	47.83	58.80	22.17	42	19.8%	49.67	55.67	39.33	213.11	24.0%	38	18.7%
Rubble	44.50	28.33	27.11	31.92	15.9%	37.33	46	23.17	34.88	16.4%	77.33	55.67	29.33	205.11	26.9%	37	18.0%
Sand	33.17	5.78	10.11	14.25	7.1%	35.00	30.40	26.17	30.53	14.4%	41.67	24.67	48	133.78	19.0%	24	11.8%
Soft Coral	18	36.78	18.00	25.04	12.5%	42.17	44.60	54.17	47.12	22.2%	5.67	9.67	11	164.56	4.4%	30	14.5%
Sponge	2.83	8.33	30.33	15.21	7.6%	5.50	11.40	15.17	10.65	5.0%	2	25.67	37.67	82.44	10.8%	15	7.2%
Tunicate	0	0.11	0.56	0.25	0.1%	0	0	0	0	0.0%	0	0	0.33	0.78	0.1%	0	0.1%
Unknown	0.50	0.67	5	2.25	1.1%	1.17	3.00	7.00	3.76	1.8%	0	0.33	0.33	13.33	0.1%	2	1.2%
Water	0	0.56	1.67	0.83	0.4%	0	0	0	0	0%	0	0	0	2.22	0	0	0.2%
No. of transects	6	9	9	24		6	5	6	17		3	3	3	9		50	

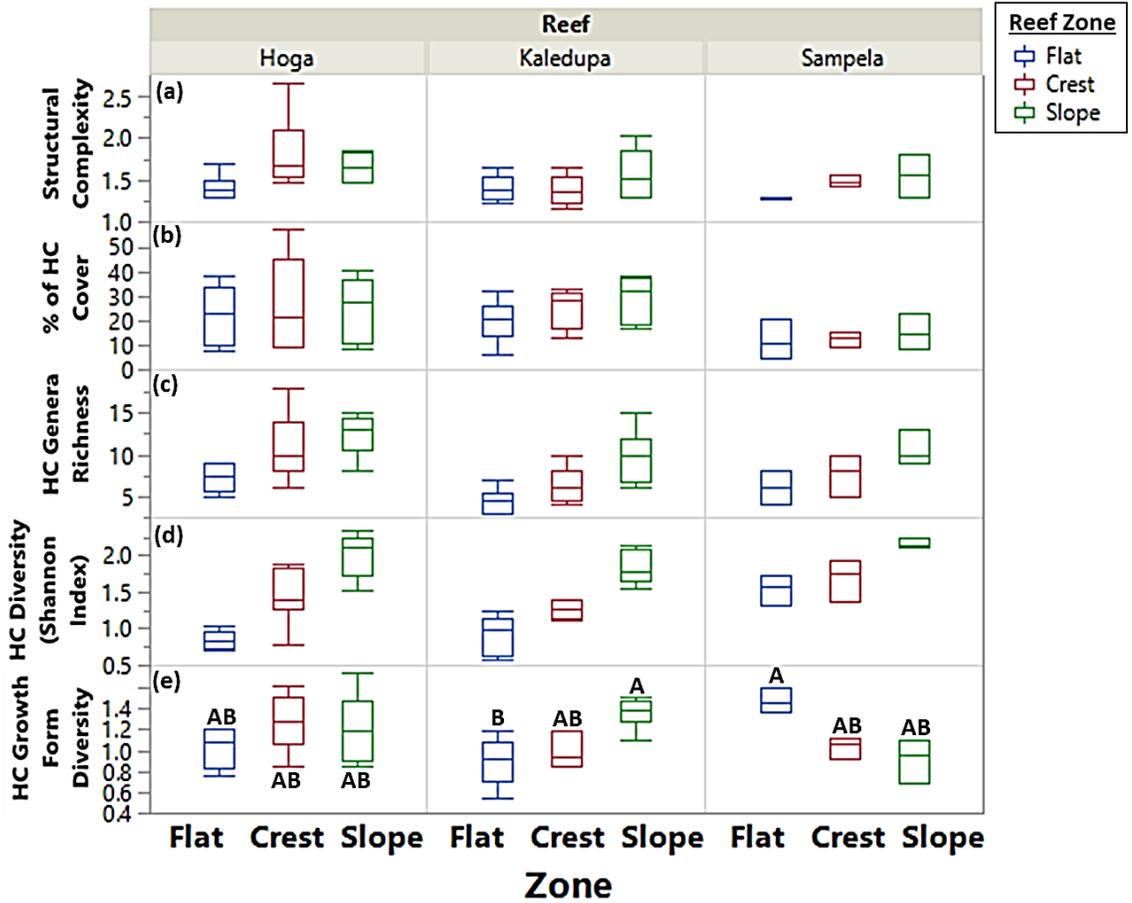


Figure 6. Variation in (a) structural complexity, (b) percentage of hard coral cover, (c) hard coral genera richness, (d) hard coral diversity (Shannon index), and (e) hard coral growth form diversity among reef zones within each reef system. Different capital letters symbolize statistically significant differences as determined by *post hoc* Tukey pairwise comparisons that were ran on significant interactions (A-AB, Tukey, all $P < 0.05$). Total number of transects across study site: $N = 50$.

3.2 Fish Community Data

This study captured 46% of all fish species and 62% of all fish families previously recorded in the WMNP. A total of 12,980 individual tropical marine fish were counted, representing 32 families, 90 genera, and at least 270 species. I calculated relative abundance of each family and species in the reef flat, crest, and slope of each reef system. The detailed data containing the list of fish families and species observed in each reef zone and reef system are in Appendix C.

Approximately 98% of all fish observed were identified to species. From the total population of fish counted, 76 individual fish could only be identified to family and 296 to genus. Fish that were only able to be identified to genus were included in calculations for fish species richness and diversity. These fish were compared against the rest of the species identified within each transect to ensure that they were in fact a different species that was not already identified. The 10 most abundant species accounted for approximately 50% of all fish recorded in this study. These species were *Pomacentrus brachialis*, *Odonus niger*, *Amblyglyphidodon curacao*, *Chromis viridis*, *Dascylus reticulatus*, *Neoglyphidodon nigroris*, *Amblyglyphidodon leucogaster*, *Pholidichthys leucotaenia*, *Ctenochaetus striatus*, and *Pterocaesio tile* (Appendix C).

Six of the 10 most abundant species were from the family Pomacentridae, commonly known as damselfish, which represented 51% of the total number of individuals and roughly 6 % of the total number of species recorded (Appendix C). The second most abundant family of tropical marine fish were Acanthuridae (surgeonfish),

which represented 11% of the total number of individuals and 2% of the total number of species recorded.

3.2.1 Variation in community composition of fish assemblages among reef zones and reef systems

The community composition of fish assemblages varied across a reef zone and reef system gradient (Figure 7). The nMDS of fish community composition revealed that adjacent reef zones (flat to crest and crest to slope) shared the most similarity in community composition. Transects within the same reef zone generally grouped together indicating their similarity in community composition of fish (Figure 7a). The community composition of fish assemblages in the Sampela reef system was most dissimilar from the other reef systems as evidenced by the minor overlap with the Hoga and Kaledupa reef system grouping (Figure 7b). The nMDS plots suggested that the community composition of fish varied more significantly between reef zones in contrast to reef systems (Figure 7).

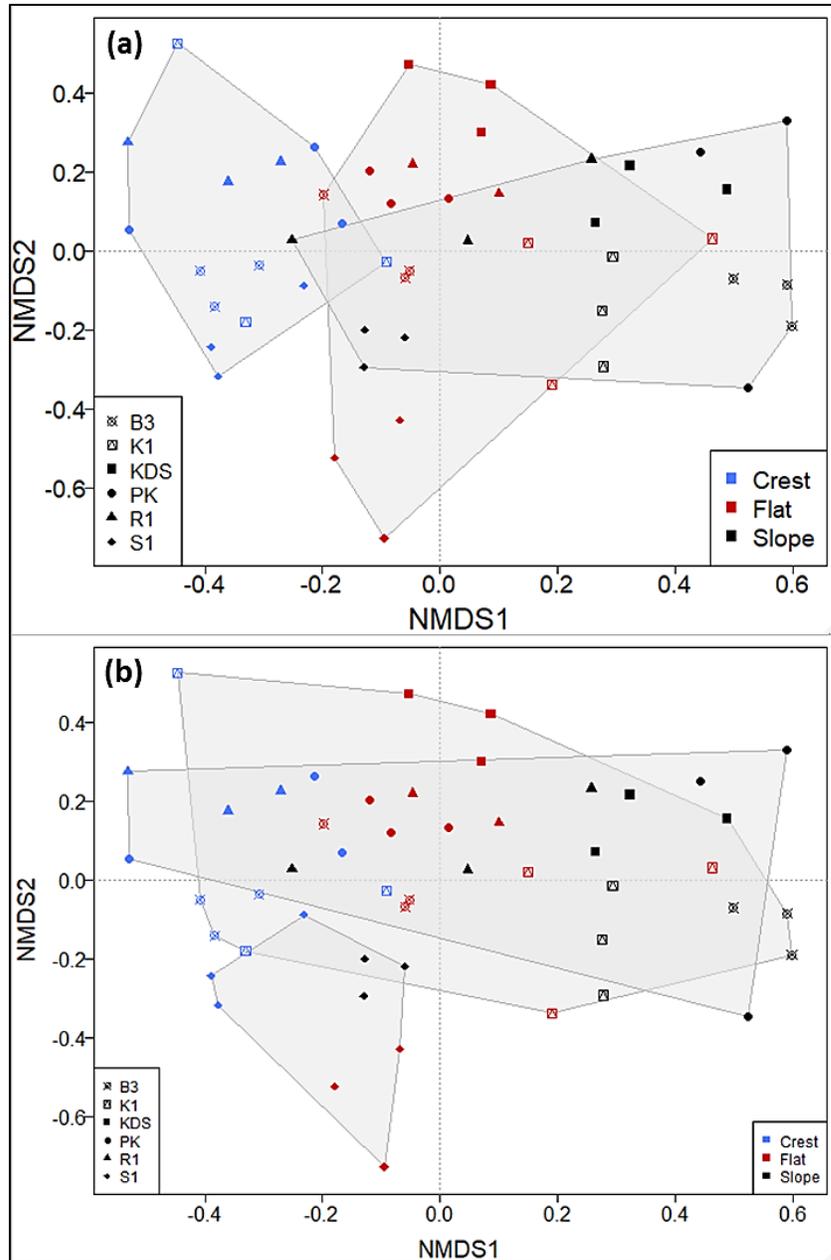


Figure 7. Non-metric multidimensional scaling analysis showing variation in fish community composition among each of the 50 transects by reef zone (a) and reef system (b). Spatial variation of fish community composition was assessed using Bray-Curtis similarity matrix. Individual symbols represent each transect. Ellipses highlight the transects clustering within each reef zone and reef system (Stress = 0.23).

Fish abundance was not significantly predicted by reef zone and reef system (Table 7). The Hoga reef system had the highest abundance of fish among reef zones (Figure 8e). Fish abundance decreased across reef zones away from the shore in the Hoga and Kaledupa reef systems (Figure 9a).

The combined effect of reef zone and reef system had a significant effect on fish species richness and Shannon diversity index scores of fish assemblages (Table 7). Fish species richness and Shannon diversity index scores decreased across reef zones away from the shore across reef systems (Figure 8b-c). The interaction effect of reef zone and reef system was significant for fish diversity (Table 7).

Table 7. Results from two-way ANOVA testing the main effects of zone and reef system on each fish community composition and structure variables. Models included the interaction of zone*reef. Combined effect reports the combined effect of reef zone and reef system on fish community data variables. N = 50 transects. Bold numbers indicate statistically significant effects on fish community variable. Main effects that did not reveal statistically significant pair-wise comparison in post hoc Tukey tests are italicized. A 0.05 criterion of statistical significance was employed for all tests.

Response variable	Main effects		Interaction	Combined effect			
	Zone (p)	Reef (p)	Zone*Reef (p)	R ²	df	F	p
Log Fish Abundance	0.22	0.08	0.15	0.29	(8,41)	2.12	0.06
Fish Species Richness	0.07	0.24	0.10	0.34	(8,41)	2.63	0.02
Fish Diversity (Shannon index)	0.24	0.64	<i>0.03</i>	0.30	(8,41)	2.23	0.04
Fish Functional Diversity (Shannon index)	<i>0.04</i>	0.48	0.27	0.31	(8,41)	3.64	0.04

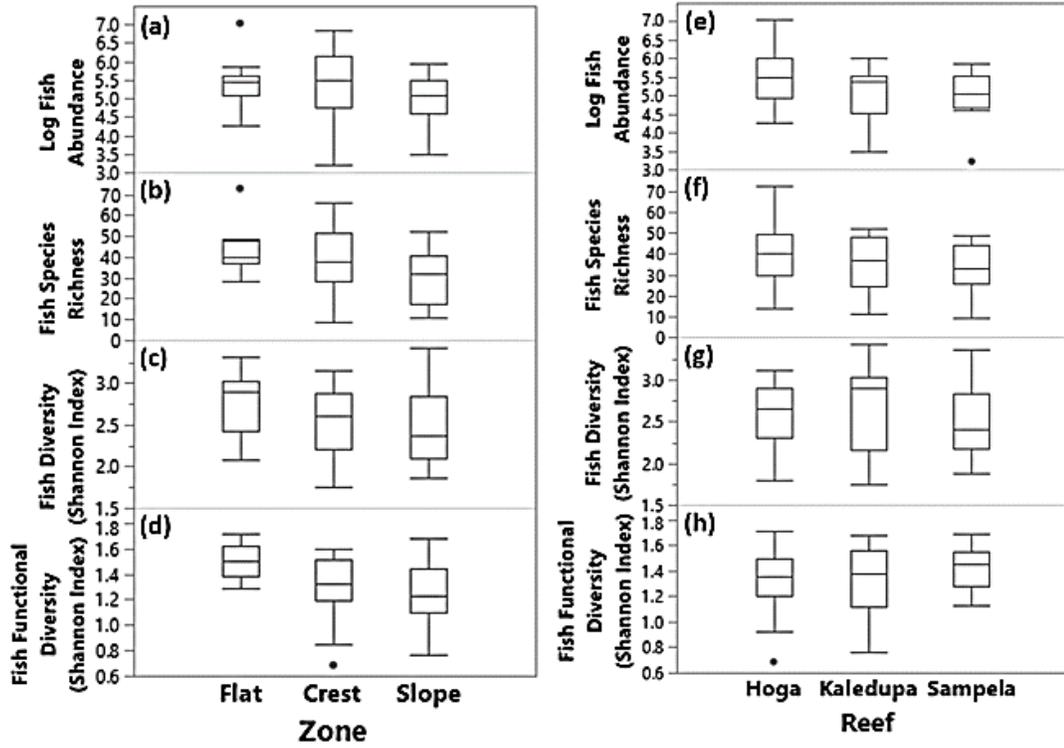


Figure 8. Variation in log fish abundance, fish species richness, fish diversity (Shannon index), and fish functional diversity (Shannon index) by reef zone (left panel) and reef system (right panel). Total number of transects across study site: N = 50.

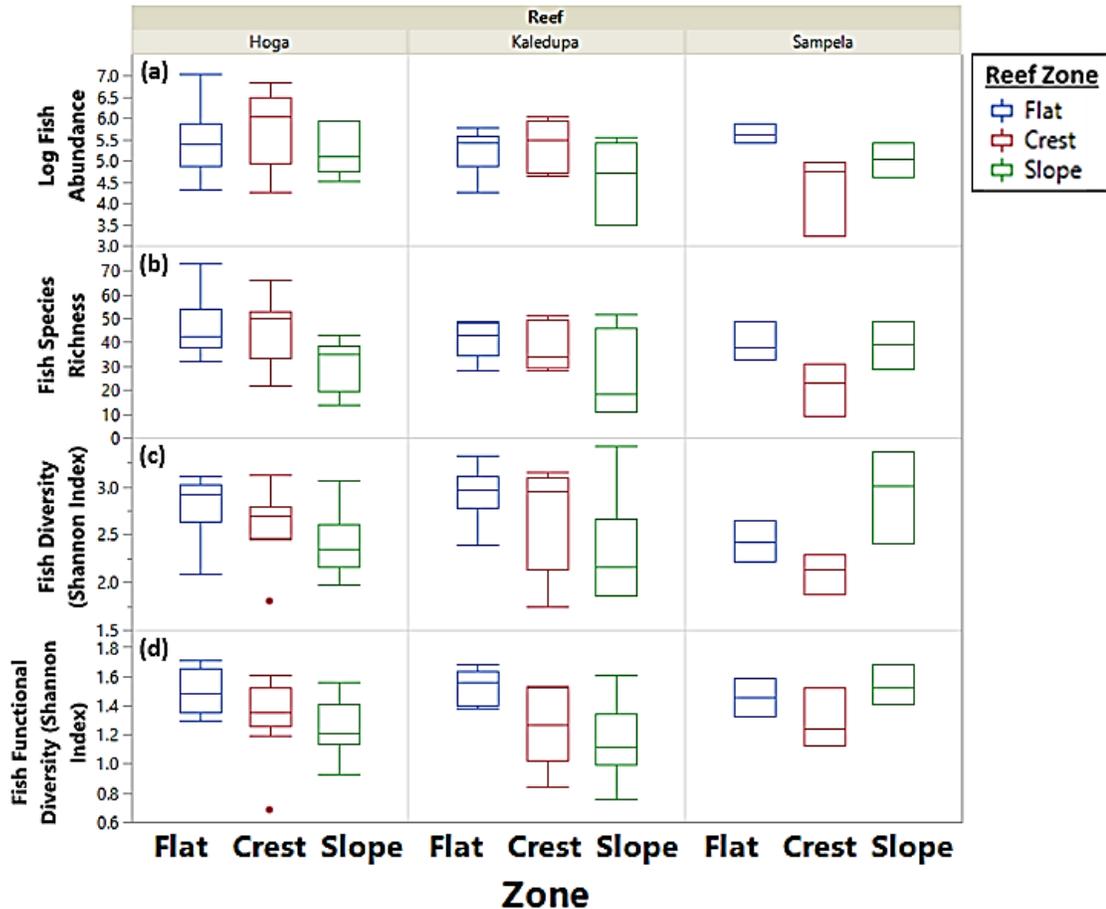


Figure 9. Variation in log fish abundance, fish species richness, fish diversity (Shannon index), and fish functional diversity (Shannon Index) among reef zones within each reef system. Total number of transects across study site: N = 50.

3.2.2 Variation in trophic group functional diversity of fish assemblages among reef zones and reef systems

Functional fish diversity varied among reef zones and reef systems. The detailed count data containing the list of fish species within each trophic group that were observed in each reef zone and reef system are presented in Appendix C.

The trophic group functional diversity of fish assemblages was highly variable within reef zones (Figure 10a) and reef systems (Figure 10b). The nMDS of fish functional diversity revealed that transects within the same reef zone (Figure 10a) and reef system (Figure 10b) did not cluster tightly together indicating their dissimilarity in trophic group structure. The nMDS plots showed that reef slopes clustered more tightly than the other reef zones which suggested that there was less variation in fish functional diversity in the reef slopes (Figure 10a).

Reef zone had a significant effect on trophic group functional diversity of fish across reef systems; however, pair-wise comparisons on the interaction effect of reef zone and reef systems for fish functional diversity did not yield significant differences (Table 7). Shannon diversity index scores for fish trophic group diversity decreased across reef zones away from the shore within the Hoga and Kaledupa reef systems (Figure 9d). The combined effect of reef zone and reef system on the functional diversity of fish assemblages was significant, whereby trophic group Shannon diversity index scores decreased across reef zones away from the shore within each reef system (Table 7).

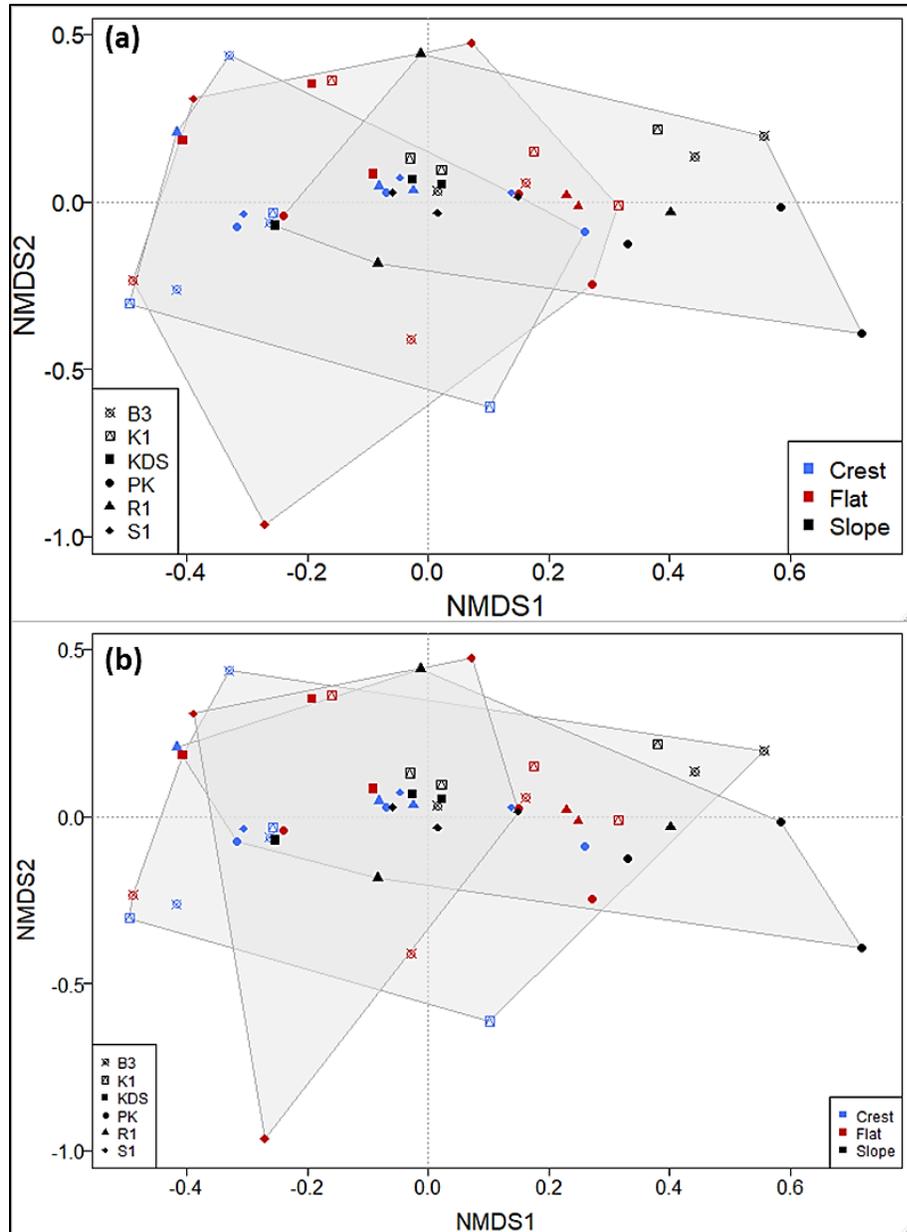


Figure 10. Non-metric multidimensional scaling analysis showing variation in fish community structure (trophic group functional diversity) between each of the 50 transects by reef zone (a) and reef system (b). Spatial variation of fish community structure was assessed using Bray-Curtis similarity matrix on fish functional diversity data. Individual symbols represent a single transect. Ellipses highlight the transects within each reef zone and reef system (Stress = 0.16).

The five most abundant and diverse trophic groups for marine fish were omnivores, planktivores, herbivores, invertivores, and carnivores (Appendix D). Omnivores were the most abundant trophic group, representing 40 % of all fish recorded, across reef zones and reef systems when calculating community proportion based on relative abundance (Appendix D). Omnivores were the fourth most diverse trophic group, with 46 species recorded across the study area. Red-toothed triggerfish (*Odonus niger*) were the most abundant omnivore recorded, representing 19 % of all omnivorous fish. Red-toothed triggerfish were only recorded in the Hoga and Kaledupa reef systems where its relative abundance significantly increased across reef zones away from the shore (Appendix D). Red-toothed triggerfish were commonly observed in large schools of fish along the reef crest and reef slope in the Hoga and Kaledupa reef systems (Personal observation). Staghorn damselfish (*Amblyglyphidodon curacao*) were the most abundant omnivore observed in all reef systems, representing 15 % of all omnivorous fish. Staghorn damselfish abundance were significantly higher in the reef crest within the Hoga reef system (Appendix D).

Planktivores were the second most abundant trophic group, representing 23 % of all fish recorded, across reef zones and reef systems (Appendix D). Planktivores were the fifth most diverse trophic group, with 42 species recorded across the study area. Charcoal damsel (*Pomacentrus brachialis*) were the most abundant planktivorous fish present in all reef systems, representing 36 % of all planktivores. Charcoal damsel relative

abundance significantly decreased from the reef crest to the reef slopes in the Hoga and Kaledupa reef systems (Appendix D).

Herbivores were the third most abundant trophic group, representing 13 % of all fish observed, across reef zones and reef systems (Appendix D). Herbivores were the most diverse trophic group for marine fish, with 63 species being recorded across the study area. Striated surgeonfish (*Ctenochaetus striatus*) were the most abundant herbivore observed, representing 27 % of all herbivorous fish. Striated surgeonfish abundance significantly decreased across zones away from the shore in each reef system (Appendix D).

Invertivores were the third most abundant trophic group, representing 12 % of all fish observed (Appendix D). Invertivores were the third most diverse trophic group for marine fish, with 51 species being recorded across the study area. Green damselfish (*Chromis viridis*) were the most abundant invertivore observed, representing 43 % of all invertivores. Green damselfish were only recorded in the Hoga reef system where its abundance significantly decreased across reef zones away from the shore (Appendix D). Yellow chromis (*Chromis analis*) were the most abundant invertivore recorded in all reef systems, representing 13 % of all invertivorous fish. Yellow chromis abundance significantly increased across reef zones away from the shore in the Hoga and Kaledupa reef systems (Appendix D).

Carnivores were the fifth most abundant trophic group, representing 9 % of all fish observed, across reef zones and reef systems (Appendix D). Carnivores were the

second most diverse trophic group for marine fish, with 63 species being recorded across the study area. Yellowfin goatfish (*Mulloidichthys vanicolensis*) were the most abundant carnivore observed, representing 20 % of all carnivorous fish. Yellowfin goatfish were only recorded in the Hoga reef system where its abundance significantly decreased from the reef crest to reef slope (Appendix D). Two-lined monocle bream (*Scolopsis bilineata*) were the most abundant carnivore observed in all reef systems, representing 7 % of all carnivorous fish. Two-lined monocle bream abundance did not significantly vary across reef zones in each reef system (Appendix D).

Overall, the reef zone had a significant effect on trophic group diversity of marine fish assemblages in the study area. The community composition and trophic group structure of fish assemblages became less diverse across reef zones away from the shore within each reef system (Table 7 and Figure 9).

3.3 Coral reef habitat complexity and its effect on the community composition and trophic structure of fish assemblages

Fish abundance was significantly predicted by hard coral genera and growth form diversity (Table 8). Fish abundance was positively related to hard coral genera ($\beta = 0.46$, $p = 0.33$ and growth form diversity ($\beta = 0.62$, $p = 0.24$). The higher levels of hard coral genera and growth form diversity in the Hoga reef system had a significant positive effect on fish abundance across reef zones ($\beta = 0.34$, $p = 0.03$). However, in contrast to my hypothesis, fish abundance decreased across reef zones away from the shore in each reef

system (flat: $\beta = 0.45$, $p = 0.08$, crest: $\beta = 0.02$, $p = 0.90$, and slope: $\beta = -0.45$, $p > 0.05$). Reef system, reef zone, hard coral genera diversity, and hard coral growth form diversity explained 35 % of the variation in fish species richness (Table 8).

Fish species richness was significantly predicted by hard coral genera and growth form diversity (Table 8). Fish species richness decreased across reef zones away from the shore in each reef system. Within the model, hard coral growth form diversity had a greater influence on fish species richness ($\beta = 12.99$, $p = 0.15$) than hard coral genera diversity ($\beta = 0.58$, $p = 0.94$) across reef zones and reef systems. Reef system, reef zone, hard coral genera diversity, and hard coral growth form diversity explained 38 % of the variation in fish species richness (Table 8).

Fish diversity (Shannon index) and fish functional diversity were not significantly related to hard coral genera diversity, hard coral growth form diversity, reef zone, or reef system (Table 8). Although the combined effect of reef zone and reef system significantly predicted structural complexity, structural complexity was omitted from the multiple linear regression models because it did not contribute significantly to explaining the variation in the community composition and structure of fish assemblages (Table 5). Hard coral cover was also omitted from the multiple linear regression models due to the weak correlation of hard coral cover to the other habitat complexity metrics and the lack of significant variation of hard coral cover between reef zones and reefs systems. Hard coral genera diversity (Shannon Index) was chosen over hard coral genera richness for model selection because it captured both genera richness and evenness across transects.

Table 8. Results for four multiple linear regression models predicting fish community composition and structure across a reef zone and reef system gradient. Models were ran using hard coral and fish community data from 50 transects. Independent variables included hard coral (HC) diversity (Shannon index), HC growth form diversity (Shannon index), reef zone (flat/crest/slope), and reef system (Hoga/Kaledupa/Sampela). All models included the interaction of zone*reef. Bold numbers indicate statistically significant effects on response variable. A 0.05 criterion of statistical significance was employed for all tests.

Response variables	Explanatory variable significance (<i>p</i>)					Overall model			
	Zone	Reef	Zone*reef	HC	HC Growth	R ²	<i>df</i>	<i>F</i>	<i>p</i>
				Diversity	Form Diversity				
Log Fish Abundance	0.18	0.08	0.18	0.33	0.24	0.35 (10,39)	2.13	0.05	
Fish Species Richness	0.34	0.35	0.06	0.94	0.15	0.38 (10,39)	2.38	0.03	
Fish Diversity (Shannon index)	0.34	0.78	0.09	0.94	0.71	0.31 (10,39)	1.73	0.11	
Fish Functional Diversity (Shannon index)	0.22	0.49	0.43	0.52	0.95	0.32 (10,39)	1.79	0.09	

4 Discussion

The main objective of this study was to examine the varied effects of coral reef habitat complexity on the community composition and trophic structure of marine fish assemblages across reef zones and reef systems. Previous research tended to focus on the impact of a single factor of coral reef habitat complexity on the community composition and trophic structure of marine fish assemblages (Komyakova et al. 2013, Gratwicke and Speight, 2005a). This study confirmed what has been shown in other studies of coral reef ecosystems: habitat complexity influences the community composition and structure of fish assemblages (Richardson et al. 2017). This study expanded on previous research by considering several habitat complexity factors simultaneously and further examining their variation across a reef zone and reef system gradient.

Coral reef habitat complexity varied across reef zones and reef systems. All the examined coral habitat complexity variables increased away from the shore from the reef flat toward to the reef slope. Alterations in habitat complexity among reef zones can result from changes in natural disturbances, which decreases with depth (Green 1996). The reef flats and crests are subjected to increased disturbances due to changes in tide, hydrodynamic stress from wave action, and anthropogenic use (McClanahan and Arthur, 2001; Letouneur et al. 1998; Parrish, 1989).

The three reef systems in this study undergo different human pressures across each of the reef zones. The reef flats and crests in the Kaledupa and Sampela Reef systems undergo high navigational and fishing pressures by local people who depend on

the reefs for subsistence fishing and transit for commerce (McMellor et al. 2010; Petsoede et al. 2003; Pet-Soede and Erdmann, 2003). These increased human pressures can directly or indirectly affect the community composition and functional diversity of both benthic substrate and fish communities (McClanahan and Arthur, 2001; Jennings and Polunin, 1996).

Protected coral reefs have higher fish species richness and numbers of individuals than unprotected reefs with the same habitat complexity (McClanahan and Arthur, 2001). Although the Hoga reef system is designated as an eco-tourism and no-take zone for fishing practices, I observed the presence of many local Indonesians fishing in the protected area. The lack of data regarding the enforcement of the marine protected zone by the Wakatobi regional government makes assessment of human disturbance unreliable (Dr. Dan Exton, personal communication). Therefore, this study did not incorporate any measures for anthropogenic disturbance into the models.

Previous studies suggest that anthropogenic effects on fish abundance and species richness are mostly indirect through damage to the habitat, rather than a direct effect to fish communities (McClanahan and Arthur, 2001; Jennings and Polunin, 1996; Russ, 1991). The Kaledupa and Sampela reef systems were previously subjected to destructive fishing practices, such as blast fishing, which has been shown to lead to the destruction of underlying benthic habitat that supports marine organisms. The Kaledupa reef system had the lowest percentage of hard coral cover across all reef systems and was dominated by soft corals (Table 7). Rock, rubble, and sand had higher percentages of cover than hard

coral in the Kaledupa reef system (Table 7). Increased rubble deposits and movement on reefs in the Indo-Pacific have been shown to be detrimental to small reef-building corals by decreasing their survivorship rates (Fox et al. 2006).

Reef-building hard corals are slow to grow back in fields of dead hard coral rubble in which soft coral or corallimorpharians, such as *Millepora* and *Tubipora*, will often become dominant on rubble (Inoue et al. 2013; Fox et al. 2003). Although these corallimorphs have structurally complex limestone skeletons they do not provide the same type of habitat complexity that is associated with higher levels of compositional and functional diversity of associated marine fish (Brooker et al. 2013). This could explain why this study did not find a strong correlation between hard coral cover and structural complexity.

Previous studies have demonstrated a diverse but low prevalence of disease in hard coral in the Wakatobi Marine National Park (Haapkylä et al. 2010 and 2007). Although I did not measure the prevalence or distribution of diseases on hard coral colonies, I personally observed many large tabular *Acropora* hard coral colonies on the reef slopes that had outbreaks of white band disease. These colonies of *Acropora* were highly structurally complex and were frequently accompanied by large schools of two-stripe damselfish (*Dascylus reticulatus*). The tabular *Acropora* colonies were fouled by filamentous algae as they were slowly killed by the disease. Although the structurally complex limestone skeleton remained after death, the tabular *Acropora* colony no longer provided suitable habitat for the two-stripe damselfish due to the decreased size in refuge

hole within the colony of hard coral. This would explain why this study did not find a strong correlation between live hard coral cover and structural complexity.

Although this study found a weak positive correlation between hard coral cover and hard coral genera richness, I expect that future losses in hard coral cover will result in declines in hard coral genera richness in the study area. Hard coral genera richness significantly varied among reef zones across all reef systems. I personally observed that the reef flats were largely dominated by large colonies of *Porites*, which suggests that this genus of hard coral can outcompete other hard corals for space due to their tolerance of the aforementioned natural and anthropogenic disturbances that occur on the reef flat of this study site (McClanahan and Arthur, 2001; Letouneur et al. 1998).

Results from this study further support the findings that hard coral genera richness significantly predicts structural complexity and overall habitat complexity on coral reefs (Komyakova et al. 2018; Fuad 2010). Similarly, hard coral Shannon diversity index scores significantly varied among reef zones, increasing with distance from shore. I expected that higher levels of diversity in hard corals would result in a greater range of habitat complexity and diversity in the community composition and structure of fish assemblages.

Complex reef habitats support diverse fish communities and the loss of habitat complexity of coral reefs can alter the composition of marine fish communities. I observed a decrease in the abundance of site-attached demersal reef fish species (e.g. two-stripe damselfish) and an increase in benthopelagic fish species (e.g. staghorn

damsel fish) as the complexity of the benthic substrate decreased across reef zones and reef systems. Benthopelagic fish species venture far away from the substrate whereas site-attached demersal fish orient close to and within the reef structure. Although these two species of damselfish are in the same family and trophic group (omnivore), each species responded differently to changes in hard coral growth form diversity across a reef zone and reef system gradient because they used the habitat differently.

The Sampela reef system had a distinctly different fish community in all 3 reef zones than the Hoga and Kaledupa reef systems. I personally observed higher levels of turbidity in the Sampela reef system. Sampela is located next to a seagrass bed and a Bajau fishing village. These adjacent environments can modify the habitat composition and consequently the fish community structure (Letouneur et al. 1998; Parrish, 1989). High-turbidity has a negative effect on school formation for some fish species because visual contact among individuals is reduced and can cause changes in the behavior of fish (Ohata et al. 2013; Miyazaki et al. 2000). Turbidity also has the potential to affect the ability of fish to locate food and detect predators.

During data collection, I did not observe large schools of benthopelagic fish, such as the red-toothed triggerfish on the Sampela reef which were present across reef zones on both the Hoga and Kaledupa reef systems. This is likely the result in how characteristically different the Sampela reef is from the other two reef systems. The Sampela reef is a lagoonal fringing reef, which maintains a significantly different water flow regime than standard fringing reefs, such as Hoga and Kaledupa (Dr. David Smith,

Personal communication). This change in flow could directly impact the feeding strategy of the red-toothed triggerfish, which inhabits reef channels and reef slopes that are subject to strong current which aid them in feeding on zooplankton (Reefbase, 2019).

The distribution of trophic groups along a reef is likely related to the availability of primary food sources. The reef zone had a significant effect on the distribution of herbivores, the most diverse trophic group of fish in this study (Appendix D). Striated surgeonfish (*Ctenochaetus striatus*), the most abundant herbivore observed, significantly decreased across zones away from the shore in each reef system (Appendix D). The decrease in overall herbivore abundance and species richness across reef zones away from the shore is likely the result of the decrease in algae, their food source, across reef zones away from the shore. This change in the distribution of herbivores across reef zones further demonstrates that specific trophic groups, such as herbivores, respond differently to changes in availability of benthic substrate.

I showed that the abundance and species richness of marine fish assemblages are significantly positively related to hard coral genera diversity, hard coral growth form diversity, reef zone, and reef system. This study found that the effects that habitat complexity has on structuring fish community composition varies spatially along the reef flat, crest, and slope. I have also shown that fish functional diversity was weakly inversely related to habitat complexity across reef zones away from the shore in each reef system. The combined effects of reef zone and reef system influenced the overall

direction and strength of relationships between the fish community and habitat complexity data.

There was a significant difference in the abundance and number of species among reef zones and reef systems but not a difference in fish functional diversity, measured as Shannon's diversity of trophic group fish data. Although we had lower relative abundance of fish and species richness across reef zones in the Kaledupa and Sampela reef systems, there was no loss of trophic groups, which fill different ecological roles. Functional redundancy in fish trophic groups may explain why the observed change in habitat complexity do not lead to changes in fish diversity. Across reef zones, species replacements occur between functionally redundant fish species but do not induce changes to the functional structure of communities, assessed here using Shannon diversity index scores for fish trophic groups. This pattern supports previous studies that have demonstrated that functional redundancy in reef fish is comparatively higher in the tropics (Mouillot et al. 2013).

My results showing a significant difference in the abundance and number of species among reef zones and reef systems but not a difference in fish functional diversity indicate that we cannot assume that a decrease in hard coral genera diversity and hard coral growth form diversity across reef zones and reef systems will result in a loss in functional diversity of marine fish assemblages in the WMNP. These results seem to conform with previous research that has shown that using the number of individuals as a measure of fish abundance within communities, in contrast to a size based metric such as

length or biomass, may have limited explanatory power in examining trophic group functional diversity (Mouillot et al. 2013). Small species tend to be more abundant on reefs than larger ones, which result in them being overrepresented in surveys for tropical marine fish (Mouillot et al. 2013). Smaller fish belonging to unique functional feeding groups are expected to be disproportionately abundant on tropical coral reefs, which may dominate this study's functional diversity index (Fisher et al. 2010).

The results of this study provide further evidence for the argument that future research should incorporate a comprehensive reef zone spatial gradient (flat, crest, and slope), when examining the relationship between habitat complexity and associated marine fish assemblages across study sites. The variation in the community composition and trophic structure of marine fish assemblages resulting from changes in habitat complexity are likely to have major impacts on ecosystem service provision by coral reefs (Done, 1992). Coral reef ecosystems provide substantial income for people in fisheries and eco-tourism and are likely to be negatively impacted by the decrease in habitat complexity of coral reefs (Costanza et al. 2013; Graham et al. 2007; Costanza et al. 1997).

From a management perspective, it is important to understand how the changes in coral and fish communities across reef zones will affect the rest of the ecosystem. This will enable future management plans to develop more spatially targeted conservation and restoration initiatives for vulnerable microhabitats that may play a key role in major ecosystem processes and services. Marine conservation and restoration efforts may need

to include specific management plans that vary among reef zones based on how varied habitat complexity and fish communities are at local scales.

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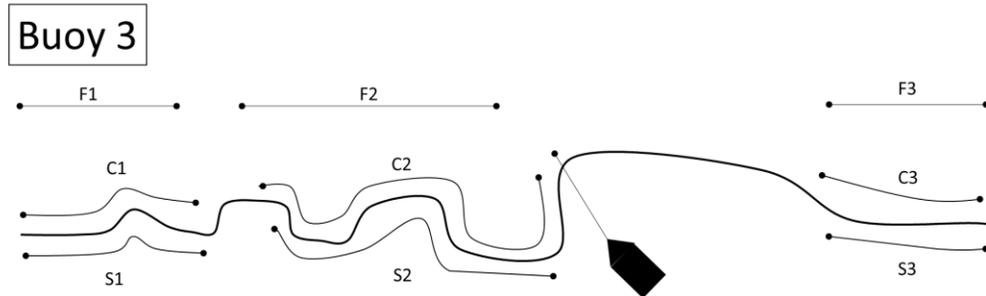
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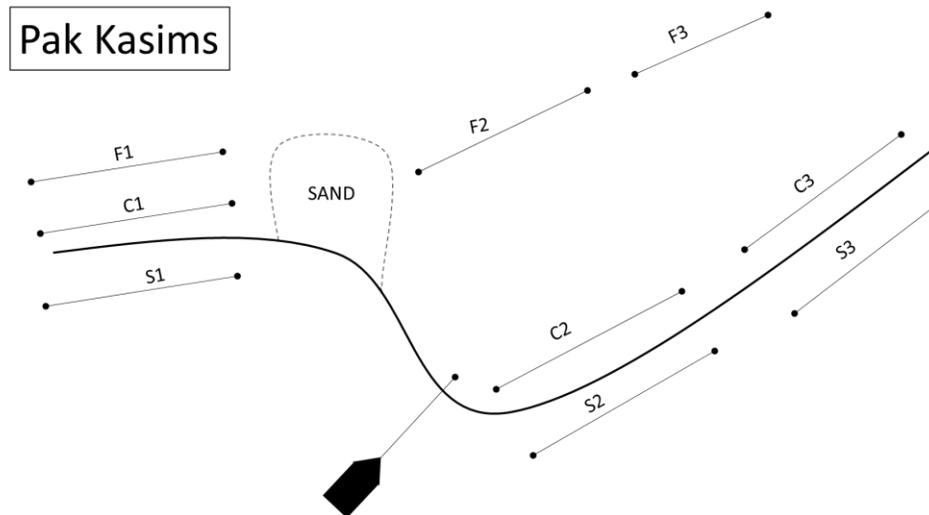
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6 Appendices

APPENDIX A

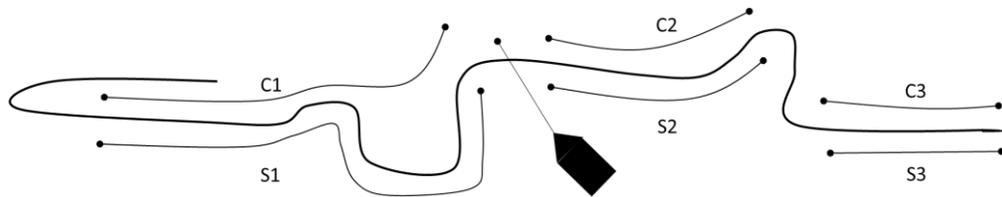


Map of Buoy 3 on the Hoga Reef System. The long solid black line illustrates the general contour of the reef. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring buoy [S05°28.40; E 123°45.45]. This figure illustrates sampling design and is not drawn to scale.



Map of Pak Kasims on the Hoga Reef System. The long solid black line illustrates the general contour of the reef. The dashed lines illustrate the edge of a large sandy area. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring buoy [S 05°27.569; E 123°45.179]. This figure illustrates sampling design and is not drawn to scale.

Ridge 1



Map of Ridge 1 on the Hoga Reef System. The long solid black line illustrates the general contour of the reef. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring buoy [S 05°26.565; E 123°45.138]. This figure illustrates sampling design and is not drawn to scale.

Kaledupa 1

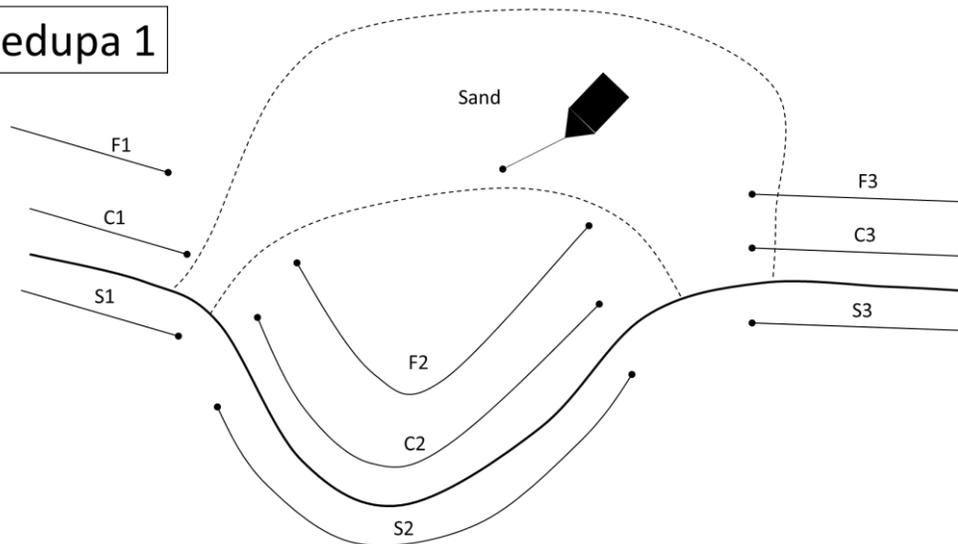
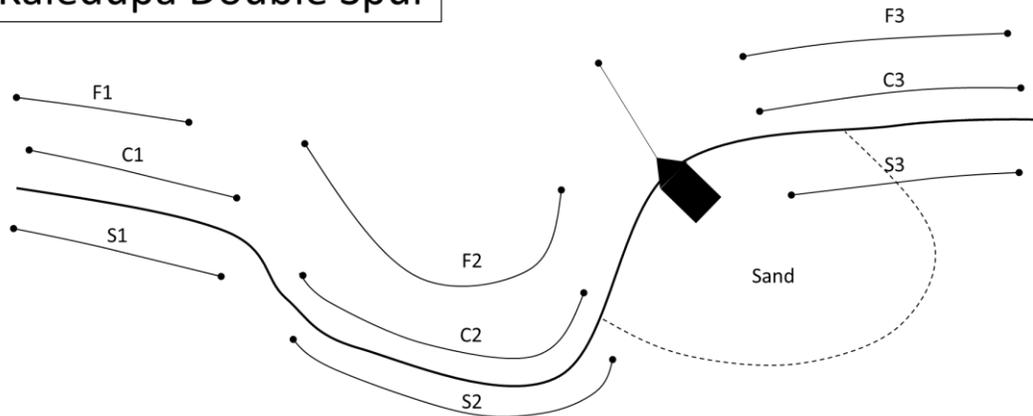


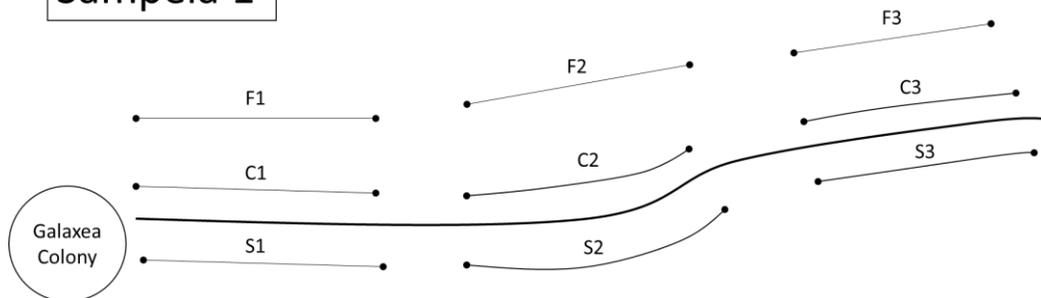
Figure 3d. Map of Kaledupa 1 on the Kaledupa Reef System. The long solid black line illustrates the general contour of the reef. The dashed lines illustrate the edge of a large sandy area. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring buoy [S 05°28.22; E133°43.47]. This figure illustrates sampling design and is not drawn to scale.

Kaledupa Double Spur



Map of Kaledupa Double Spur on the Kaledupa Reef System. The long solid black line illustrates the general contour of the reef. The dashed lines illustrate the edge of a large sandy area. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring [S 05°27.432; E 123°42.412]. This figure illustrates sampling design and is not drawn to scale.

Sampela 1



Map of Sampela 1 on the Sampela Reef System. The long solid black line illustrates the general contour of the reef. The circle represents a very large colony of *Galaxea* that was used as a reference point for underwater navigation. Symbols and numbers indicate transect number within each reef zone (flat = F, reef crest = C, and slope = S). The black polygon represents the boat anchored on mooring buoy [S 05°28.975; E 123°44.95]. This figure illustrates sampling design and is not drawn to scale.

APPENDIX B

Appendix B. Total abundance for hard coral genera by growth form. The percentage of cover was calculated for each genus within each growth form for 50 transects. Individual numbers represents the sum of all count data for all three transects within each reef zone. Numbers in parentheses next to growth form type indicate total genera richness recorded across entire study site.

Genus recorded in each growth form	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Branching (10)	22	159	59	6	9	8	26	30	9	328	14.9%
Acropora	10	14	10			4	8	4	4	54	16.5%
Anacropora		1								1	0.3%
Favia								1		1	0.3%
Galaxea			2							2	0.6%
Montipora	1	69	1		4					75	22.9%
Pocillopora	10	16	11	2	1	3	15	11	3	72	22.0%
Porites		52	1	4	1		1	8		67	20.4%
Psammocora		1								1	0.3%
Stylophora		3	6				2	4		15	4.6%
Tubastraea		3	26							29	8.8%
Unknown	1				3	1		2		7	2.1%
Digitate (3)	3	3	4			1	4		2	17	0.8%
Acropora	3	1				1	4			9	52.9%
Montipora			4							4	23.5%
Pocillopora		2								2	11.8%

Bold numbers indicate the percentage of cover for each growth form.

Appendix B. Continued.

Genus recorded in each growth form	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Encrusting (22)	7	62	210	17	12	77	8	18		411	18.7%
Astrea			1						20	21	5.1%
Astreopora		1	4				1			6	1.5%
Cyphastrea			1							1	0.2%
Echinopora		2	2							4	1.0%
Favia		1	5							6	1.5%
Favites		1	6					2		9	2.2%
Gardineroseris			2						1	3	0.7%
Goniastrea	2	2								4	1.0%
Goniopora			7							7	1.7%
Leptastrea		1								1	0.2%
Leptoseris			3							3	0.7%
Merulina		2								2	0.5%
Montipora	2	25	58	1	1	6	1	4		98	23.8%
Mycedium			5		1			1	11	18	4.4%
Pachyseris		1	9	1		4				16	3.9%
Pavona	1	2	5						1	9	2.2%
Plesiastrea										0	0.0%
Porites		12	29		2	2		4	1	50	12.2%
Psammocora			3				3		1	7	1.7%
Symphyllia			1							1	0.2%

Bold numbers indicate the percentage of cover for each growth form.

Appendix B. Continued.

Genus recorded in each growth form	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Tubastraea			20		1	4				25	6.1%
Turbinaria		1	4							5	1.2%
Unknown	2	11	45	15	7	60	3	7		150	36.5%
Foliose (8)		23	31		6	24			4	88	4.0%
Echinophyllia		3								3	3.4%
Echinopora		1							2	3	3.4%
Montipora		5								5	5.7%
Mycedium		2	6		1	5				14	15.9%
Oxypora		2	7			2				11	12.5%
Pachyseris		5	8		4	11				28	31.8%
Pectinia		1	3						1	5	5.7%
Turbinaria					1	2			1	4	4.5%
Unknown		4	7			4				15	17.0%
Massive (22)	117	171	133	85	93	125	16	26		766	34.8%
Astrea			1							1	0.1%
Astreopora		2	4						59	65	8.5%
Coscinaraea	1	1								2	0.3%
Diploastrea		10	11		10			1	3	35	4.6%
Euphyllia				1		1				2	0.3%
Favia	3	6	8	3	4	14	1	2	8	49	6.4%

Bold numbers indicate the percentage of cover for each growth form.

Appendix B. Continued.

Genus recorded in each growth form	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Favites	1	13	3	1	5	5		2		30	3.9%
Galaxea		4	1	1	2	2	1		11	22	2.9%
Goniastrea	3	12	1	3	1	2		5	5	32	4.2%
Goniopora		3	25	3	2	5				38	5.0%
Lobophyllia	1		1			1			3	6	0.8%
Montastraea		1							6	7	0.9%
Montipora		7	2					2	1	12	1.6%
Oulophyllia			1							1	0.1%
Pavona	1									1	0.1%
Physogyra			1			1				2	0.3%
Platygyra			3	1						4	0.5%
Plerogyra			1							1	0.1%
Porites	102	98	43	52	50	19	10	13	4	391	51.0%
Psammocora	2	1								3	0.4%
Symphyllia		1	1			1			18	21	2.7%
Turbinaria			1							1	0.1%
Unknown	3	5	23		4	10	4	1		50	6.5%

Bold numbers indicate the percentage of cover for each growth form.

Appendix B. Continued.

Genus recorded in each growth form	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Mushroom (4)	7	5	4	1	3	6	1			27	1.2%
Ctenactis	1	1								2	7.4%
Fungia	5	4	3	1	3	5	1			22	81.5%
Heliofungia			1							1	3.7%
Unknown	1					1				2	7.4%
Submassive (7)	173	211	25	36	24	18	8	1		496	22.5%
Acropora					1					1	0.2%
Favia		1							3	4	0.8%
Galaxea										0	0.0%
Montipora		16	2		1	2	1			22	4.4%
Porites	168	185	19	26	20	15	4	1	2	440	88.7%
Psammocora	2	4								6	1.2%
Stylophora	1								1	2	0.4%
Unknown	2	5	4	1	1	1	3			17	3.4%
Tabular (6)	10	15	16		1	18	9			69	3.1%
Acropora	10	6	7		1	18	9			51	73.9%
Echinopora		1								1	1.4%
Montipora		2	4							6	8.7%
Mycedium			4							4	5.8%
Pachyseris		5								5	7.2%
Turbinaria		1								1	1.4%
Unknown			1							1	1.4%

APPENDIX C

Appendix C. Total abundance for each fish species by Family. The frequency of observation (F.O.) percentages were calculated for each fish species within each family. Individual numbers represent the mean of all count data for all three transects within each reef zone. Fish species are listed in descending order of highest total abundance within each Family. Total species richness for each Family is in parentheses next to Family heading.

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Acanthuridae (3)	40.17	35.89	21.89	34.67	35.00	11.67	27.33	11.00	24.00	28.72	11.1%
Ctenochaetus striatus	18.17	8.89	0.78	17.00	4.50	0.50	21.33	7.00	9.33	8.82	30.7%
Zebrasoma scopas	4.00	5.67	0.22	7.00	6.00	1.17	3.00	1.67	1.33	3.60	12.5%
Acanthurus nigrofuscus	5.83	5.56	1.33	2.67	2.50	1.83	1.00	2.33	3.00	3.16	11.0%
Naso vlamingii	1.50	2.78	5.00	0.00	12.50	0.50	0.00	0.00	0.00	3.14	10.9%
Acanthurus auranticavus	3.00	0.33	1.11	3.00	1.00	0.17	0.67	0.00	8.00	1.64	5.7%
Acanthurus pyroferus	0.83	0.89	2.22	1.83	1.67	0.83	0.00	0.00	1.33	1.26	4.4%
Naso caeruleacauda	0.00	2.22	1.33	0.33	2.50	0.33	0.00	0.00	0.00	1.02	3.6%
Acanthurus nubilus	0.00	0.22	1.89	0.00	0.00	4.17	0.00	0.00	0.00	0.88	3.1%
Naso sp	0.00	2.56	0.00	0.50	2.83	0.17	0.00	0.00	0.00	0.88	3.1%
Acanthus thompsoni	0.17	1.22	1.67	0.00	0.50	0.83	0.00	0.00	0.00	0.70	2.4%
Acanthurus thompsoni	0.17	0.78	1.89	0.00	0.00	0.00	0.00	0.00	0.00	0.50	1.7%
Ctenochaetus binotatus	1.33	0.78	0.11	0.50	0.00	0.17	0.00	0.00	0.33	0.42	1.5%
Acanthurus sp	0.33	0.00	1.56	0.00	0.17	0.00	0.00	0.00	0.00	0.34	1.2%
Ctenochaetus cyanocheilus	1.50	0.22	0.00	0.50	0.00	0.33	0.00	0.00	0.33	0.34	1.2%
Zebrasoma veliferum	0.50	0.44	0.00	0.50	0.83	0.17	0.33	0.00	0.00	0.34	1.2%
Acanthurus blochii	1.50	0.44	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.26	0.9%
Acanthurus leucocheilus	0.17	0.33	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.24	0.8%
Acanthurus nigricans	0.33	0.22	0.44	0.33	0.00	0.00	0.00	0.00	0.00	0.20	0.7%
Naso hexacanthus	0.17	0.44	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.7%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Acanthurus bariene	0.00	0.11	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.04	0.1%
Ctenochaetus sp	0.00	0.11	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.04	0.1%
Acanthurus nigricaudus	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.1%
Acanthurus triostegus	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.1%
Naso unicornis	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.1%
Paracanthurus hepatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.02	0.1%
Anthinae (3)	3.50	8.56	8.00	6.50	0.00	0.17	0.00	0.00	0.00	4.20	1.6%
Pseudanthias huchtii	3.50	8.22	0.56	6.50	0.00	0.17	0.00	0.00	0.00	2.80	66.7%
Pseudanthias pleurotaenia	0.00	0.33	7.11	0.00	0.00	0.00	0.00	0.00	0.00	1.34	31.9%
Pseudanthias tuka	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.06	1.4%
Aulostomidae (1)	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01%
Aulostomus chinensis	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	100.0%
Balistidae (9)	4.17	37.67	52.44	4.00	35.50	39.67	3.33	1.33	1.67	26.60	10.2%
Odonus niger	0.00	10.11	49.67	3.00	34.17	38.50	0.00	0.00	0.00	19.84	74.6%
Melichthys niger	1.00	24.56	0.44	0.00	0.00	0.00	0.00	0.00	0.00	4.62	17.4%
Melichthys vidua	0.83	2.33	1.67	0.50	1.00	0.33	0.00	0.00	0.33	1.06	4.0%
Balistapus undulatus	1.50	0.56	0.44	0.00	0.33	0.67	0.33	1.00	0.00	0.56	2.1%
Sufflamen chrysopterus	0.50	0.00	0.00	0.33	0.00	0.17	2.00	0.33	0.33	0.28	1.1%
Sufflamen bursa	0.17	0.11	0.22	0.00	0.00	0.00	0.67	0.00	1.00	0.18	0.7%
Balistoides conspicillum	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.1%
Balistoides viridescens	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.1%
Rhinecanthus aculeatus	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.02	0.1%
Caesionidae (7)	0.00	11.89	22.67	0.00	24.00	2.17	0.00	1.67	0.00	9.46	3.6%
Pterocaesio tile	0.00	3.11	20.00	0.00	20.83	2.17	0.00	0.00	0.00	6.92	73.2%
Pterocaesio tessellata	0.00	4.56	2.11	0.00	0.00	0.00	0.00	1.00	0.00	1.26	13.3%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Caesio teres	0.00	3.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.66	7.0%
Pterocaesio diagramma	0.00	0.56	0.00	0.00	3.17	0.00	0.00	0.33	0.00	0.50	5.3%
Caesio cuning	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.6%
Pterocaesio randalli	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.4%
Pterocaesio trilineata	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.02	0.2%
Carangidae (1)	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.02%
Caranx melampygus	0.00	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.04	100.0%
Chaetodontidae (28)	6.50	19.44	9.11	6.50	6.00	15.33	9.00	2.67	6.67	10.36	4.0%
Hemitaenichthys polylepis	0.00	8.44	4.22	0.00	1.00	10.17	0.00	0.00	0.00	3.62	34.9%
Forcipiger flavissimus	0.83	2.33	2.33	1.00	1.83	1.67	0.00	0.00	0.67	1.52	14.7%
Chaetodon kleinii	0.67	1.56	1.22	1.83	1.17	1.67	1.33	0.67	1.33	1.34	12.9%
Chaetodon lunulatus	0.83	0.78	0.33	0.67	0.67	0.50	2.00	0.00	0.00	0.64	6.2%
Chaetodon vagabundus	0.00	0.11	0.00	1.83	0.50	0.17	0.33	0.33	0.67	0.40	3.9%
Chaetodon ulietensis	0.17	1.22	0.11	0.17	0.00	0.33	0.33	0.00	0.67	0.38	3.7%
Heniochus varius	0.33	0.67	0.11	0.00	0.50	0.17	0.00	0.00	1.67	0.36	3.5%
Chaetodon rafflesi	0.67	0.67	0.00	0.17	0.00	0.00	0.67	0.33	0.00	0.28	2.7%
Chaetodon melannotus	1.33	0.22	0.00	0.17	0.17	0.00	0.00	0.33	0.00	0.26	2.5%
Forcipiger longirostris	0.00	0.78	0.33	0.17	0.17	0.00	0.00	0.00	0.00	0.24	2.3%
Chaetodon baronessa	0.67	0.00	0.00	0.00	0.00	0.00	1.33	1.00	0.00	0.22	2.1%
Chaetodon lineolatus	0.00	0.78	0.11	0.00	0.00	0.33	0.33	0.00	0.00	0.22	2.1%
Chaetodon speculum	0.17	0.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.18	1.7%
Chaetodon trifascialis	0.33	0.00	0.00	0.00	0.00	0.17	1.33	0.00	0.00	0.14	1.4%
Chaetodon ocellicaudus	0.00	0.00	0.00	0.50	0.00	0.17	0.00	0.00	0.00	0.08	0.8%
Chaetodon punctatofasciatus	0.33	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.8%
Chaetodon semeion	0.00	0.22	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.08	0.8%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Chaetodon sp	0.17	0.11	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.06	0.6%
Heniochus acuminatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.06	0.6%
Chaetodon unimaculatus	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.4%
Chaetodon adiergastos	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
Chaetodon auriga	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
Chaetodon bennetti	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
Chaetodon citrinellus	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.02	0.2%
Chaetodon lunula	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.02	0.2%
Chaetodon meyeri	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
Chaetodon oxycephalus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.02	0.2%
Heniochus monoceros	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
Cirrhitidae (2)	0.00	0.56	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.14	0.1%
Paracirrhites forsteri	0.00	0.22	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.08	57.1%
Paracirrhites sp	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	42.9%
Ephippidae (2)	1.50	5.56	0.78	0.00	0.00	0.00	0.00	0.00	0.00	1.32	0.5%
Platax pinnatus	0.00	4.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.76	57.6%
Platax teira	1.50	1.33	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.56	42.4%
Haemulidae (14)	0.17	0.78	0.00	0.50	3.67	0.00	0.33	0.00	0.33	0.70	0.3%
Plectorhinchus lineatus	0.00	0.78	0.00	0.33	3.67	0.00	0.00	0.00	0.00	0.62	88.6%
Holocentridae	0.00	2.22	0.11	0.00	0.00	0.17	0.00	0.33	0.33	0.48	68.6%
Hemiramphidae	0.17	0.00	0.11	0.00	0.50	0.33	0.00	0.00	0.00	0.14	20.0%
Neoniphon sammara	0.00	0.67	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.14	20.0%
Myripristis violacea	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	17.1%
Sargocentron caudimaculatum	0.00	0.22	0.00	0.00	0.00	0.17	0.00	0.33	0.00	0.08	11.4%
Plectorhinchus vittatus	0.17	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.06	8.6%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Neoniphon sp	0.00	0.00	0.00	0.00	0.17	0.33	0.00	0.00	0.00	0.06	8.6%
Sargocentron sp	0.00	0.00	0.11	0.00	0.33	0.00	0.00	0.00	0.00	0.06	8.6%
Myripristis hexagona	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	8.6%
Myripristis kuntee	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.04	5.7%
Sargocentron ittodai	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	5.7%
Haemulidae sp	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	2.9%
Neoniphon sammara	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	2.9%
Labridae (41)	7.83	7.22	0.22	20.50	5.00	3.17	6.00	0.67	0.33	6.14	2.4%
Thalassoma lunare	1.67	1.78	0.00	2.83	1.83	0.83	1.33	0.00	0.33	1.28	20.8%
Thalassoma hardwicke	1.83	3.11	0.00	1.17	0.00	0.00	2.00	0.00	0.00	1.04	16.9%
Labroides dimidiatus	0.83	0.22	0.00	3.50	0.00	0.17	2.00	0.33	0.00	0.72	11.7%
Halichoeres hortulanus	0.50	0.33	0.11	1.17	1.00	0.33	0.00	0.00	0.00	0.44	7.2%
Labridae sp	0.17	0.22	0.00	2.67	0.00	0.00	0.00	0.00	0.00	0.38	6.2%
Hemigymnus melapterus	1.00	0.11	0.00	0.83	0.50	0.17	0.00	0.00	0.00	0.32	5.2%
Labriodes bicolor	0.50	0.00	0.00	1.67	0.00	0.00	0.00	0.00	0.00	0.26	4.2%
Thalassoma sp	0.00	0.00	0.00	1.33	0.00	0.00	0.00	0.00	0.00	0.16	2.6%
Halichoeres chrysus	0.00	0.00	0.00	0.17	0.00	0.83	0.00	0.00	0.00	0.12	2.0%
Hemigymnus fasciatus	0.00	0.11	0.00	0.67	0.17	0.00	0.00	0.00	0.00	0.12	2.0%
Anampses meleagrides	0.00	0.00	0.00	0.33	0.17	0.17	0.00	0.00	0.00	0.08	1.3%
Choerodon anchorago	0.17	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	1.3%
Halichoeres sp	0.17	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.08	1.3%
Hologymnosus annulatus	0.00	0.11	0.00	0.17	0.00	0.17	0.00	0.33	0.00	0.08	1.3%
Thalassoma sp	0.00	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.08	1.3%
Cheilinus chlorurus	0.17	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00	0.06	1.0%
Coris gaimard	0.17	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.06	1.0%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Gomphosus varius</i>	0.00	0.00	0.00	0.00	0.33	0.00	0.33	0.00	0.00	0.06	1.0%
<i>Halichoeres hartzfeldii</i>	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.06	1.0%
<i>Halichoeres scapularis</i>	0.17	0.00	0.00	0.17	0.00	0.17	0.00	0.00	0.00	0.06	1.0%
<i>Oxycheilinus unifasciatus</i>	0.17	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.06	1.0%
<i>Stethojulis bandanensis</i>	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.06	1.0%
<i>Anampses geograpicus</i>	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.04	0.7%
<i>Bodianus</i> sp	0.00	0.00	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.04	0.7%
<i>Cheilinus</i> sp	0.00	0.11	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.04	0.7%
<i>Labriodes</i> sp	0.00	0.00	0.00	0.17	0.00	0.00	0.33	0.00	0.00	0.04	0.7%
<i>Thalassoma lutescens</i>	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.7%
<i>Anampses caeruleopunctatus</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Anampses</i> sp	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Anampses twisti</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Cheilinus fasciatus</i>	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Cheilinus trilobatus</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Diproctacanthus xanthurus</i>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Halichoeres dussumieri</i>	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Halichoeres nebulosus</i>	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Halichoeres prosopeion</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Halichoeres solorensis</i>	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Halichoeres trimaculatus</i>	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Pseudodax moluccanus</i>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
<i>Stethojulis</i> sp	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.02	0.3%
<i>Stethojulis strigiventer</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Lethrinidae (7)	0.33	1.11	0.22	0.17	1.50	0.17	0.33	0.33	2.33	0.68	0.3%
Lethrinus harak	0.17	0.44	0.00	0.00	0.00	0.17	0.00	0.33	1.00	0.20	29.4%
Monotaxis grandoculis	0.00	0.33	0.22	0.17	0.17	0.00	0.33	0.00	0.00	0.16	23.5%
Lethrinus sp	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	1.33	0.12	17.6%
Monotaxis sp	0.17	0.33	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.10	14.7%
Lethrinus erythracanthus	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.06	8.8%
Lethrinus erythropterus	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	2.9%
Lethrinus microdon	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	2.9%
Lutjanidae (11)	2.50	2.67	9.11	2.33	4.83	1.67	0.00	0.67	1.00	3.58	1.4%
Lutjanus ehrenbergii	0.83	1.67	3.33	0.83	0.50	1.00	0.00	0.00	0.00	1.28	35.8%
Lutjanus monostigma	0.17	0.00	3.22	0.00	0.00	0.00	0.00	0.00	0.00	0.60	16.8%
Macolor niger	0.00	0.11	0.22	0.00	3.00	0.00	0.00	0.00	0.00	0.42	11.7%
Lutjanus decussatus	0.67	0.22	0.22	0.00	0.67	0.00	0.00	0.33	0.33	0.28	7.8%
Macolor macularis	0.00	0.00	0.33	0.17	0.67	0.67	0.00	0.00	0.33	0.26	7.3%
Lutjanus fulviflamma	0.00	0.56	0.56	0.00	0.00	0.00	0.00	0.33	0.00	0.22	6.1%
Lutjanidae sp	0.00	0.00	0.11	1.17	0.00	0.00	0.00	0.00	0.00	0.16	4.5%
Lutjanus biguttatus	0.00	0.00	0.78	0.00	0.00	0.00	0.00	0.00	0.00	0.14	3.9%
Lutjanus semicinctus	0.17	0.11	0.22	0.17	0.00	0.00	0.00	0.00	0.00	0.10	2.8%
Lutjanus sp	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.10	2.8%
Lutjanus carponotatus	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.6%
Monacanthidae (1)	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01%
Paraluteres prionurus	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	100.0%
Mullidae (9)	2.00	18.44	23.00	1.00	1.00	0.33	5.00	0.00	7.00	8.70	3.4%
Mulloidichthys vanicolensis	0.00	16.22	10.56	0.00	0.00	0.00	0.00	0.00	0.00	4.82	55.4%
Mulloidichthys flavolineatus	0.17	1.00	12.11	0.00	0.00	0.00	0.00	0.00	2.67	2.54	29.2%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Parupeneus multifasciatus</i>	0.83	0.56	0.22	0.17	0.33	0.17	2.67	0.00	0.67	0.52	6.0%
<i>Parupeneus barberinus</i>	0.17	0.33	0.00	0.33	0.50	0.17	2.00	0.00	3.00	0.50	5.7%
<i>Parupeneus bifasciatus</i>	0.50	0.33	0.00	0.17	0.17	0.00	0.33	0.00	0.33	0.20	2.3%
<i>Parupeneus macronemua</i>	0.33	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.7%
<i>Parupeneus cyclostomus</i>	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
<i>Parupeneus macronema</i>	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.2%
<i>Upeneus tragula</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.02	0.2%
Muraenidae (1)	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.02	0.01%
<i>Gymnothorax javanicus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.02	100.0%
Nemipteridae (9)	8.33	1.56	2.78	1.50	0.50	1.00	8.67	1.00	2.33	2.86	1.1%
<i>Scolopsis bilineata</i>	3.17	1.33	2.67	1.33	0.50	0.50	2.33	0.33	0.67	1.58	55.2%
<i>Scolopsis affinis</i>	2.67	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.34	11.9%
<i>Scolopsis lineatus</i>	1.33	0.11	0.00	0.00	0.00	0.33	1.33	0.00	0.00	0.30	10.5%
<i>Scolopsis trilineatus</i>	0.17	0.00	0.00	0.00	0.00	0.00	4.00	0.33	0.00	0.28	9.8%
<i>Scolopsis ciliatus</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	1.33	0.10	3.5%
<i>Scolopsis sp</i>	0.33	0.00	0.00	0.00	0.00	0.17	0.33	0.00	0.33	0.10	3.5%
<i>Scolopsis margaritifera</i>	0.17	0.00	0.11	0.00	0.00	0.00	0.33	0.33	0.00	0.08	2.8%
<i>Scolopsis temporalis</i>	0.33	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.06	2.1%
<i>Scolopsis trilineata</i>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.7%
Ostraciidae (1)	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.01%
<i>Ostracion meleagris</i>	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	100.0%
Pholidichthyidae (1)	0.00	47.22	0.00	10.17	1.00	0.00	0.00	0.00	0.00	9.84	3.8%
<i>Pholidichthys leucotaenia</i>	0.00	47.22	0.00	10.17	1.00	0.00	0.00	0.00	0.00	9.84	100.0%
Pomacanthidae (8)	3.83	1.56	3.67	0.50	1.17	1.67	17.33	1.00	8.00	3.38	1.3%
<i>Apolemichthys trimaculatus</i>	0.83	0.11	1.11	0.00	0.00	0.00	14.00	0.33	3.67	1.40	41.4%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Centropyge bicolor</i>	0.67	0.44	0.00	0.33	0.67	0.67	1.33	0.00	1.67	0.54	16.0%
<i>Pygoplites diacanthus</i>	0.67	0.44	1.00	0.00	0.33	0.00	0.00	0.00	0.67	0.42	12.4%
<i>Centropyge vroliki</i>	1.00	0.00	0.11	0.17	0.00	0.17	1.67	0.67	1.00	0.38	11.2%
<i>Centropyge tibicen</i>	0.67	0.11	0.00	0.00	0.00	0.50	0.33	0.00	1.00	0.24	7.1%
<i>Pomacanthus semicirculatus</i>	0.00	0.00	1.22	0.00	0.00	0.00	0.00	0.00	0.00	0.22	6.5%
<i>Pomacanthus xanthometopon</i>	0.00	0.44	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.12	3.6%
<i>Pomacanthus sexstriatus</i>	0.00	0.00	0.22	0.00	0.00	0.17	0.00	0.00	0.00	0.06	1.8%
Pomacentridae (75)	246.83	233.56	69.56	103.17	69.67	48.17	200.33	68.67	97.33	132.68	51.1%
<i>Pomacentrus brachialis</i>	28.50	39.11	5.89	24.50	18.17	6.00	30.67	19.33	23.33	21.76	16.4%
<i>Amblyglyphidodon curacao</i>	9.00	66.22	0.56	8.67	3.67	0.00	6.67	1.33	5.33	15.38	11.6%
<i>Chromis viridis</i>	101.50	5.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	13.10	9.9%
<i>Dascylus reticulatus</i>	2.67	1.44	2.56	0.00	0.67	4.00	116.33	26.33	34.33	12.22	9.2%
<i>Neoglyphidodon nigroris</i>	0.67	30.67	18.33	6.17	9.67	9.83	0.00	0.00	0.33	12.00	9.0%
<i>Amblyglyphidodon leucogaster</i>	0.00	25.56	13.44	0.67	16.33	6.00	0.00	0.33	1.67	9.90	7.5%
<i>Pomacentrus moluccensis</i>	31.67	11.78	0.11	1.17	0.83	0.00	1.67	0.00	0.00	6.28	4.7%
<i>Chromis analis</i>	0.17	4.11	12.33	0.17	0.17	3.83	0.00	2.67	3.33	3.84	2.9%
<i>Chromis xanthochira</i>	0.00	8.56	0.00	6.50	9.17	0.67	0.33	0.00	1.33	3.60	2.7%
<i>Chromis ternatensis</i>	16.50	2.33	0.56	1.33	3.00	3.67	1.67	0.00	0.00	3.56	2.7%
<i>Dascylus aruanus</i>	12.83	0.00	0.00	0.00	0.00	0.00	8.33	0.00	1.00	2.10	1.6%
<i>Chromis caudalis</i>	0.33	3.67	0.44	5.33	2.00	2.17	0.00	0.00	0.33	1.94	1.5%
<i>Dascylus trimaculatus</i>	0.67	1.00	0.67	3.00	0.50	0.83	13.33	0.00	3.00	1.88	1.4%
<i>Pomacentrus reidi</i>	1.83	0.56	4.11	1.00	0.67	2.50	1.33	0.00	4.00	1.88	1.4%
<i>Chrysiptera</i> sp	1.50	0.78	0.00	8.17	0.00	2.17	0.33	0.00	0.67	1.62	1.2%
<i>Chrysiptera cyanea</i>	7.33	1.56	0.11	0.00	0.00	0.00	5.67	0.00	1.33	1.60	1.2%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Chromis margaritifer</i>	0.33	0.22	0.00	11.67	0.83	0.00	0.00	0.00	0.00	1.58	1.2%
<i>Abudefduf vaigiensis</i>	1.83	6.00	0.11	0.00	0.00	0.17	0.00	0.67	0.33	1.40	1.1%
<i>Chromis xanthura</i>	0.00	0.33	0.11	5.17	1.83	0.83	1.67	0.00	3.67	1.34	1.0%
<i>Pomacentrus coelestis</i>	4.00	0.00	0.00	4.50	0.00	0.00	3.33	2.00	0.00	1.34	1.0%
<i>Plectroglyphidodon lacrymatus</i>	6.50	1.00	0.22	0.50	0.33	0.33	2.00	0.00	0.00	1.26	0.9%
<i>Abudefduf sexfasciatus</i>	4.83	2.11	0.00	0.00	0.00	1.50	0.00	0.00	1.00	1.20	0.9%
<i>Chrysiptera parasema</i>	0.00	0.00	0.00	9.83	0.00	0.00	0.00	0.00	0.00	1.18	0.9%
<i>Chromis lepidolepis</i>	0.83	5.00	0.11	0.17	0.00	0.00	0.67	0.00	1.00	1.14	0.9%
<i>Amblyglyphidodon aureus</i>	0.00	0.11	4.00	0.17	0.33	1.50	0.00	0.00	0.00	0.98	0.7%
<i>Chromis weberi</i>	0.50	4.11	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.92	0.7%
<i>Pomacentrus pavo</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	13.67	0.00	0.82	0.6%
<i>Chromis sp</i>	0.00	3.00	0.33	1.00	0.00	0.17	0.00	0.00	0.33	0.76	0.6%
<i>Neoglyphidodon crossi</i>	1.17	0.67	0.56	0.00	0.00	0.00	0.00	1.00	0.00	0.42	0.3%
<i>Pomacentridae sp</i>	1.17	0.22	0.44	0.17	0.17	0.00	0.00	0.00	1.67	0.40	0.3%
<i>Dischistodus melanotus</i>	1.00	1.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.36	0.3%
<i>Chromis amboinensis</i>	0.67	0.00	0.78	0.33	0.50	0.00	0.33	0.00	0.00	0.34	0.3%
<i>Chromis opercularis</i>	0.00	1.33	0.11	0.00	0.00	0.67	0.00	0.00	0.00	0.34	0.3%
<i>Chrysiptera unimaculata</i>	2.00	0.00	0.11	0.00	0.00	0.00	0.67	0.00	0.67	0.34	0.3%
<i>Pomacentrus alexanderae</i>	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	4.00	0.30	0.2%
<i>Abudefduf septemfasciatus</i>	0.00	1.44	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.28	0.2%
<i>Pomacentrus sp</i>	0.50	0.00	0.11	0.17	0.00	0.33	0.33	0.33	1.33	0.26	0.2%
<i>Acanthochromis polycanthus</i>	0.17	0.22	0.56	0.00	0.00	0.00	0.00	0.00	1.33	0.24	0.2%
<i>Pomacentrus lepidogenys</i>	0.00	0.44	0.11	0.33	0.00	0.00	0.00	0.33	1.33	0.24	0.2%
<i>Chromis atripes</i>	0.00	0.78	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.2%
<i>Chrysiptera rex</i>	1.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.20	0.2%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Chrysiptera rollandi</i>	1.17	0.11	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.18	0.1%
<i>Pomacentrus nigromarginatus</i>	0.00	0.78	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.18	0.1%
<i>Amphiprion clarkii</i>	0.00	0.11	0.33	0.17	0.17	0.00	0.33	0.00	0.00	0.14	0.1%
<i>Amblyglyphidodon ternatensis</i>	0.00	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.1%
<i>Chromis fumea</i>	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.1%
<i>Chrysiptera springeri</i>	0.00	0.00	0.00	0.00	0.00	0.00	2.00	0.00	0.00	0.12	0.1%
<i>Hemiglyphidodon plagiometopon</i>	0.00	0.22	0.11	0.17	0.00	0.00	0.33	0.00	0.33	0.12	0.1%
<i>Neopomacentrus azysron</i>	0.00	0.67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.12	0.1%
<i>Amphirion sp</i>	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.1%
<i>Pomacentrus auriventris</i>	0.67	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.10	0.1%
<i>Pomacentrus nigromanus</i>	0.00	0.00	0.56	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.1%
<i>Amphirion perideraion</i>	0.00	0.00	0.00	0.50	0.17	0.00	0.00	0.00	0.00	0.08	0.1%
<i>Amphirion ocellaris</i>	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.06	0.0%
<i>Plectroglyphidodon dickii</i>	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.06	0.0%
<i>Pomacentrus littoralis</i>	0.00	0.00	0.11	0.00	0.00	0.17	0.00	0.00	0.33	0.06	0.0%
<i>Amblyglyphidodon sp</i>	0.00	0.00	0.11	0.17	0.00	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Amphiprion sp</i>	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Chromis lineata</i>	0.00	0.22	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Chrysiptera talboti</i>	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Dischistodus chrysopoecilus</i>	0.00	0.00	0.00	0.17	0.00	0.17	0.00	0.00	0.00	0.04	0.0%
<i>Pomacentrus amboinensis</i>	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Pomacentrus armillatus</i>	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.0%
<i>Chromis agilis</i>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.02	0.0%
<i>Chromis alpha</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Chromis delta	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.0%
Chromis retrofasciata	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Chrysiptera glauca	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Dascylus sp	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Dischistodus perspiciliatus	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Dischistodus fasciatus	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Neoglyphidodon melas	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Neoglyphidodon thoracotaeniatus	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Neopomacentrus cyanomos	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Pomacentrus tripunctatus	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.0%
Pseudochromidae (1)	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01%
Pseudochromidae sp	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	100.0%
Scaridae (22)	11.00	5.89	1.33	12.67	7.67	3.00	5.00	1.33	2.67	5.96	2.3%
Chlorurus sordidus	1.67	1.22	0.11	5.17	1.67	1.33	1.00	0.00	0.33	1.50	25.2%
Chlorurus bleekeri	3.50	1.67	0.11	1.83	0.67	0.33	0.00	0.00	0.33	1.10	18.5%
Scarus tricolor	1.50	0.56	0.11	0.83	1.67	0.33	0.00	0.00	0.00	0.64	10.7%
Scarus dimidiatus	2.67	0.67	0.00	0.33	0.50	0.00	1.33	0.00	0.00	0.62	10.4%
Scarus sp	0.17	0.44	0.00	2.00	0.50	0.50	0.33	0.00	0.00	0.48	8.1%
Scaridae sp	0.33	0.78	0.44	0.00	0.00	0.00	2.00	0.00	0.00	0.38	6.4%
Scarus schlegeli	0.17	0.11	0.00	0.17	1.83	0.00	0.00	0.33	0.00	0.30	5.0%
Scarus oviceps	0.17	0.11	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.14	2.3%
Scarus spinus	0.33	0.00	0.11	0.00	0.00	0.33	0.00	0.00	0.33	0.12	2.0%
Scarus flavipectoralis	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.33	1.00	0.10	1.7%
Scarus psittacus	0.17	0.00	0.22	0.00	0.00	0.00	0.00	0.33	0.33	0.10	1.7%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Scarus rivulatus	0.00	0.00	0.00	0.17	0.00	0.00	0.33	0.33	0.33	0.08	1.3%
Chlorurus microrhinos	0.00	0.11	0.00	0.17	0.00	0.17	0.00	0.00	0.00	0.06	1.0%
Scarus prasinathus	0.00	0.11	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.06	1.0%
Scarus ghobban	0.00	0.00	0.00	0.17	0.17	0.00	0.00	0.00	0.00	0.04	0.7%
Scarus hypselopterus	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.00	0.04	0.7%
Scarus quoyi	0.17	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.7%
Hipposcarus longiceps	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
Scarus chameleon	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
Scarus rubroviolaceus	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
Scarus russeli	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.3%
Scorpaenidae (2)	0.00	0.00	0.00	0.00	0.17	0.00	0.33	0.00	0.00	0.04	0.02%
Pterois antennata	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.02	50.0%
Taenianotus triacanthus	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	50.0%
Serranidae (8)	0.83	0.56	0.00	0.83	0.33	0.17	1.33	1.00	0.00	0.50	0.2%
Cephalopholis urodeta	0.33	0.11	0.00	0.67	0.33	0.17	0.33	0.00	0.00	0.22	44.0%
Epinephelus merra	0.33	0.11	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.12	24.0%
Serranidae sp	0.00	0.11	0.00	0.00	0.00	0.00	0.67	0.00	0.00	0.06	12.0%
Anyperodon leucogrammicus	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	4.0%
Cephalopholis boenak	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	4.0%
Cephalopholis cyanostigma	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	4.0%
Epinephelus fasciatus	0.00	0.00	0.00	0.00	0.00	0.00	0.33	0.00	0.00	0.02	4.0%
Plectropomus areolatus	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	4.0%

Appendix C. Continued

Relative abundance of each species by Family	Hoga			Kaledupa			Sampela			Grand Total	%
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Siganidae (8)	1.17	0.78	0.44	1.17	2.17	0.50	0.67	0.33	3.00	1.06	0.4%
<i>Siganus vulpinus</i>	0.33	0.56	0.00	0.83	1.67	0.33	0.67	0.00	1.00	0.58	54.7%
<i>Siganus doliatus</i>	0.00	0.22	0.22	0.33	0.00	0.00	0.00	0.33	1.00	0.20	18.9%
<i>Siganus</i> sp	0.67	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.10	9.4%
<i>Siganus fuscescens</i>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.08	7.5%
<i>Siganus guttatus</i>	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.06	5.7%
<i>Siganus argenteus</i>	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.02	1.9%
<i>Siganus puellus</i>	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.02	1.9%
Tetraodontidae (8)	1.00	0.56	0.00	0.17	0.50	0.00	0.00	0.67	0.00	0.34	0.1%
<i>Canthigaster epilampra</i>	0.33	0.22	0.00	0.00	0.00	0.00	0.00	0.67	0.00	0.12	35.3%
<i>Arothron nigropunctatus</i>	0.00	0.11	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.06	17.6%
<i>Canthigaster papua</i>	0.17	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.04	11.8%
<i>Tetraodontidae</i> sp	0.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04	11.8%
<i>Arothron hispidus</i>	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	5.9%
<i>Arothron</i> sp	0.00	0.11	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	5.9%
<i>Canthigaster solandri</i>	0.17	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	5.9%
<i>Canthigaster valentini</i>	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	5.9%
Tripterygiidae (1)	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	0.01%
<i>Helcogramma striata</i>	0.00	0.00	0.00	0.00	0.17	0.00	0.00	0.00	0.00	0.02	100.0%
Zanclidae (1)	0.33	0.89	0.33	3.17	3.50	1.33	1.67	1.67	2.33	1.56	0.6%
<i>Zanclus comutus</i>	0.33	0.89	0.33	3.17	3.50	1.33	1.67	1.67	2.33	1.56	100.0%

APPENDIX D

Appendix D. Total abundance for each fish species by functional feeding group. The frequency of observation (F.O.) percentages were calculated for each fish species within each functional feeding group from 50 transects. Individual numbers represent the sum of all count data for all three transects within each reef zone. Fish species are listed in descending order of highest total abundance within each functional feeding group.

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Carnivore (63)	30.5	35.7	44.9	15.3	9.2	4.0	26.3	3.3	14.7	24.2	9.34%
Mulloidichthys vanicolensis	0.0	16.2	10.6	0.0	0.0	0.0	0.0	0.0	0.0	4.8	19.88%
Pseudanthias huchtii	3.5	8.2	0.6	6.5	0.0	0.2	0.0	0.0	0.0	2.8	11.55%
Mulloidichthys flavolineatus	0.2	1.0	12.1	0.0	0.0	0.0	0.0	0.0	2.7	2.5	10.48%
Dascylus aruanus	12.8	0.0	0.0	0.0	0.0	0.0	8.3	0.0	1.0	2.1	8.66%
Scolopsis bilineata	3.2	1.3	2.7	1.3	0.5	0.5	2.3	0.3	0.7	1.6	6.52%
Pseudanthias pleurotaenia	0.0	0.3	7.1	0.0	0.0	0.0	0.0	0.0	0.0	1.3	5.53%
Lutjanus ehrenbergii	0.8	1.7	3.3	0.8	0.5	1.0	0.0	0.0	0.0	1.3	5.28%
Lutjanus monostigma	0.2	0.0	3.2	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.48%
Platax teira	1.5	1.3	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.6	2.31%
Parupeneus multifasciatus	0.8	0.6	0.2	0.2	0.3	0.2	2.7	0.0	0.7	0.5	2.15%
Parupeneus barberinus	0.2	0.3	0.0	0.3	0.5	0.2	2.0	0.0	3.0	0.5	2.06%
Macolor niger	0.0	0.1	0.2	0.0	3.0	0.0	0.0	0.0	0.0	0.4	1.73%
Pygoplites diacanthus	0.7	0.4	1.0	0.0	0.3	0.0	0.0	0.0	0.7	0.4	1.73%
Scolopsis lineatus	1.3	0.1	0.0	0.0	0.0	0.3	1.3	0.0	0.0	0.3	1.24%
Lutjanus decussatus	0.7	0.2	0.2	0.0	0.7	0.0	0.0	0.3	0.3	0.3	1.16%
Scolopsis trilineatus	0.2	0.0	0.0	0.0	0.0	0.0	4.0	0.3	0.0	0.3	1.16%
Sufflamen chrysopterus	0.5	0.0	0.0	0.3	0.0	0.2	2.0	0.3	0.3	0.3	1.16%
Labriodes bicolor	0.5	0.0	0.0	1.7	0.0	0.0	0.0	0.0	0.0	0.3	1.07%
Macolor macularis	0.0	0.0	0.3	0.2	0.7	0.7	0.0	0.0	0.3	0.3	1.07%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Cephalopholis urodeta</i>	0.3	0.1	0.0	0.7	0.3	0.2	0.3	0.0	0.0	0.2	0.91%
<i>Lutjanus fulviflamma</i>	0.0	0.6	0.6	0.0	0.0	0.0	0.0	0.3	0.0	0.2	0.91%
<i>Hemigymnus melapterus</i>	0.0	0.1	0.0	0.8	0.5	0.2	0.0	0.0	0.0	0.2	0.83%
<i>Lethrinus harak</i>	0.2	0.4	0.0	0.0	0.0	0.2	0.0	0.3	1.0	0.2	0.83%
<i>Parupeneus bifasciatus</i>	0.5	0.3	0.0	0.2	0.2	0.0	0.3	0.0	0.3	0.2	0.83%
<i>Lutjanus biguttatus</i>	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.58%
<i>Epinephelus merra</i>	0.3	0.1	0.0	0.0	0.0	0.0	0.0	1.0	0.0	0.1	0.50%
<i>Lethrinus sp</i>	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	1.3	0.1	0.50%
<i>Myripristis violacea</i>	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.50%
<i>Lutjanus semicinctus</i>	0.2	0.1	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.41%
<i>Lutjanus sp</i>	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.1	0.41%
<i>Scolopsis ciliatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	1.3	0.1	0.41%
<i>Scolopsis sp</i>	0.3	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.3	0.1	0.41%
<i>Scolopsis margaritifera</i>	0.2	0.0	0.1	0.0	0.0	0.0	0.3	0.3	0.0	0.1	0.33%
<i>Thalassoma sp</i>	0.0	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.1	0.33%
<i>Gomphosus varius</i>	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.0	0.0	0.1	0.25%
<i>Lethrinus erythracanthus</i>	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.1	0.25%
<i>Myripristis hexagona</i>	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.25%
<i>Oxycheilinus unifasciatus</i>	0.2	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.25%
<i>Plectorhinchus vittatus</i>	0.2	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.1	0.25%
<i>Plectroglyphidodon dickii</i>	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.25%
<i>Pomacanthus sexstriatus</i>	0.0	0.0	0.2	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.25%
<i>Pseudanthias tuka</i>	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.25%
<i>Scolopsis temporalis</i>	0.3	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.25%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Caranx melampygus	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.17%
Labriodes sp	0.0	0.0	0.0	0.2	0.0	0.0	0.3	0.0	0.0	0.0	0.17%
Pomacanthus xanthometopon	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.17%
Anyperodon leucogrammicus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Arothron sp	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Aulostomus chinensis	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Balistoides conspicillum	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Cephalopholis boenak	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Cephalopholis cyanostigma	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Cheilinus trilobatus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Epinephelus fasciatus	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.08%
Lethrinus erythropterus	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.08%
Lethrinus microdon	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.08%
Lutjanus carponotatus	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Parupeneus cyclostomus	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Pterois antennata	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.08%
Scarus sp	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.08%
Scolopsis trilineata	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Stethojulis strigiventer	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.08%
Taenianotus triacanthus	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.08%
Detritivore (1)	1.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.10%
Acanthurus blochii	1.5	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	100.00%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Facultative Coralivore (34)	7.0	9.8	2.8	5.0	3.8	5.2	10.3	3.0	8.0	6.1	2.33%
Chaetodon kleinii	0.7	1.6	1.2	1.8	1.2	1.7	1.3	0.7	1.3	1.3	22.11%
Chaetodon lunulatus	0.8	0.8	0.3	0.7	0.7	0.5	2.0	0.0	0.0	0.6	10.56%
Balistapus undulatus	1.5	0.6	0.4	0.0	0.3	0.7	0.3	1.0	0.0	0.6	9.24%
Chaetodon vagabundus	0.0	0.1	0.0	1.8	0.5	0.2	0.3	0.3	0.7	0.4	6.60%
Centropyge vroliki	1.0	0.0	0.1	0.2	0.0	0.2	1.7	0.7	1.0	0.4	6.27%
Chaetodon ulietensis	0.2	1.2	0.1	0.2	0.0	0.3	0.3	0.0	0.7	0.4	6.27%
Heniochus varius	0.3	0.7	0.1	0.0	0.5	0.2	0.0	0.0	1.7	0.4	5.94%
Chaetodon rafflesi	0.7	0.7	0.0	0.2	0.0	0.0	0.7	0.3	0.0	0.3	4.62%
Centropyge tibicen	0.7	0.1	0.0	0.0	0.0	0.5	0.3	0.0	1.0	0.2	3.96%
Chaetodon lineolatus	0.0	0.8	0.1	0.0	0.0	0.3	0.3	0.0	0.0	0.2	3.63%
Chaetodon speculum	0.2	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	2.97%
Neoniphon sammara	0.2	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	2.64%
Chaetodon trifascialis	0.3	0.0	0.0	0.0	0.0	0.2	1.3	0.0	0.0	0.1	2.31%
Neopomacentrus azysron	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	1.98%
Chaetodon semeion	0.0	0.2	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.1	1.32%
Arothron nigropunctatus	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.99%
Halichoeres scapularis	0.2	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.1	0.99%
Heniochus acuminatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1	0.99%
Neoniphon sp	0.0	0.0	0.0	0.0	0.2	0.3	0.0	0.0	0.0	0.1	0.99%
Chaetodon sp	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.66%
Chaetodon unimaculatus	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.66%
Acanthurus nigricaudus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
Arothron hispidus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Balistoides viridescens</i>	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Chaetodon adiergastos</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Chaetodon auriga</i>	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Chaetodon bennetti</i>	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Chaetodon citrinellus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.33%
<i>Chaetodon lunula</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.33%
<i>Chaetodon oxycephalus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.33%
<i>Halichoeres</i> sp	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Halichoeres trimaculatus</i>	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Neopomacentrus cyanomos</i>	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.33%
<i>Rhinecanthus aculeatus</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.33%
Herbivore (64)	60.0	33.6	16.0	59.0	26.2	14.7	34.0	11.0	30.3	32.6	12.57%
<i>Ctenochaetus striatus</i>	18.2	8.9	0.8	17.0	4.5	0.5	21.3	7.0	9.3	8.8	27.04%
<i>Acanthurus nigrofuscus</i>	5.8	5.6	1.3	2.7	2.5	1.8	1.0	2.3	3.0	3.2	9.69%
<i>Zebrasoma scopas</i>	0.0	2.6	0.0	7.0	2.7	1.2	0.0	0.0	0.0	1.8	5.40%
<i>Acanthurus auranticavus</i>	3.0	0.3	1.1	3.0	1.0	0.2	0.7	0.0	8.0	1.6	5.03%
<i>Chrysiptera cyanea</i>	7.3	1.6	0.1	0.0	0.0	0.0	5.7	0.0	1.3	1.6	4.90%
<i>Chlorurus sordidus</i>	1.7	1.2	0.1	5.2	1.7	1.3	1.0	0.0	0.3	1.5	4.60%
<i>Acanthurus pyroferus</i>	0.8	0.9	2.2	1.8	1.7	0.8	0.0	0.0	1.3	1.3	3.86%
<i>Chrysiptera parasema</i>	0.0	0.0	0.0	9.8	0.0	0.0	0.0	0.0	0.0	1.2	3.62%
<i>Chlorurus bleekeri</i>	3.5	1.7	0.1	1.8	0.7	0.3	0.0	0.0	0.3	1.1	3.37%
<i>Naso caeruleacauda</i>	0.0	2.2	1.3	0.3	2.5	0.3	0.0	0.0	0.0	1.0	3.13%
<i>Acanthurus nubilus</i>	0.0	0.2	1.9	0.0	0.0	4.2	0.0	0.0	0.0	0.9	2.70%
<i>Scarus tricolor</i>	1.5	0.6	0.1	0.8	1.7	0.3	0.0	0.0	0.0	0.6	1.96%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Scarus dimidiatus</i>	2.7	0.7	0.0	0.3	0.5	0.0	1.3	0.0	0.0	0.6	1.90%
<i>Siganus vulpinus</i>	0.3	0.6	0.0	0.8	1.7	0.3	0.7	0.0	1.0	0.6	1.78%
<i>Acanthurus thompsoni</i>	0.2	0.8	1.9	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.53%
<i>Scarus</i> sp	0.2	0.4	0.0	2.0	0.5	0.5	0.0	0.0	0.0	0.5	1.41%
<i>Ctenochaetus binotatus</i>	1.3	0.8	0.1	0.5	0.0	0.2	0.0	0.0	0.3	0.4	1.29%
<i>Dischistodus melanotus</i>	1.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	1.10%
<i>Acanthurus</i> sp	0.3	0.0	1.6	0.0	0.2	0.0	0.0	0.0	0.0	0.3	1.04%
<i>Chrysiptera unimaculata</i>	2.0	0.0	0.1	0.0	0.0	0.0	0.7	0.0	0.7	0.3	1.04%
<i>Ctenochaetus cyanocheilus</i>	1.5	0.2	0.0	0.5	0.0	0.3	0.0	0.0	0.3	0.3	1.04%
<i>Scolopsis affinis</i>	2.7	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.3	1.04%
<i>Scarus schlegeli</i>	0.2	0.1	0.0	0.2	1.8	0.0	0.0	0.3	0.0	0.3	0.92%
<i>Acanthurus leucocheilus</i>	0.2	0.3	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.74%
<i>Acanthurus nigricans</i>	0.3	0.2	0.4	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.61%
<i>Chrysiptera rex</i>	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.61%
<i>Naso lituratus</i>	0.3	0.2	0.6	0.2	0.0	0.0	0.0	0.0	0.0	0.2	0.61%
<i>Siganus doliatus</i>	0.0	0.2	0.2	0.3	0.0	0.0	0.0	0.3	1.0	0.2	0.61%
<i>Zebrasoma veliferum</i>	0.0	0.2	0.0	0.5	0.7	0.2	0.0	0.0	0.0	0.2	0.61%
<i>Acanthus thompsoni</i>	0.0	0.0	0.0	0.0	0.5	0.8	0.0	0.0	0.0	0.2	0.49%
<i>Scarus oviceps</i>	0.2	0.1	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.1	0.43%
<i>Acanthurus grammoptilus</i>	0.0	0.3	0.2	0.0	0.0	0.0	0.3	0.0	0.0	0.1	0.37%
<i>Hemiglyphidodon plagiometopon</i>	0.0	0.2	0.1	0.2	0.0	0.0	0.3	0.0	0.3	0.1	0.37%
<i>Hemigymnus fasciatus</i>	0.0	0.1	0.0	0.7	0.2	0.0	0.0	0.0	0.0	0.1	0.37%
<i>Hemigymnus melapterus</i>	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.37%
<i>Scarus spinus</i>	0.3	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.3	0.1	0.37%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Scarus flavipectoralis	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.3	1.0	0.1	0.31%
Scarus psittacus	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.3	0.3	0.1	0.31%
Siganus sp	0.7	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.31%
Acanthurus nigroris	0.0	0.1	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.1	0.25%
Chlorurus sp	0.0	0.0	0.0	0.3	0.3	0.0	0.0	0.0	0.0	0.1	0.25%
Scarus rivulatus	0.0	0.0	0.0	0.2	0.0	0.0	0.3	0.3	0.3	0.1	0.25%
Siganus fuscescens	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.1	0.25%
Acanthuridae sp	0.0	0.1	0.0	0.0	0.0	0.0	0.7	0.0	0.0	0.1	0.18%
Chlorurus microrhinos	0.0	0.1	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.1	0.18%
Scarus prasignathus	0.0	0.1	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.18%
Siganus guttatus	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.1	0.18%
Acanthurus bariene	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.12%
Ctenochaetus sp	0.0	0.1	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.12%
Dischistodus chrysopoecilus	0.0	0.0	0.0	0.2	0.0	0.2	0.0	0.0	0.0	0.0	0.12%
Scarus ghobban	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.12%
Scarus hypselopterus	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.12%
Scarus quoyi	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.12%
Acanthurus triostegus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Chaetodon sp	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Chrysiptera glauca	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Dischistodus perspiciliatus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Dischistodus fasciatus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Hipposcarus longiceps	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Naso unicornis	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Scarus chameleon	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Scarus rubroviolaceus	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Scarus russeli	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.06%
Siganus argenteus	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.06%
Invertivore (51)	110.5	27.9	20.1	27.8	14.7	9.0	20.0	4.0	8.7	30.0	11.57%
Chromis viridis	101.5	4.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.0	43.34%
Chromis analis	0.2	4.1	12.3	0.2	0.2	3.8	0.0	2.7	3.3	3.8	12.78%
Chromis margaritifer	0.0	0.2	0.0	11.7	0.8	0.0	0.0	0.0	0.0	1.5	5.13%
Forcipiger flavissimus	0.8	2.3	2.3	1.0	1.8	1.7	0.0	0.0	0.7	1.5	5.06%
Apolemichthys trimaculatus	0.8	0.1	1.1	0.0	0.0	0.0	14.0	0.3	3.7	1.4	4.66%
Thalassoma lunare	1.7	1.8	0.0	2.8	1.8	0.8	1.3	0.0	0.3	1.3	4.26%
Thalassoma hardwicke	1.8	3.1	0.0	1.2	0.0	0.0	2.0	0.0	0.0	1.0	3.46%
Chromis sp	0.0	3.0	0.3	1.0	0.0	0.2	0.0	0.0	0.3	0.8	2.53%
Labroides dimidiatus	0.8	0.2	0.0	3.5	0.0	0.2	2.0	0.3	0.0	0.7	2.40%
Plectorhinchus lineatus	0.0	0.8	0.0	0.3	3.7	0.0	0.0	0.0	0.0	0.6	2.06%
Pterocaesio diagramma	0.0	0.6	0.0	0.0	3.2	0.0	0.0	0.3	0.0	0.5	1.66%
Chromis caudalis	0.3	1.9	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.5	1.53%
Halichoeres hortulanus	0.5	0.3	0.1	1.2	1.0	0.3	0.0	0.0	0.0	0.4	1.46%
Chromis amboinensis	0.7	0.0	0.8	0.3	0.5	0.0	0.3	0.0	0.0	0.3	1.13%
Chromis opercularis	0.0	1.3	0.1	0.0	0.0	0.7	0.0	0.0	0.0	0.3	1.13%
Forcipiger longirostris	0.0	0.8	0.3	0.2	0.2	0.0	0.0	0.0	0.0	0.2	0.80%
Pomacanthus semicirculatus	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.73%
Chromis atripes	0.0	0.8	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.67%
Monotaxis grandoculis	0.0	0.3	0.2	0.2	0.2	0.0	0.3	0.0	0.0	0.2	0.53%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Thalassoma sp	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.2	0.53%
Halichoeres chrysus	0.0	0.0	0.0	0.2	0.0	0.8	0.0	0.0	0.0	0.1	0.40%
Monotaxis sp	0.2	0.3	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.1	0.33%
Anampses meleagrides	0.0	0.0	0.0	0.3	0.2	0.2	0.0	0.0	0.0	0.1	0.27%
Choerodon anchorago	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.27%
Cheilinus chlorurus	0.2	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.1	0.20%
Coris gaimard	0.2	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.20%
Halichoeres sp	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.20%
Parupeneus macronemua	0.3	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.20%
Sargocentron sp	0.0	0.0	0.1	0.0	0.3	0.0	0.0	0.0	0.0	0.1	0.20%
Stethojulis bandanensis	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.20%
Anampses geograpicus	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.13%
Bodianus sp	0.0	0.0	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.0	0.13%
Cheilinus sp	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.13%
Thalassoma lutescens	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.13%
Anampses caeruleopunctatus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Anampses sp	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Anampses twisti	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Canthigaster solandri	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Canthigaster valentini	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Cheilinus fasciatus	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Chromis agilis	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.07%
Chromis alpha	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Chromis retrofasciata	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Diproctacanthus xanthurus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Halichoeres nebulosus	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Halichoeres prosopeion	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Halichoeres solorensis	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.07%
Heniochus monoceros	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Parupeneus macronema	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Stethojulis sp	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.07%
Upeneus tragula	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.07%
Obligate Coralivore (4)	2.0	0.2	0.1	0.7	0.2	0.2	1.3	1.3	0.0	0.6	0.22%
Chaetodon melannotus	1.3	0.2	0.0	0.2	0.2	0.0	0.0	0.3	0.0	0.3	44.83%
Chaetodon baronessa	0.7	0.0	0.0	0.0	0.0	0.0	1.3	1.0	0.0	0.2	37.93%
Chaetodon ocellicaudus	0.0	0.0	0.0	0.5	0.0	0.2	0.0	0.0	0.0	0.1	13.79%
Chaetodon meyeri	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.45%
Omnivore (46)	36.2	243.8	100.2	38.8	80.3	76.0	145.7	34.0	53.0	103.6	39.92%
Odonus niger	0.0	10.1	49.7	3.0	34.2	38.5	0.0	0.0	0.0	19.8	19.14%
Amblyglyphidodon curacao	9.0	66.2	0.6	8.7	3.7	0.0	6.7	1.3	5.3	15.4	14.84%
Dascylus reticulatus	2.7	1.4	2.6	0.0	0.7	4.0	116.3	26.3	34.3	12.2	11.79%
Neoglyphidodon nigroris	0.7	30.7	18.3	6.2	9.7	9.8	0.0	0.0	0.3	12.0	11.58%
Amblyglyphidodon leucogaster	0.0	25.6	13.4	0.7	16.3	6.0	0.0	0.3	1.7	9.9	9.55%
Pholidictys leucotaenia	0.0	47.2	0.0	10.2	1.0	0.0	0.0	0.0	0.0	9.8	9.49%
Melichthys niger	1.0	24.6	0.4	0.0	0.0	0.0	0.0	0.0	0.0	4.6	4.46%
Hemitaurichthys polylepis	0.0	8.4	4.2	0.0	1.0	10.2	0.0	0.0	0.0	3.6	3.49%
Dascylus trimaculatus	0.7	1.0	0.7	3.0	0.5	0.8	13.3	0.0	3.0	1.9	1.81%
Zebrasoma scopas	4.0	3.1	0.2	0.0	3.3	0.0	3.0	1.7	1.3	1.8	1.78%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Zanclus comutus</i>	0.3	0.9	0.3	3.2	3.5	1.3	1.7	1.7	2.3	1.6	1.51%
<i>Abudefduf vaigiensis</i>	1.8	6.0	0.1	0.0	0.0	0.2	0.0	0.7	0.3	1.4	1.35%
<i>Plectroglyphidodon lacrymatus</i>	6.5	1.0	0.2	0.5	0.3	0.3	2.0	0.0	0.0	1.3	1.22%
<i>Abudefduf sexfasciatus</i>	4.8	2.1	0.0	0.0	0.0	1.5	0.0	0.0	1.0	1.2	1.16%
<i>Melichthys vidua</i>	0.8	2.3	1.7	0.5	1.0	0.3	0.0	0.0	0.3	1.1	1.02%
<i>Amblyglyphidodon aureus</i>	0.0	0.1	4.0	0.2	0.3	1.5	0.0	0.0	0.0	1.0	0.95%
<i>Naso sp</i>	0.0	2.6	0.0	0.5	2.8	0.2	0.0	0.0	0.0	0.9	0.85%
<i>Platax pinnatus</i>	0.0	4.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.73%
<i>Acanthus thompsoni</i>	0.2	1.2	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.52%
<i>Centropyge bicolor</i>	0.7	0.4	0.0	0.3	0.7	0.7	1.3	0.0	1.7	0.5	0.52%
<i>Neoglyphidodon crossi</i>	1.2	0.7	0.6	0.0	0.0	0.0	0.0	1.0	0.0	0.4	0.41%
<i>Abudefduf septemfasciatus</i>	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.3	0.27%
<i>Sufflamen bursa</i>	0.2	0.1	0.2	0.0	0.0	0.0	0.7	0.0	1.0	0.2	0.17%
<i>Naso caesius</i>	0.2	0.7	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.15%
<i>Amphiprion clarkii</i>	0.0	0.1	0.3	0.2	0.2	0.0	0.3	0.0	0.0	0.1	0.14%
<i>Zebrasoma veliferum</i>	0.5	0.2	0.0	0.0	0.2	0.0	0.3	0.0	0.0	0.1	0.14%
<i>Amblyglyphidodon ternatensis</i>	0.0	0.0	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.12%
<i>Canthigaster epilampra</i>	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.1	0.12%
<i>Amphirion perideraion</i>	0.0	0.0	0.0	0.5	0.2	0.0	0.0	0.0	0.0	0.1	0.08%
<i>Chaetodon punctatofasciatus</i>	0.3	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.08%
<i>Chromis viridis</i>	0.0	0.3	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.1	0.08%
<i>Pomacanthus xanthometopon</i>	0.0	0.2	0.0	0.0	0.2	0.2	0.0	0.0	0.0	0.1	0.08%
<i>Amphirion ocellaris</i>	0.0	0.0	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.1	0.06%
<i>Halichoeres hartzfeldii</i>	0.0	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.1	0.06%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Amblyglyphidodon sp	0.0	0.0	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.04%
Amphiprion sp	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.04%
Canthigaster papua	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.04%
Chrysiptera talboti	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.04%
Dascylus sp	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Halichoeres dussumieri	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.02%
Neoglyphidodon melas	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Neoglyphidodon thoracotaeniatus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Ostracion meleagris	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Paracanthurus hepatus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.02%
Pseudodax moluccanus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Siganus puellus	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.02%
Piscivore (5)	0.2	0.6	0.0	0.2	0.0	0.3	0.0	1.0	0.0	0.2	0.09%
Hologymnosus annulatus	0.0	0.1	0.0	0.2	0.0	0.2	0.0	0.3	0.0	0.1	33.33%
Sargocentron caudimaculatum	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.3	0.0	0.1	33.33%
Sargocentron ittodai	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.67%
Gymnothorax javanicus	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	8.33%
Plectropomus areolatus	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.33%
Planktivore (42)	91.5	91.4	41.0	59.0	69.3	21.3	46.3	37.0	43.0	60.4	23.25%
Pomacentrus brachialis	28.5	39.1	5.9	24.5	18.2	6.0	30.7	19.3	23.3	21.8	36.05%
Pterocaesio tile	0.0	3.1	20.0	0.0	20.8	2.2	0.0	0.0	0.0	6.9	11.46%
Pomacentrus moluccensis	31.7	11.8	0.1	1.2	0.8	0.0	1.7	0.0	0.0	6.3	10.40%
Chromis xanthochira	0.0	8.6	0.0	6.5	9.2	0.7	0.3	0.0	1.3	3.6	5.96%
Chromis ternatensis	16.5	2.3	0.6	1.3	3.0	3.7	1.7	0.0	0.0	3.6	5.90%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
<i>Naso vlamingii</i>	1.5	2.8	5.0	0.0	12.5	0.5	0.0	0.0	0.0	3.1	5.20%
<i>Pomacentrus reidi</i>	1.8	0.6	4.1	1.0	0.7	2.5	1.3	0.0	4.0	1.9	3.11%
<i>Chrysiptera</i> sp	1.5	0.8	0.0	8.2	0.0	2.2	0.3	0.0	0.7	1.6	2.68%
<i>Chromis caudalis</i>	0.0	1.8	0.0	5.3	2.0	2.2	0.0	0.0	0.3	1.5	2.45%
<i>Chromis xanthura</i>	0.0	0.3	0.1	5.2	1.8	0.8	1.7	0.0	3.7	1.3	2.22%
<i>Pomacentrus coelestis</i>	4.0	0.0	0.0	4.5	0.0	0.0	3.3	2.0	0.0	1.3	2.22%
<i>Pterocaesio tessellata</i>	0.0	4.6	2.1	0.0	0.0	0.0	0.0	1.0	0.0	1.3	2.09%
<i>Chromis lepidolepis</i>	0.8	5.0	0.1	0.2	0.0	0.0	0.7	0.0	1.0	1.1	1.89%
<i>Chromis weberi</i>	0.5	4.1	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.9	1.52%
<i>Pomacentrus pavo</i>	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.7	0.0	0.8	1.36%
<i>Caesio teres</i>	0.0	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	1.09%
<i>Pomacentrus alexanderae</i>	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	4.0	0.3	0.50%
<i>Pomacentrus</i> sp	0.5	0.0	0.1	0.2	0.0	0.3	0.3	0.3	1.3	0.3	0.43%
<i>Acanthochromis polycanthus</i>	0.2	0.2	0.6	0.0	0.0	0.0	0.0	0.0	1.3	0.2	0.40%
<i>Pomacentrus lepidogenys</i>	0.0	0.4	0.1	0.3	0.0	0.0	0.0	0.3	1.3	0.2	0.40%
<i>Naso hexacanthus</i>	0.2	0.4	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.33%
<i>Chrysiptera rollandi</i>	1.2	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.2	0.30%
<i>Pomacentrus nigromarginatus</i>	0.0	0.8	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.2	0.30%
<i>Chromis fumea</i>	1.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.20%
<i>Chrysiptera springeri</i>	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	0.0	0.1	0.20%
<i>Pomacentrus auriventris</i>	0.7	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.1	0.17%
<i>Pomacentrus nigromanus</i>	0.0	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.17%
<i>Paracirrhites forsteri</i>	0.0	0.2	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.13%
<i>Caesio cuning</i>	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.10%

Appendix D. Continued

Species observed in each functional feeding group	Hoga			Kaledupa			Sampela			Mean	F.O. %
	Flat	Crest	Slope	Flat	Crest	Slope	Flat	Crest	Slope		
Paracirrhites sp	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.10%
Pomacentrus littoralis	0.0	0.0	0.1	0.0	0.0	0.2	0.0	0.0	0.3	0.1	0.10%
Chromis lineata	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Chromis margaritifer	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Myripristis kuntee	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.07%
Pomacentrus amboinensis	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Pomacentrus armillatus	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Pterocaesio randalli	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.07%
Chromis delta	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.03%
Helcogramma striata	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.03%
Paraluteres prionurus	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03%
Pomacentrus tripunctatus	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.03%
Pterocaesio trilineata	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.03%
Unknown (NA)	2.8	1.3	1.1	4.2	0.2	0.0	1.3	0.0	0.8	1.6	0.60%
Pomacentridae sp	1.2	0.2	0.4	0.2	0.2	0.0	0.0	0.0	0.8	0.4	25.64%
Labridae sp	0.2	0.2	0.0	2.7	0.0	0.0	0.0	0.0	0.0	0.4	24.36%
Scaridae sp	0.3	0.8	0.4	0.0	0.0	0.0	1.0	0.0	0.0	0.4	24.36%
Lutjanidae sp	0.0	0.0	0.1	1.2	0.0	0.0	0.0	0.0	0.0	0.2	10.26%
Amphirion sp	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1	6.41%
Serranidae sp	0.0	0.1	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.1	3.85%
Tetraodontidae sp	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.56%
Haemulidae sp	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0	1.28%
Pseudochromidae sp	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.28%