School of Molecular and Life Sciences

Faculty of Science and Engineering

Ecological and Socioeconomic Impacts of Cyclone Winston to Coral Reef Ecosystems and Coastal Communities in Fiji

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This thesis is presented for the Degree of

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Author's Declaration

To the best of my knowledge and belief this thesis contains no material previously published by any other person, except where due acknowledgment has been made. This thesis contains no material which has been accepted for the award of any other degree or diploma in any university.

The research presented and reported in this thesis was conducted in accordance with the National Health and Medical Research Council National Statement on Ethical Conduct in Human Research (2007) – updated March 2014. The proposed research study received human research ethics approval from the Curtin University Human Research Ethics Committee (EC00262), Approval Number #CTR-13281 Harvey/Wildlife Conservation Society data sharing agreement.

This research was conducted under the Wildlife Conservation Society's animal ethics policy and Institutional Review Board approval and University of Western Australia Animal Ethics Committee, Approval Number # RA/3/100/1161

Signature:

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Abstract

Cyclones are a global natural disturbance which can cause severe damage to natural resources such as coral reefs ecosystems. Cyclones directly impact coral reefs through damaging waves which break or dislodge corals. Any damage to corals can affect the structural complexity of reefs which may affect fish assemblages which are intrinsically linked with habitat diversity and complexity. People who live near coral reefs may also be impacted through a loss of infrastructure (buildings, boats, water, farms, communication), but also due to changes to the ecological function and ecosystem services that coral reef ecosystems provide. The benefits that people gain include food and income from fishing, sediment generation, coastal protection, but also a sense of identity.

In February 2016 Fiji was impacted by category 5 tropical cyclone Winston, currently one of the most severe cyclones recorded in the southern hemisphere. The objectives of this research were to: (a) assess the relationship of Fijian coastal communities with coral reef goods and services, perceptions on ocean resources and management, and the impact that cyclone Winston had on these relationships; and (b) assess the impact of cyclone Winston on coral reef habitat, fish assemblages and changes in fish communities associated with habitat change.

Socio-economic interviews were completed in 2015 (pre-cyclone Winston) and 2016 (post-cyclone Winston) at four villages in Kubulau (Kiobo and Navatu) and Levuka districts (Arovudi and Taviya), in Fiji. Fijians, similar to other Pacific coastal communities, have a high reliance on ocean resources for subsistence and livelihoods. Overall cyclone Winston had minimal, but varying impacts between districts on a range of socio-economic metrics including fishing equipment, fishing catches and fish catch value. Notable increases were observed in fishing effort and catch sold, and decreases in catch given away in Kubulau District and in seafood consumption in Levuka

District after the cyclone. Perceptions on the status of fish stocks, preferable food fish and other fish stock perceptions varied between districts and pre/post-cyclone.

Baseline data on coral reef habitat and fish assemblages was collected twice before and after cyclone Winston at two locations, Kubulau and Levuka Districts. Modelling of maximum wave heights, exposure and duration of waves generated by cyclone Winston was a useful method to explain cyclone damage. We observed spatially variable impacts in habitat composition, with the loss of live coral cover and structural complexity greatest at sites exposed to the highest magnitude wave height and exposure from cyclone Winston. Despite large habitat changes, few significant changes were observed in the fish assemblages, apart from decreases in obligate corallivores due to a strong relationship with coral cover. Overall, the cyclone impacts to fish assemblages at all sites were minor and were not discernible from high levels of natural year to year variation.

Cyclone Winston did not have substantial short-term impacts to fish assemblages, catches and uses of these catches in surveyed villages, which is positive for these communities. However, Fijian coastal communities are vulnerable to predicted future degradation of coral reef ecosystems from the cumulative impacts of anthropogenic disturbances and increases in the number of cyclones which reach maximum intensity given the communities dependence on marine resources. As such it is important that more research is undertaken which investigates human community and coral reef recovery from cyclones to develop mitigation/adaptation strategies to ensure communities and their vulnerable livelihoods can be sustained in future.

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Statement of Contributions

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Author contributions: BP, SM and EH designed the study. SM collected and compiled the 2015 and 2016 survey data. BP conducted statistical analyses with assistance from BS, EH, SM and JG. BP wrote the manuscript. All co-authors reviewed, edited and commented on the manuscript.

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Table of Context

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Definition of Terminology

* Definitions provided here are to provide context to terminology being used throughout this thesis and may differ from definitions of these terms used in other literature.

General

MPA - Marine protection area. A spatial area which is permanently closed to all types of fishing and extraction of marine life.

PHC - Periodically Harvested Closure. A form of marine protection spatial area that is closed to fishing for varying temporal periods (from predominantly closed to temporarily closed) as a strategy to improve conservation of reef resources or harvest yield.

Social

Exposure - Exposure to events/disturbances that will impact the system. e.g. increasing cyclone intensities and changing behaviour could increase exposure of communities.

Sensitivity/risk - How sensitive a community or natural resource is to change in the system. For example, social systems are more likely to be sensitive to climate change if they are highly dependent on a climate vulnerable natural resource (Marshall et al. 2007).

Adaptive capacity - Describes the ability to respond to challenges through learning, managing risk and impacts, developing new knowledge and devising effective approaches. Adaptive capacity greatly influences the vulnerability of communities and regions to climate change effects and hazards (Adger 2006; Adger et al. 2005; Rapport et al. 1998).

Vulnerability (opposite of resilience) - A function of exposure, sensitivity/risk and adaptive capacity used to determine the social vulnerability of communities to changes in the ecological system.

Ecological

Cyclone magnitude - The wave climate that develops from a cyclone caused by the combination of cyclone intensity, size and speed.

Cyclone exposure - The relative location of a coral community with respect to incoming cyclone wave direction and distance from reefs and other wave obstacles. Regardless of the distance from the cyclone wave energy is lost upon interaction with shallow water features like reefs, islands and coastlines, creating a wave shadow which can leave corals undamaged.

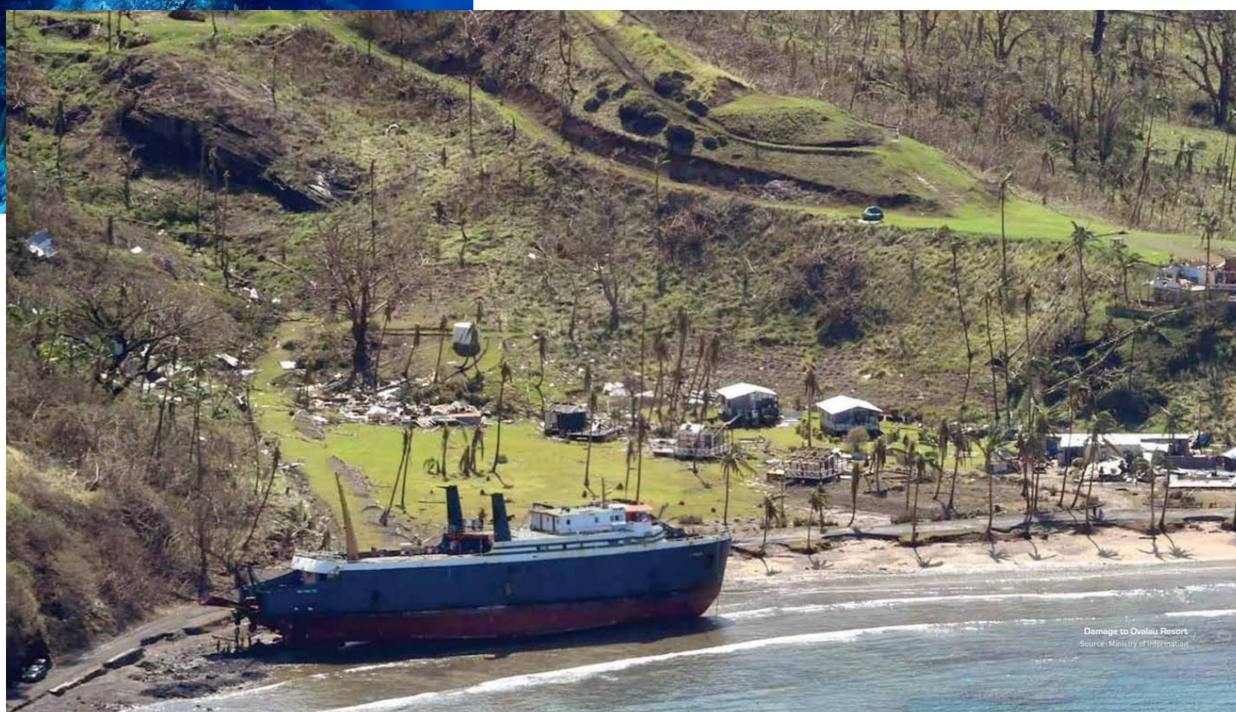
Sensitivity - How prone a coral colony is to cyclone wave action based on their shape, size and attachment to the substrate. Generally larger coral colonies are easier to dislodge (Done 1992) while stream-lined colonies oriented in the direction of the flow are more resistant. However branching type species of Acropora are more prone to breakage.

Vulnerability - A function of cyclone exposure and magnitude, sensitivity and adaptive capacity used to determine the vulnerability of coral reef ecosystems to changes in disturbances (cyclones) which affect the ecological system.

Stereo DOV - Diver operated stereo-video system (Goetze et al. 2019b).

Chapter 1

General Introduction



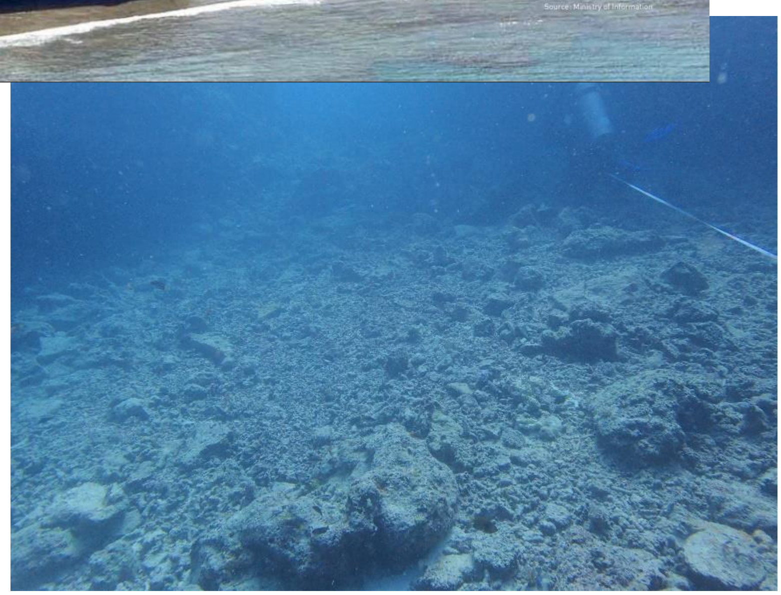


Photo 1 & 3: S. Mangubhai/WCS;
Photo 2: Government of Fiji

1.1 Introduction

Cyclones (typhoons, hurricanes) are a devastating natural disturbance in tropical marine ecosystems (Stoddart 1971; Harmelin-Vivien 1994), producing strong winds that create large swells which exert substantial mechanical forces on the reef directly impacting corals and benthic structure (Done 1992). This can significantly decrease the structural complexity of a coral reef, often leading to widespread, but variable damage to marine benthos (Alvarez-Filip et al. 2009). Other physical processes associated with cyclones, such as heavy rainfall can induce secondary impacts such as high nutrient runoff, freshwater flood plumes and high turbidity. These impacts can create anoxic, hyposaline conditions and sedimentation causing additional stress to corals and can lead to widespread mortality, impacting reefs over an extended period of time (Stoddart 1971; Harmelin-Vivien 1994).

Tropical cyclones influence the structure and function of coral reef ecosystems, playing an important role in maintaining reef diversity (Rogers 1993; Hughes and Connell 1999; Gardner et al. 2005). Cyclone damage is spatially patchy with the severity and variability of the damage dependent on several characteristics associated with the cyclone magnitude, exposure and vulnerability of the coral reef (Done 1992; Harmelin-Vivien 1994). Characteristics associated with the cyclone such as size, intensity and speed are more influential to habitat damage over broader scales. Whereby, slow moving, intense and spatially large cyclones that track close to reefs have the potential to cause the greatest damage (Puotinen et al. 2016). At localised scales, reef characteristics such as depth, topography, coral species composition, and reef profile can cause variability in damage over scales of 10s of metres. Less streamlined colonies suffer the most breakage with large colonies, or colonies with weak substrate attachment, subject to dislodgement and toppling (Tunnicliffe 1981; Done 1992). Coral forms that are commonly destroyed often include tabulate, branching and plate type morphologies, which provide the majority of structural complexity and habitat on a reef (Madin and Connolly 2006; Alvarez-Filip et al. 2009). The history of disturbance and recovery in a particular location is also important (Hubbard et al. 1991; Done 1992; Hughes and Connell 1999) as damage from thermal stress, predation and disease can weaken coral skeletons and make them easier to break and dislodge affecting resilience to future disturbances (Madin et al. 2012; Cheal et al. 2017).

Cyclone impacts to fish are more variable, largely due to their mobile nature allowing them to take refuge in deeper water or intact reefs (Harmelin-Vivien 1994). Most of the changes observed in fish assemblages after cyclones are longer term and due to substantial habitat damage and a lack of recovery in corals (Gardner et al. 2005). Live coral and its inherent structural complexity are often the most important drivers in structuring coral reef fish assemblages (Emslie et al. 2014; Darling et al. 2017). For example, live coral provides critical food sources, and shelter for corallivorous species and planktivorous damselfish (Munday 2004; Coker et al. 2014). Whereas structural complexity provides refuge for larger reef fish (Kerry and Bellwood 2015; Khan et al. 2017).

The history and cumulative impact of different disturbances in a particular location is important in determining ecosystem recovery (Hubbard et al. 1991; Done 1992; Hughes and Connell 1999). Historically, cyclone regimes have occurred at infrequent temporal scales allowing coral populations time to recover between disturbances, maintaining diversity and composition within the ecosystem (Hughes 1989; Rogers 1993). With the influence of climate change, researchers are predicting a greater number of tropical cyclones will reach maximum intensities (e.g. Category 5) (Knutson et al. 2019), which may decrease the time between damaging cyclones on coral reefs around the world (Puotinen et al. 2020). In recent history, many anthropogenic impacts have had a global influence (ocean warming, overfishing, ocean acidification and invasive species), with negative impacts on coral reefs (Richmond 1993; Hughes and Connell 1999; Hughes et al. 2003). It is unknown how the interaction between increased cyclone intensity and other anthropogenic impacts will affect coral reefs long term, however, there is the potential to exacerbate declines in fish and coral populations, increasing degradation of reef ecosystems (Cheal et al. 2017).

Cyclones regularly cause severe impacts to infrastructure, agriculture, property, resources and the environment, leading to significant economic and social losses (Terry 2007). Reported damage costs from cyclones are estimated to increase annually from US$56 billion (Mendelsohn et al. 2012) to US$223 billion (Bakkensen 2014) by 2100 with predicted climate change impacts. More regular maximum intensity cyclones have the potential to increase exposure to communities and cause serious socio-economic losses in tropical regions which are supported by coral reef ecosystems. Given island nations have high resource dependency on seafood as a primary resource, this poses issues for food security and the livelihood of these communities.

Pacific Island nations are at high risk due to their dependence on reef ecosystems for coastal protection, subsistence and generation of income (Hunt 1999; Sulu et al. 2015). Fish assemblages and the livelihoods of Pacific Islanders are susceptible to significant changes from climate change and altered cyclone regimes, which could cause long-term degradation of coral reef ecosystems (Pratchett et al. 2011; Cinner et al. 2012). Throughout the Pacific, Islander people consume approximately 25-113 kg of fish per person annually (Morris and Mackay 2008). This high consumption of ocean resources can make communities sensitive to ecosystem impacts if alternative subsistence options are not available (Fig. 2.1). A recent study on the impact of cyclone Winston to fisheries dependent communities in Fiji showed agriculture and the environment were the top two most affected sectors in terms of losses (Government of Fiji 2016). These resources are at higher risk of being impacted given their natural variability and sensitivity to weather and anthropogenic impacts with a changing climate. Possible degradation of coral reefs by cyclones causing declines in fish stocks will not only pose a serious threat to the livelihoods of coastal island communities, but will also have flow on effects through increased reliance on fish as a food source whilst land crops regenerate (Morris and Mackay 2008; Government of Fiji 2016). Having multiple sources of subsistence and income would help to lower sensitivity of communities to future disturbances given the likelihood of increasing exposure to future natural disturbance events system (Marshall et al. 2009). Alternatively increasing adaptive capacity with communities can act as an important method to mitigate the vulnerability of coastal communities to climate change (Marshall et al. 2013). However, to determine vulnerability requires the determination of exposure and sensitivity of social as well as ecological components within the system, in which limited data of this nature exists on Fijian communities (Fig. 2.1, 4.1; Marshall et al. 2009).

There is minimal knowledge known on the ecological and social systems in Fiji which limits the ability to determine what impact large disturbances will have on Fijian communities and management strategies can be implemented to minimise these impacts (Fig. 2.1, 4.1). As such, quantifying cyclone impacts in human communities should consider economic social and ecological information to determine the magnitude and trajectory of impacts and vulnerability. This will facilitate the development and implementation of management and conservation strategies to preserve Indo-Pacific reefs and Islander livelihoods.

1.2 Study area and research design

Fiji is located in the South Pacific Ocean and is made up of more than 300 islands with many of them inhabited. The country has a tropical marine climate with minimal temperature variation and two primary seasons; the dry season, which is cooler with minimal rain; and the wet season, which is hotter and more humid with the occurrence of numerous storms and cyclones. This study was conducted in Fiji within two districts Kubulau and Levuka, and their adjacent customary waters (Fig. 2.2; 3.1; 3.2). Kubulau District is located on the second largest island in Fiji, Vanua Levu, while Levuka District is located on Ovalau Island to the east of the Fijian capital, Suva. Socioeconomic surveys were conducted in the villages Kiobo and Navatu in Kubulau District, and Arovudi and Taviya in Levuka District (Fig. 2.2). Ecological surveys using diver operated stereo-video (stereo-DOV) were conducted on shallow inshore coral reefs adjacent to the villages of Kiobo and Natokalau in Kubulau and Nauouo in Levuka (Fig. 3.1; 3.2). More details on the sampling locations and research design are presented in each chapter.

1.3 Thesis aims and objectives

The main objective of this thesis is to contribute to a greater understanding of the ecological and social vulnerability to cyclone disturbance events. To address this, I investigate the impacts of cyclone Winston from both an ecological and socio-economic perspective. I assess impacts to coral reefs in Fiji and the adjacent coastal communities which depend on these reef resources. The aims of this research were to (a) investigate the coral reef resource dependency of coastal Fijian communities and if cyclone Winston impacted livelihoods and subsistence i.e., community sensitivity; (b) determine ecological impacts from cyclone Winston to coral reef benthic and fish communities (Fig. 1.1).

1.4 Socioeconomic assessment of ocean reliance and community fisheries in the Kubulau and Levuka districts, Fiji (Chapter 2)

Chapter 2 investigates the relationship and reliance that Fijian coastal communities have with coral reef ecosystems and the goods and services they provide (Fig. 1.1). I investigate the perceptions of respondents on the species of fish targeted for consumption and the abundance status of these species, and also local fish populations (Fig. 1.1). I assess the community's perception of changes in fish abundances and hypothetical actions that communities would take if fish stocks declined (Fig. 1.1). I also investigate whether cyclone Winston had any impact on these relationships of communities with perceptions and dependence on coral reef resources.

1.5 Responses of benthic habitat and fish to severe tropical cyclone Winston in Fiji (Chapter 3)

In chapter 3 I assess the impact of cyclone Winston on coral reefs in Fiji. I investigate the changes to habitat composition, habitat complexity and coral cover at broad and morphological classification levels, and the impacts upon composition and trophic structure of fish assemblages (Fig. 1.1). I also investigate the relationship between fish and habitat to see if any changes which occurred to habitat variables correlate with fish assemblage changes (Fig. 1.1).

1.6 Thesis Layout

Research for this thesis has been presented in two chapters (Chapter 2 and 3) set out as two manuscripts for publication in peer reviewed journals (Fig. 1.1). As such there is similar themes and content through the introductions of each chapter due to the need to present information about cyclone processes and damages. Terminology in these chapters is also discussed in a publication format using terms "we" and 'our' as opposed to 'I'. The significance of this research and chapter findings are integrated in a general discussion (Chapter 4), along with limitations and future research directions.

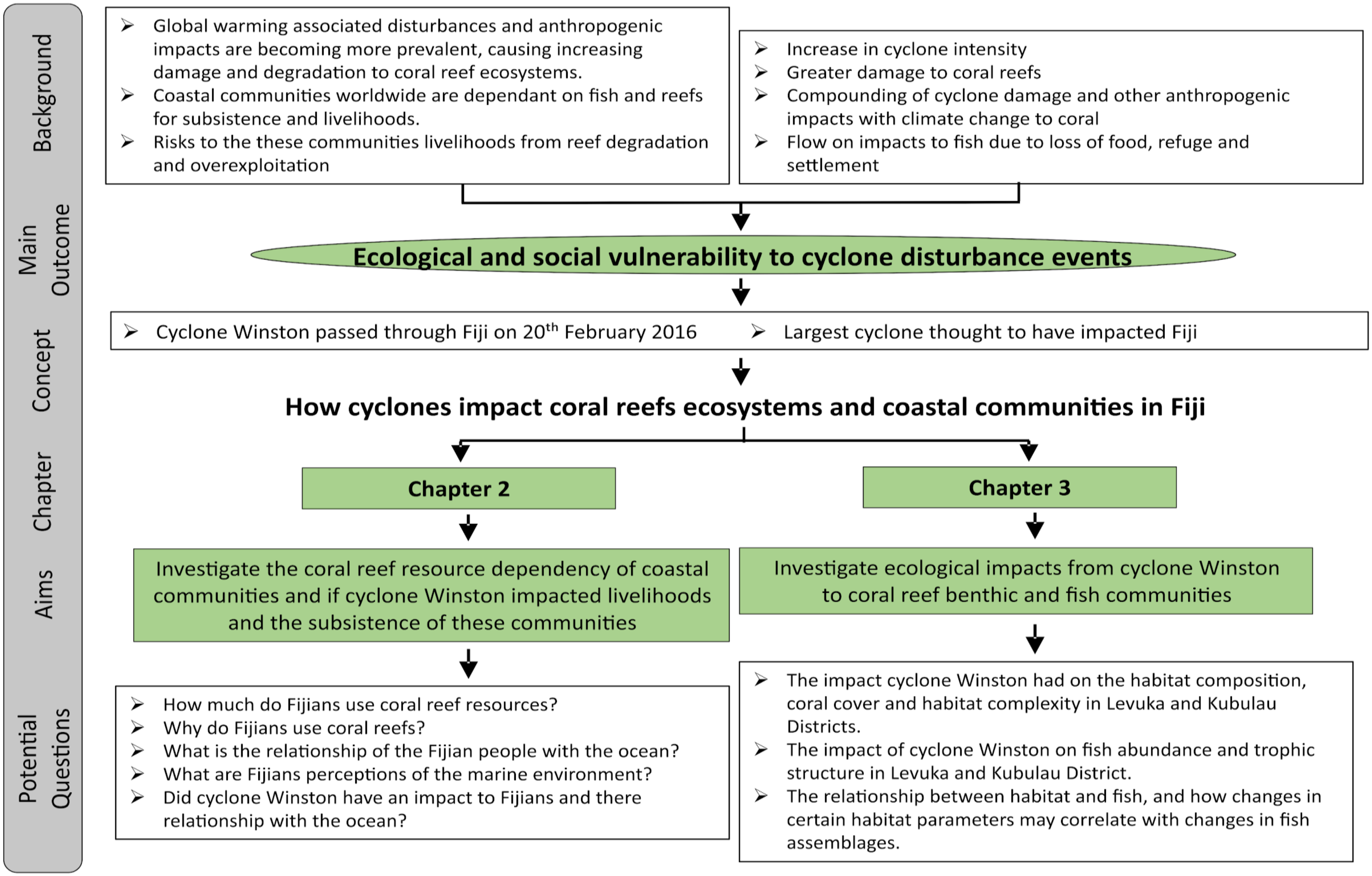


Fig. 1. 1 Flow diagram describing the background, context, structure and aims of the thesis

Chapter 2

Socioeconomic assessment of ocean reliance and community fisheries in the Kubulau and Levuka districts, Fiji

Photo: S. Mangubhai/WCS

2.1 Abstract

Cyclones are a common occurrence throughout the tropical Pacific impacting infrastructure, agriculture and natural ecosystems. Coastal communities may become more vulnerable with the predicted increases in cyclone intensity due to possible increased degradation of the local environment. Fiji suffered extensive widespread damage after cyclone Winston in 2016, which is the most severe cyclone to affect the island nation to date. We assessed the dependence of Fijian coastal communities on coral reef resources and their perceptions about the impact that cyclone Winston had on local fisheries. We also assessed their perceptions about the status and management of the fisheries. Fiji, like many other small-island tropical nations with coastal communities, utilise coral reef goods and services which provide a food and income to local villages. Communities in Kubulau District had a greater reliance on fish and income provided by fishing than Levuka and experienced minimal, but variable impacts on fish catches and consumption as a consequence of cyclone Winston. Significant changes were observed in the way fish catches were used where more fish was sold and less was given away in Kubulau. We believe this is driven by cyclone associated damages to fishing equipment and infrastructure causing increased fishing effort. Overall, the socio-economic impacts from cyclone Winston were more severe in Levuka compared to Kubulau most likely because of the greater cyclone damage in Levuka. As a result, respondents in Levuka were less optimistic about their recovery post-cyclone and susceptibility to future disturbances. In both districts perceptions about hypothetical fish declines were variable, however, similar responses were observed pre- and post-cyclone. As such Fijian communities which were more reliant on coral reef resources might be at increased risk to future cyclone disturbances which may degrade coral reef ecosystem goods and services. Providing coastal communities with knowledge and resilience strategies and opportunities for

supplementary livelihoods is important to ensure coastal communities can mitigate future impacts and adapt their livelihoods.

2.2 Introduction

Cyclones are one of the most common and destructive natural disturbances worldwide causing billions of dollars of damage to resources, infrastructure and other sectors annually (Nordhaus 2010; Mendelsohn et al. 2012). Damage from these storms has the greatest impact in tropical coastal communities due to their proximity to the sea and dependence on coastal resources for food and income. The environmental impacts of cyclones on coral reefs are relatively well documented and can affect both the biodiversity and productivity of a particular reef and the ecosystem services which local populations depend upon (Harmelin-Vivien 1994; Marshall et al. 2013). When substantial habitat changes occur (i.e. bleaching - Great Barrier Reef, Cyclones and Crown of Thorns Starfish - Caribbean) it can cause flow on effects on the abundance and assemblage structure of reef fauna long term (Hughes 1994; Alvarez-Filip et al. 2009; Bellwood et al. 2012; Emslie et al. 2014). This is because the majority of reef fauna, especially fish, have a strong relationship with habitat structure and live coral (Graham and Nash 2013; Coker et al. 2014). Previous research has documented that the cumulative impacts of cyclones, global warming related disturbances (ocean acidification) and anthropogenic impacts (fishing, runoff) will probably exacerbate the degradation of coral reefs (De'ath et al. 2012). The recovery of coral reef communities is thought to be a slow process taking between decades to centuries (Hughes and Connell 1999; Beeden et al. 2015). Recovery times could take even longer if the predicted changes in cyclone behaviour and increases in cyclone intensity associated with global warming materialise (Knutson et al. 2019; Puotinen et al. 2020). Environmental damage to marine areas can compound social and economic impacts, significantly impeding the recovery of communities for long time periods (Cinner et al. 2016).

Hundreds of millions of people in coastal communities rely directly upon the goods and services provided by coral reefs for income and their livelihoods (Wilkinson 2008; Teh et al. 2013). Reefs not only provide communities with a valuable food source, but also coastal protection (Harris et al. 2018) and can generate income through tourism and fisheries (Marshall et al. 2013). Natural disasters can pose serious risks to the day to day lives of communities with direct impacts on infrastructure, food supplies, sanitation, and can have lasting impacts on health, wellbeing of communities due to repairs to infrastructure and the injury and mortality of residents (Cinner et al. 2012; Khan and Nahar 2014). Fishers are especially at risk with likely impacts on fishing equipment (including boats) and the reefs in which they fish (Nirupama 2009; Marshall et al. 2013). A study on the Great Barrier Reef found that tourism operators and commercial fishers were at high risk due to their resource dependency and had limited capacity to adapt after cyclone Yasi (Marshall et al. 2013). Fishers from poorer socio-economic backgrounds in coastal communities may have higher risk due to a greater reliance on these resources for income and subsistence.

Coral reefs are of high cultural, social and economic importance (Hicks 2011; Cinner 2014). Although strong connections with coral reef goods and services is common throughout many coastal communities, the magnitude of reliance on these resources can vary considerably. The direct and indirect dependency on a resource, resource perceptions, the number of jobs within a family and alternative income sources can significantly affect a person’s or family's capacity to be resilient to climate change impacts and actively adapt. Consequently, it is important to consider the social and economic background among and within households and communities when determining the vulnerability to a disturbance. Assessment of vulnerability is important because it allows the risk of future disturbances to communities to be evaluated (Pratchett et al. 2011; Cinner et al. 2013). Vulnerability can be determined by assessing the interaction between exposure (likelihood of disturbances impacting the system), sensitivity (how reliant a community is on natural resources) and adaptive capacity (ability of a community to react to changes in the system, manage impacts and effectively adapt) of a community to a potential impact as per the Intergovernmental Panel on Climate Change (IPCC) vulnerability model (Fig. 2.1; Marshall et al. 2009).

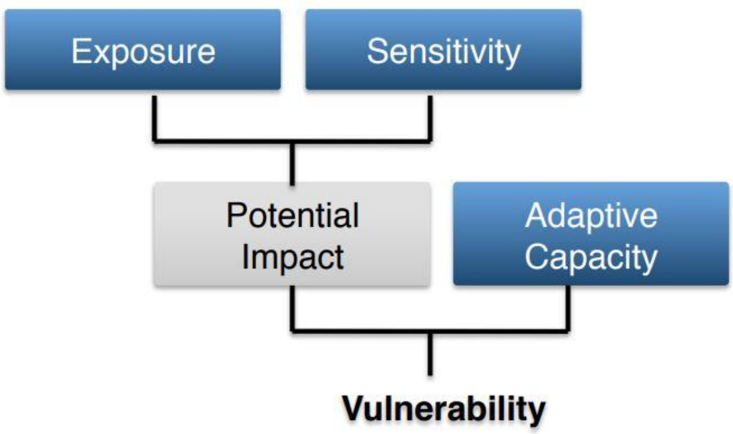


Fig. 2. 1 Framework for assessing social vulnerability within a community. Taken from (Marshall et al. 2009)

There is a lack of knowledge about how the physical and ecological impacts of cyclones influence the exposure, sensitivity and adaptive capacity of coastal communities throughout the Pacific. Cyclones have historically been a common occurrence throughout the Pacific. However, with cyclone intensity predicted to increase this knowledge is important for establishing the risk future cyclones pose to coastal communities, their adaptive capacity to future disturbances, and management strategies for sustaining future fish stocks. On the 20 February 2016 tropical cyclone Winston (a category 5 storm on the saffir simpson scale) passed through the islands of Fiji. Winston was one of the most destructive cyclones ever recorded in Fiji, and one of the strongest recorded in the Southern Hemisphere. Cyclone Winston caused major destruction of infrastructure, housing and resources/assets throughout Fiji, with total losses and damage costs estimated at over US$ 0.9 billion (Government of Fiji 2016). Two of the most affected sectors were agriculture and the environment (ecosystem service losses for native forests, mangroves and coral reefs), which are the primary two sources of subsistence and income for Fijians. It has been suggested that the damage to coral reef habitat from cyclone Winston may have had knock-on effects on fish stocks and the livelihoods of Fijians (Chaston Radway et al. 2016; Mangubhai 2016). Socio-economic data collected prior to cyclone Winston created an opportunity to resurvey four local communities to assess the impacts of the cyclone on the coastal communities in Fiji. The aims of this research were to: (a) investigate the dependence of four coastal Fijian communities on coral reef resources with a focus on the use of resources for income, subsistence and social purpose, (b) examine perceptions of Fijians on the state of their fish stocks and management strategies, and (c) investigate how Fijian fisheries and seafood consumption were impacted by cyclone Winston.

2.3 Methods

Socioeconomic surveys were conducted in February - April 2015, (pre-cyclone Winston) and in November 2016 (post-cyclone Winston) using face to face interviews. Surveys in 2015 consisted of 41 questions which focused on socioeconomic factors that affect the sustainable use of natural resources in rural communities (Jupiter et al. 2017; Kim et al. 2017). The 2016 surveys contained 49 questions selected from the global social-ecological systems monitoring framework for coastal fisheries management handbook with a focus on social and ecological indicators of natural resource management with the ability to evaluate disturbance impacts (Gurney and Darling 2017). Although surveys had a different context, many questions were similar between years with additional questions relating to cyclone response and impacts incorporated into the 2016 surveys. A subset of similar or matching questions (16 from 2015 and 17 from 2016) relating to fishing, fishing equipment, seafood consumption and fish stock perceptions, were selected to assess Fijian community and coral reef relationships and the socio-economic impacts of cyclone Winston. Survey questions relating to fish catches were investigated in two metrics based on respondents reporting their catches in either kilograms (kgs) or as whole fish (fish).

Surveys were conducted in Fourteen villages in 2015 and in Eight villages in 2016 across Fiji. However, only responses from 4 villages; Kiobo and Navatu in Kubulau District (hereafter "Kubulau") on the Island of Vanua Levu; and, Arovudi and Taviya in Levuka District on Ovalau island (hereafter "Levuka"), were used, which corresponded to the ecological survey sites in Chapter 3 (Fig. 2.2). A total of 69 households were surveyed in 2015 and 63 in 2016 across these 4 villages (Fig. 2.2). Only one representative/respondent for each household was interviewed. With the inclusion of family members in households counts of the respondents, surveys accounted for 53% of the population in 2015 and 49% in 2016 of these villages (based on 2015 population reports) (591 people across the 4 survey villages) (Kim et al. 2017). Surveys in each household typically lasted approximately 60 minutes and were conducted in *iTaukei* language by trained Wildlife Conservation Society (WCS) staff. Surveys were conducted in compliance with legal requirements concerning *iTaukei* affairs, the WCS institutional board and with the approval of community leaders. Personal identifiers such as names were removed from the data to ensure confidentiality for the respondent's privacy and identity.

2.4 Statistical analysis

Data were primarily grouped and presented at district level. However, in some instances data were grouped to village level, or only one district was presented due to differences between the 2015 and 2016 data and survey methods. Fish catch data couldn't be analysed for villages in Levuka due to inconsistencies among fish units (fish and kgs). Statistical analyses on catch and fishing data were conducted using PRIMER statistical analysis software (Clarke and Gorley 2017), and the PERMANOVA+ add on to PRIMER (Anderson et al. 2008). A permutational analysis of variance

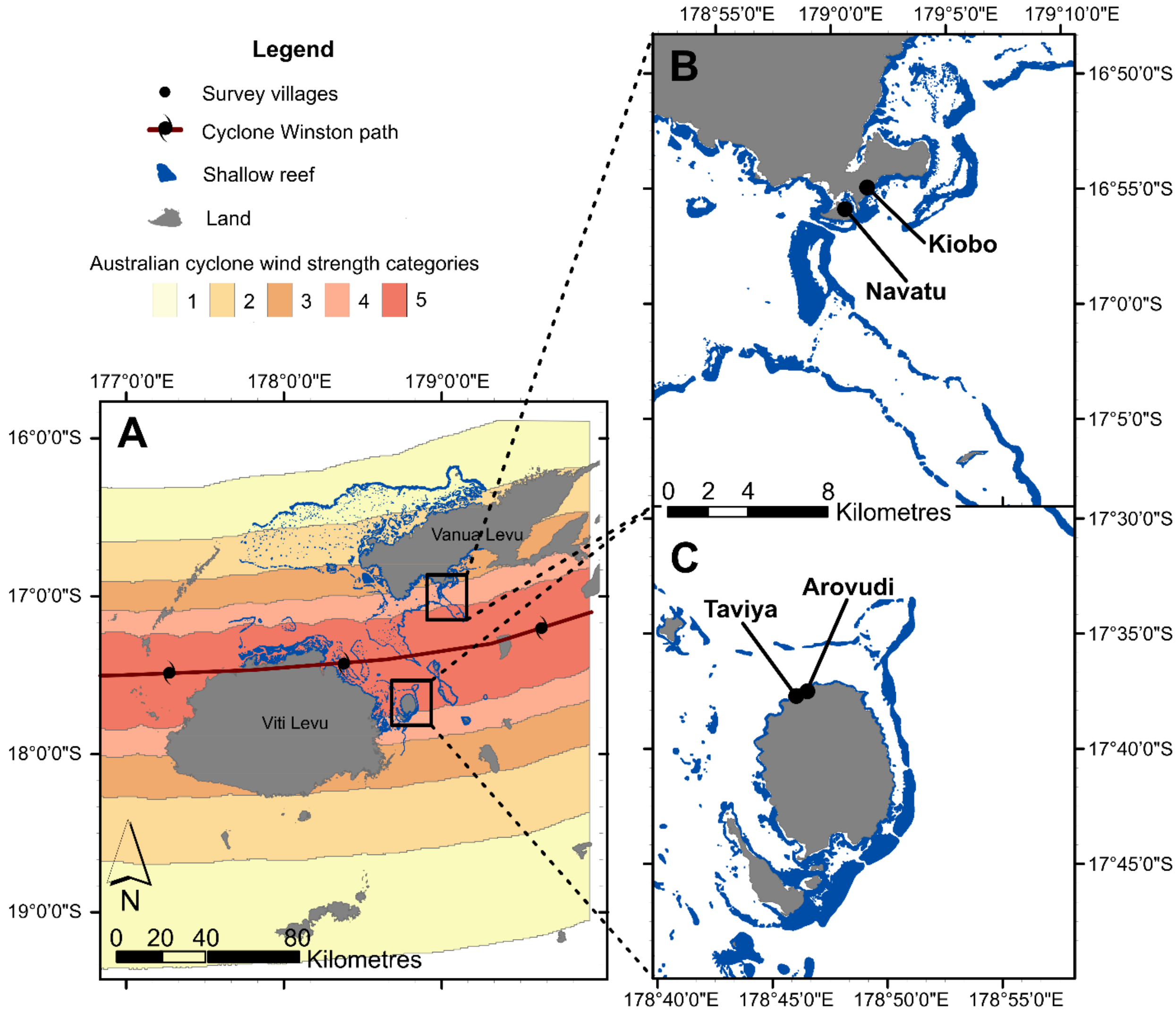


Fig. 2. 2 The position of **A** study sites in Kubulau and Levuka districts, Fiji, relative to the path of tropical cyclone Winston. Australian cyclone wind categories modeled based on Puotinen et al. (2016) were overlaid to indicate the spatial extent of likely exposure to conditions likely to cause severe wave damage. Insets show the survey villages **B** Kiobo and Navatu in Kubulau District and **C** Taviya and Arovudi in Levuka District relative to the surrounding reefs

(PERMANOVA) was completed using a one-factor design (*Years*: fixed, 2 levels: 2015, 2016) to test for differences between years for each of the fishing catch variables (average daily fishing effort (hours spent fishing) and fish catch value) in Kubulau. A two-factor design (*District*: fixed, 2 levels: Kubulau, Levuka; *Years*: fixed, 2 levels: 2015, 2016) was used to test for differences in the use of a fishers catch between years in each district. PERMANOVAs were completed using a Euclidean distance dissimilarity matrix and 9999 permutations (Anderson et al. 2008). Pairwise post-hoc tests were used to explore significant interactions or differences obtained from the PERMANOVA. When there were insufficient permutations (<100) to conduct a rigorous statistical test Monte Carlo bootstrapping was used to obtain a suitable p-value (PMC)(Anderson et al. 2008). Chi-square tests (α=0.05 for all tests) were used on all statistical tests where count or percentage data was present for both survey years (2015 and 2016) and unable to be averaged. Chi-square tests for associations between districts and years were initially conducted, however, if no significant association was detected then a Chi-square test for differences between years was used and presented. Yate's corrections were applied to data with expected frequencies less than 5, dichotomous tables and/or one degree of freedom (Yates 1934).

2.5 Results

2.5.1 Fishing and fish consumption

Survey respondents with fishing related occupations made up 27.5% (19/69) of the representative respondents surveyed in 2015, and 19.0% (12/63) in 2016. Families of respondents which were supported by these fishers, incomes accounted for 24.2% (59/244) of the population in 2015 and 27.3% (62/227) in 2016.

From the 2016 surveys an analysis of how much fish is consumed regularly was completed (Fig. 2.3). Consumption of fish was not limited to respondents and families whose occupation was fishing, with 98.3% of respondents consuming fish more than once per month. Fish was consumed more regularly in Kubulau with 89% of respondents eating fish more than once per week compared to Levuka where only 54% ate fish this regularly. Respondents were asked how much fresh seafood they had consumed in the 24 hours prior in 2015 and 2016 surveys. A chi-square test indicated this consumption changed significantly between 2015 and 2016 (Table 2.1; $X^2 = 24.53$, df = 3, $P < 0.001$).

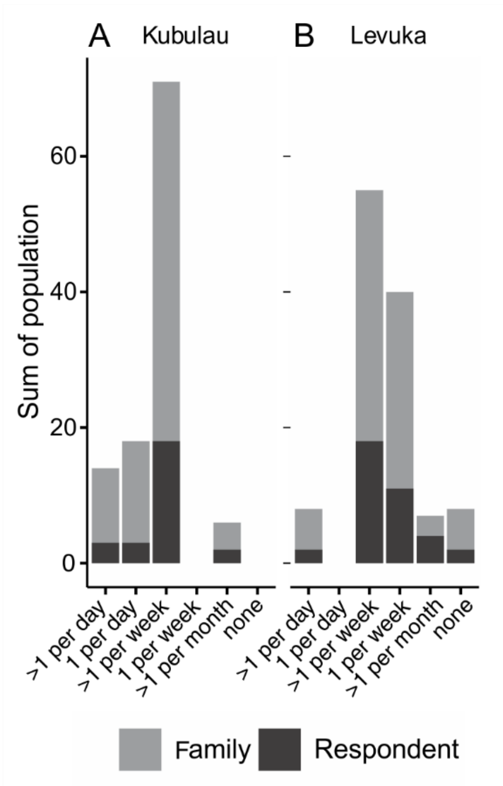


Fig. 2. 3 Frequency which locally caught fish or seafood (caught by respondent or community members) was consumed by respondents and their families in 2016 in **A** Kubulau and **B** Levuka districts

This difference was primarily driven by respondents in Arovudi where consumption of seafood (at least once a day) declined from 69% in 2015 to 19% in 2016 (Table 2.1), whereas consumption of fresh seafood in all other villages varied by < 6% (Table 2.1).

Table 2. 1 Descriptive, fish consumption and fishing related data and perceptions from survey questions answered by respondents in Kubulau and Levuka districts in surveys before (2015) and after (2016) cyclone Winston

Survey Question	**Kubulau**				**Levuka**			
Mean age	43.38 ± 3.29 yrs				50.05 ± 3.26 yrs			
Mean time residing in Village	27.06 ± 4.53 yrs				29.86 ± 4.66 yrs			
	Pre-cyclone (2015)		Post-cyclone (2016)		Pre-cyclone (2015)		Post-cyclone (2016)	
Economic status of respondents 12 months prior to 2015 surveys and 6 months prior to 2016 surveys (9 months post-cyclone)								
Much Better	0%		0%		15%		0%	
Slightly Better	57%		15%		13%		35%	
The same	32%		8%		67%		16%	
Slightly worse	11%		58%		6%		43%	
Much Worse	0%		19%		0%		5%	
Mean use of fishers' catches								
Eat	39.81 ± 6.36%		21.58 ± 6.53%		77.50 ± 9.22%		69.23 ± 6.15%	
Sell	52.50 ± 6.59%		77.26 ± 6.46%		14.17 ± 9.57%		18.81 ± 6.07%	
Giveaway	7.69 ± 1.76%		1.16 ± 0.82%		8.33 ± 3.86%		11.92 ± 4.26%	
Boats owned by respondents	14		6		3		3	
Respondent perceptions on the state of fish stocks in the 5yrs proceeding surveys								
Increased	39%		65%		17%		35%	
Decreased	25%		4%		67%		35%	
No change	21%		27%		17%		22%	
Unsure	14%		4%		0%		8%	
Percentage of the respondents which consumed fresh seafood in the 24hrs preceding surveys	Pre-cyclone (2015)		Post-cyclone (2016)		Pre-cyclone (2015)		Post-cyclone (2016)	
	Navatu	Kiobo	Navatu	Kiobo	Arovudi	Taviya	Arovudi	Taviya
	88	73	94	70	69	44	19	43

In Kubulau, the effort to catch 1 kg of fish was significantly higher in 2016 (6.1 hrs/kg) compared to 2015 (3.5 hrs/kg) (Table 2.2; Pseudo-$F_{1, 26}$ = 16.558, MS = 40.042, P_{MC} < 0.001). The effort required per day to catch fish reported in whole fish (fish) and the mean catch and value of fish (fish and kgs) on a normal day was similar in 2015 and 2016 (Table 2.2).

The amount of catch in Kubulau that was sold was significantly higher (Pseudo-$F_{1, 44}$ = 6.809, MS = 6731.7, P = 0.014), and the amount given away significantly lower (Pseudo-$F_{1, 44}$ = 8.998, MS = 468.74, P_{MC} = 0.004) in 2016 compared to 2015 (Table 2.1). The mean percentage of fishers

Table 2. 2 Fishing related survey questions of fisher respondents before (2015) and after (2016) cyclone Winston in Kubulau District

Survey Question	**Kubulau** Pre-cyclone (2015)	Post-cyclone (2016)
Proportion of total income provided by fishing to support fisher families	89.44%	-
Opinion of fishers to being able to stop fishing and provide a living from the land		
Strongly agree	-	9%
Somewhat agree	-	27%
Neither	-	9%
Somewhat disagree	-	0%
Strongly disagree	-	55%
Mean catch reported in Kilograms		
Catch on a normal fishing day (kgs)	24.33 ± 5.74	21.72 ± 7.24
Fishing effort on a normal day (hrs)	3.47 ± 0.82	6.06 ± 2.02
Value of catch on a normal day ($FJ/kg)	3.90 ± 1.01	4.19 ± 1.40
Mean catch reported in whole fish		
Catch on a normal fishing day (fish)	30.63 ± 10.63	28.00 ± 9.56
Fishing effort on a normal day (hrs)	3.06 ± 0.41	3.59 ± 0.96
Value of catch on a normal day ($FJ/fish)	1.38 ± 0.24	2.66 ± 0.68

catches that were eaten in both Kubulau and Levuka was similar between 2015 and 2016 (Table 2.1). Likewise, the percentage of catch sold and given away in Levuka didn't change significantly between years (Table 2.1). The number of boats owned was highest in Kubulau in 2015 with 14, compared to 6 owned in 2016, whereas the numbers of boats remained the same in both years in Levuka (Table 2.1). The amount of fishing equipment owned and types used were similar in both Kubulau (X^2 = 10.757, df = 5, P = 0.0564) and Levuka (X^2 = 1.318 x 10^{-31}, df = 7, P = 0.4071) between 2015 and 2016 (Fig. 2.4). Handlines were the most commonly used fishing equipment in both districts, with spearguns also used regularly in Kubulau (Fig. 2.4). A greater diversity of gear was used in Levuka compared to Kubulau (Fig. 2.4). After cyclone Winston, support in the form of fishing gear (cast and gill nets, fishing line, hooks and handlines) was provided to respondents in Levuka, but not Kubulau by the Fijian Government.

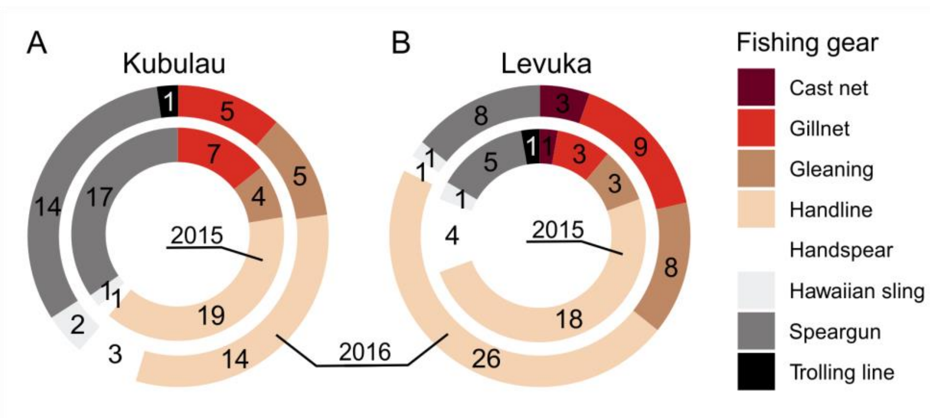


Fig. 2. 4 Breakdown of the number and types of fishing gear used by fishers in 2015 (inner circle) and 2016 (outer circle) in **A** Kubulau district showing a general decline and **B** Levuka district showing a general increase

Reported damages to sectors (i.e., infrastructure, environment, utilities) from cyclone Winston were proportionally consistent between districts, withinfrastructure and agriculture worst affected (Fig. 2.5A). A large majority (85-95%) of respondents thought the cyclone caused strong - very strong damage to their households (Fig. 2.5B). Prior to cyclone Winston 89% of respondents in Kubulau and 94.5% in Levuka were the same or better off economically than post-cyclone. Nine months post-cyclone 77% of respondents in Kubulau and 49% in Levuka reported being economically worse off (Table 2.1). At the time of the 2016 surveys 35% of respondents in Kubulau had mostly - fully recovered from the damages caused by cyclone Winston compared to 16% in Levuka (Fig. 2.5C). Almost half (49%) of respondents in Levuka and 29% of respondents in Kubulau had achieved very little to no recovery from cyclone Winston impacts. However, 65% of respondents in Levuka thought they would recover the same or better after a future cyclone of similar severity to cyclone Winston compared to 46% of respondents in Kubulau (Fig. 2.5D).

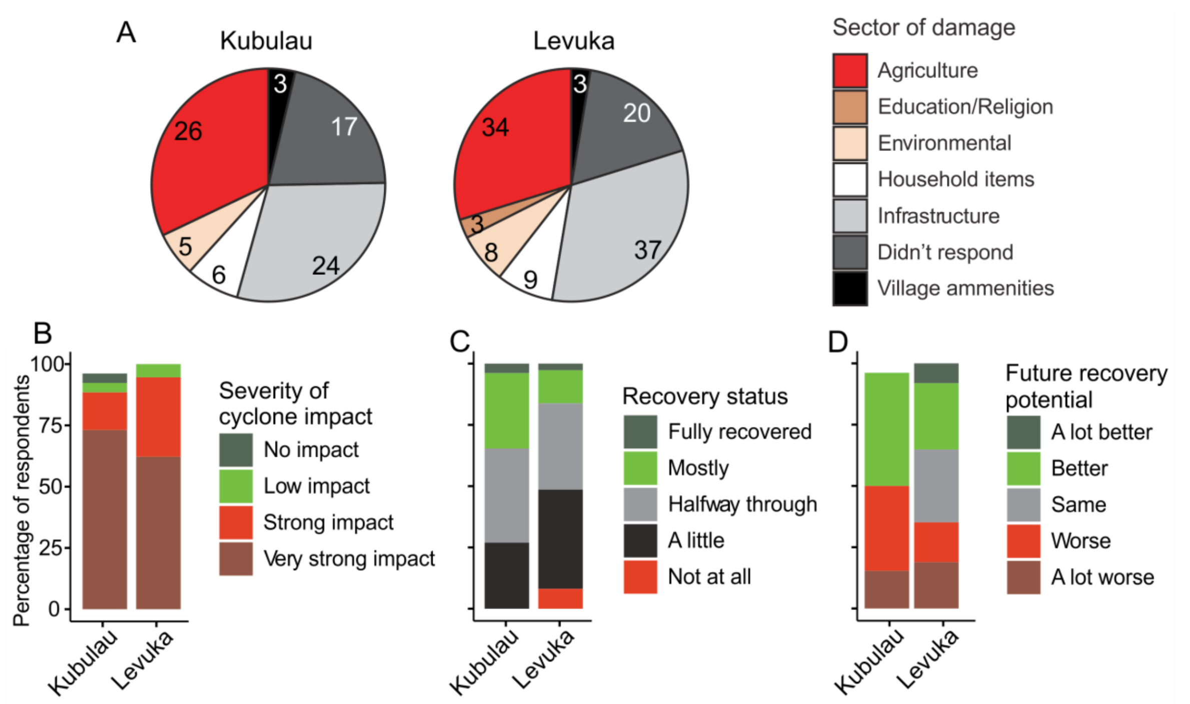


Fig. 2. 5 Responses of respondents regarding impacts from cyclone Winston in Kubulau and Levuka districts. **A** Sectors which respondents were impacted the greatest in by the cyclone. **B** Severity in which respondents were impacted by cyclone Winston. **C** respondents recovery status based on damage done by the cyclone. **D** How respondents would recover if another future severe cyclone occurred

2.5.2 Fishing perceptions - 2015 and 2016 comparison

Fisher respondents in 2015 and 2016 surveys were asked their opinion on the state of fish stocks over the past 5 years (Table 2.1). Responses in Kubulau across the two survey years were similar, with a large proportion of respondents assuming fish stocks had increased or remained the same (Table 2.1; $X^2 = 7.599$, df = 3, $P = 0.0551$). Opinions were more variable in Levuka where there was a significant change in viewpoints with respondents in 2016 having a more even spread of responses to survey answers than in 2015 (Table 2.1; $X^2 = 9.123$, df = 3, $P = 0.0277$). In 2015 the majority of fishers in Levuka fishers thought fish stocks had decreased over the last 5 years, however in 2016 most fishers thought fish stocks had increased or remained the same (Table 2.1). In both survey years respondents were asked how they thought fish stocks could be increased. In Kubulau similar responses were given in 2015 and 2016 ($X^2 = 15.471$, df = 9, P = 0.0788) with implementation or extension of periodically harvested closures (PHCs) or marine protection areas (MPAs) thought to be the most effective way to increase fish stocks (Fig. 2.6A).

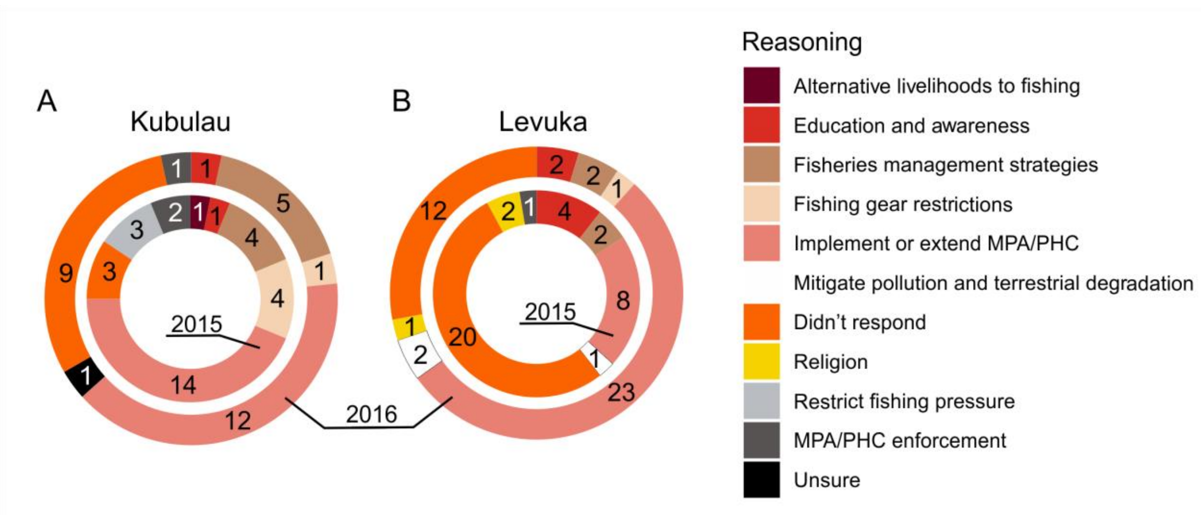


Fig. 2. 6 Perceptions of respondents on how fish stocks can be increased taken in surveys from 2015 and 2016 in **A** Kubulau and **B** Levuka districts

Respondents in Levuka gave significantly different answers in 2015 and 2016 (Fig. 2.6B; $X^2 = 41.415$, df = 8, $P < 0.001$). The majority of the Levuka respondents (53%) didn't respond to the question in 2015, where 53% thought implementation or extension and 28% thought enforcement of PHCs or MPAs to be the most effective way to increase fish stocks in 2016 (Fig. 2.6B). Changes in hypothetical actions of respondents was greater in the Levuka with a chi-square test showing a statistical difference in perception between 2015 and 2016 (Fig. 2.7B; $X^2 = 25.371$, df = 6, $P < 0.001$). However, in Kubulau responses to hypothetical actions of respondents were similar (Fig. 2.7A; $X^2 = 10.757$, df = 5, $P = 0.056$). In both districts hypothetical actions were less variable in 2015, with the majority of respondents stating they would change fishing grounds in Kubulau and most respondents not answering the question in Levuka (Fig. 2.7). In 2016 most respondents in Kubulau stated they would hypothetically change fishing grounds, fish less and choose alternate livelihood activities or other actions if fish stocks were to decrease (Fig. 2.7A). In Levuka majority of respondents also stated they would change fishing grounds, with a large percentage not responding (28%) to hypothetical 50% fish stock declines (Fig. 2.7B).

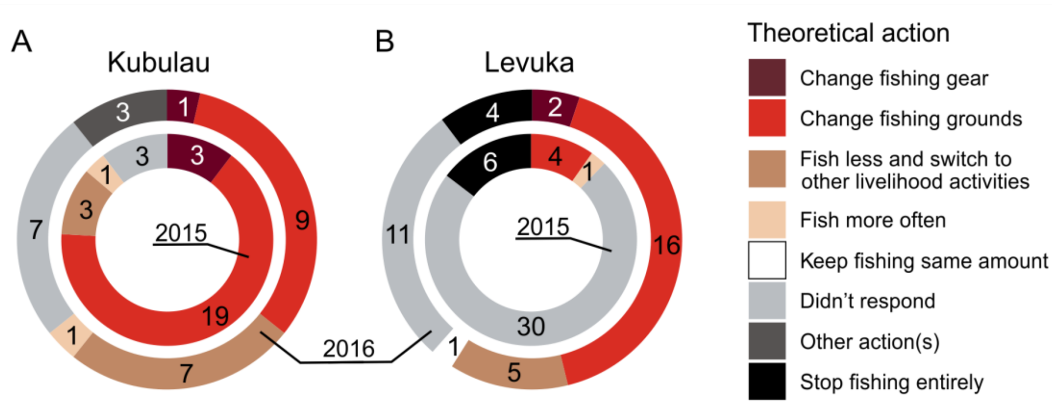


Fig. 2. 7 The hypothetical actions fishers in **A** Kubulau and **B** Levuka would take if daily catches declined by 50%. Responses in the inner circle are from surveys conducted in 2015 and outer circle from 2016 surveys

2.5.3 2015 Perceptions on popular fish species

Fishers in 2015 surveys were asked about their preferred catch for consumption and sale, the hypothetical abundance change of these fish in the previous 10 yrs, and what may have caused these changes (Fig. 2.8, 2.9). Lethrinidae, Acanthuridae and Serranidae species of fish were viewed as the most popular to be consumed and sold by Fijians in Kubulau (Fig. 2.8A). These were followed by other common reef fish species in the families Carangidae and Scaridae (Fig. 2.8A). In Levuka Lethrinidae, Acanthuridae, Clupeidae and Serranidae species of fish were the most preferred to eat, and Lethrinidae, Acanthuridae, Carangidae and Siganidae species the most preferred to sell (Fig. 2.9A). There were differing perceptions between districts on the status of the 10 most popular fish families through the past 10 years (Fig. 2.8, 2.9). In Kubulau, the majority of

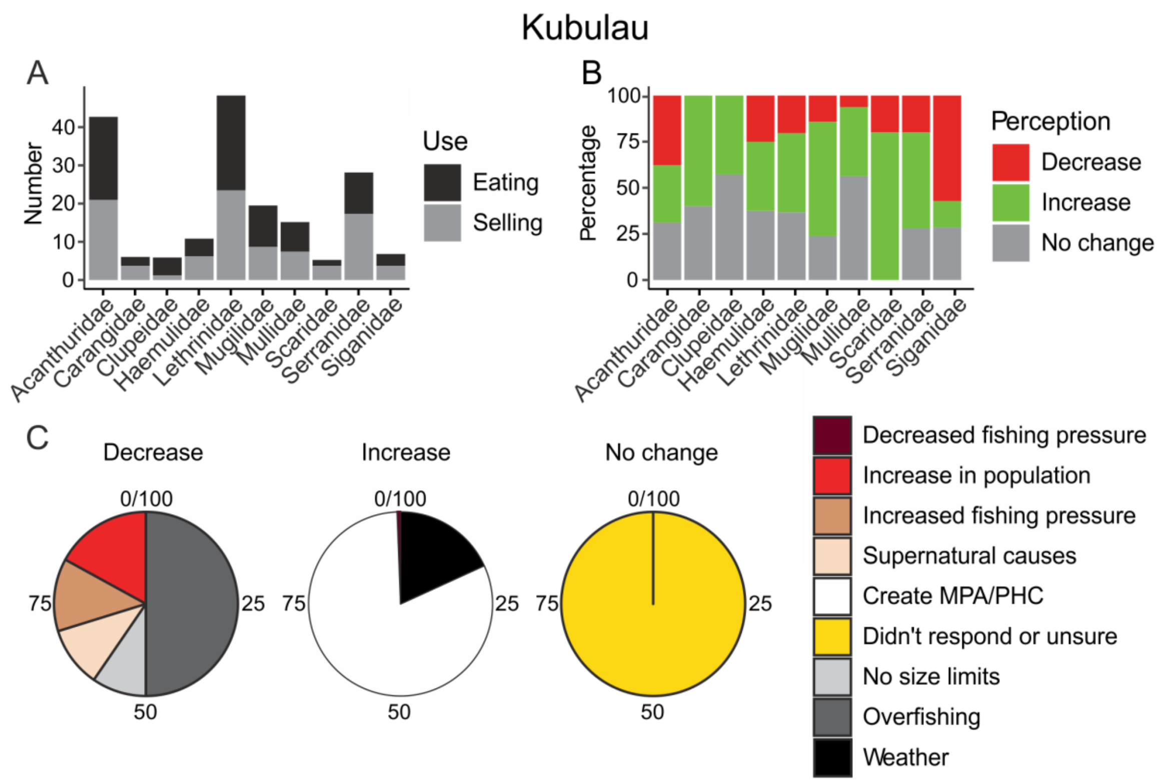


Fig. 2. 8 Kubulau respondent responses from 2015 surveys on their most preferred fish (grouped to family) for **A** consumption and sale, **B** perceptions on if their availability has increased, decreased or stayed the same over the past 10 years, and **C** reasonings for these changes graphed in percentage

fish families were perceived to have increased or remained stable in abundance, except for Siganidae which decreased over the previous 10 years (Fig. 2.8B). Contrary to this, perceptions in

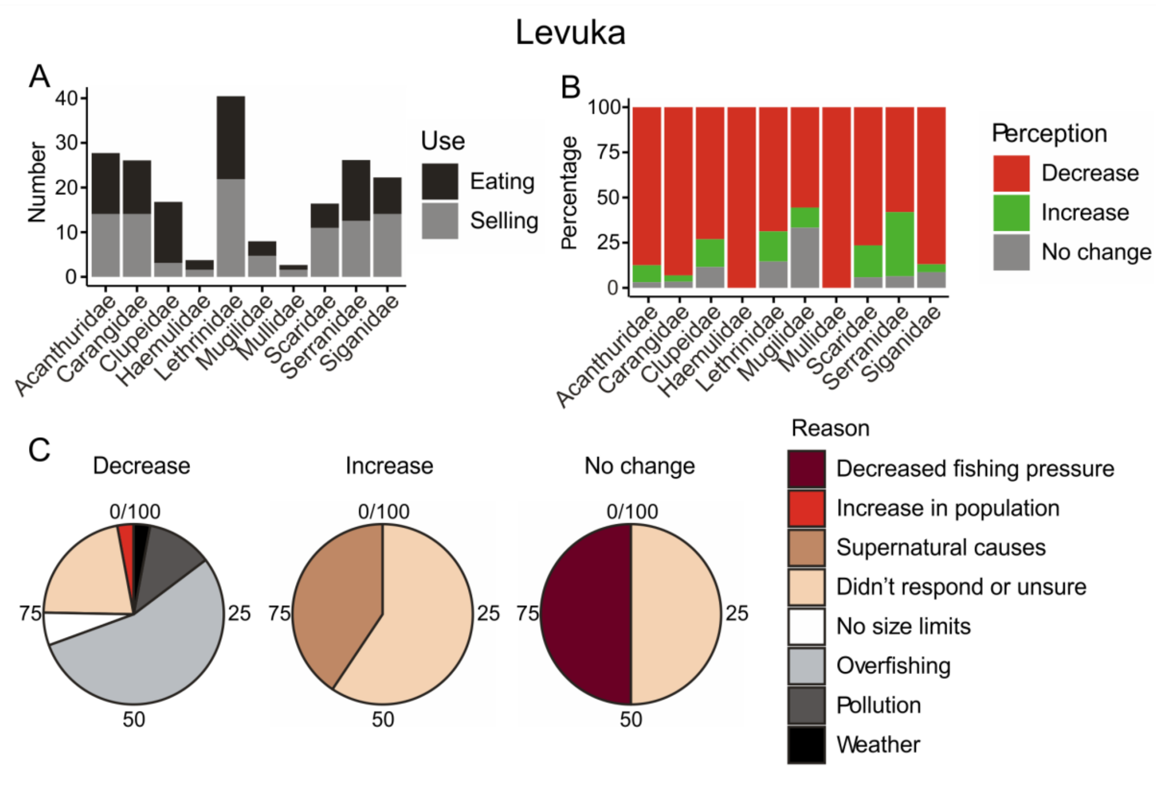


Fig. 2. 9 Levuka respondent responses from 2015 surveys on their most preferred fish (grouped to family) for **A** consumption and sale, **B** perceptions on if their availability has increased, decreased or stayed the same over the past 10 years, and **C** reasonings for these changes

Levuka were that the majority of the fish families had decreased in abundance (Fig. 2.9B). In both districts overfishing was thought to be the main reason why abundance of the preferred fish families had decreased over the past 10 years (Fig. 2.8, 2.9C). Kubulau respondents thought the implementation of MPAs or PHCs were the main reasoning behind increases in abundance and were unsure on the reason why fish abundance had remained the same (Fig. 2.8C). Similarly, in Levuka a large proportion of respondents were unsure why the abundance of their preferred species had increased, decreased or hadn't changed (Fig. 2.9C). Inexhaustible fish stocks and decreased fishing pressure were also strongly attributed to why perceived abundance increases and no changes to abundance had occurred (Fig. 2.9C).

2.6 Discussion

We found that people in our survey villages and their livelihoods, particularly those with stronger ocean relationships are vulnerable to future changes and degradation of coral reef ecosystems. People in Kubulau and Levuka were dependent on reef goods and services which provided a proportion of their subsistence and many economic and social benefits. Despite this and the damage caused by cyclone Winston, there appeared to be minimal impact on fishers' usual day to day lives and relationships with reef goods and services, nine months post-cyclone. Conversely, in surveys directly after cyclone Winston, Chaston Radway et al. (2016) observed large decreases in fishing gear, the weekly consumption of fish and the number of people which a consumed fish as a primary protein source in both Kubulau and Levuka. Considering that our results do not show these decreases could indicate human communities have naturally recovered or cyclone mitigation strategies recommended by Chaston Radway et al. (2016) have been implemented by the Fijian government assisting in the recovery of respondents lifestyles. Our research did show that respondents were impacted severely by cyclone Winston in non-marine sectors including agriculture, infrastructure and economically.

We did not observe any impacts on the relationships between ocean resources and surveyed communities in Kubulau. Changes in these relationships could not be discerned accurately in Levuka given the large proportion of participants which didn’t respond to survey questions. Cyclone impacts appeared to be mitigated more in Levuka through government and NGO disaster support which provided fishing gear, money and food among other things. Supplying fishing gear was a recommendation in a cyclone Winston community fisheries impact survey and may explain changes observed (increase in Levuka vs decrease in Kubulau) in this study in fishing gear quantities (Chaston Radway et al. 2016). The provision of these support packages may have also provided an alternative income and food source to limit the reliance on environmental or agriculture resources after cyclone Winston. Kubulau respondents did not receive as much support which could be attributed to less cyclone damage compared to Levuka and explain why Kubulau residents recovered quicker and believed they would recover better after future disturbances. A history of cyclones in Fiji may have equipped indigenous elders with knowledge of past experiences dealing with cyclone damage, where knowledge passed from elders to younger generations regarding preparation, response and rehabilitation to cyclones could minimise the potential mortality, injury and destruction of infrastructure (Senimoli et al. 2020). A lack of knowledge being passed on was reported in other parts of Fiji after cyclone Winston, and could affect a community's ability to be resilient and adapt after future cyclone impacts (Senimoli et al. 2020). People in this survey had a strong sense of place, having stayed in their villages for extended periods of time. Often people prefer the stability, familiarity and sense of belonging associated with a location or community which could inhibit movement of people to avoid future storms or reef degradation (Marshall et al. 2012).

The cyclone impacts on fishers appeared to be variable affecting different aspects of respondents' livelihoods in each district. Regardless of this, the impacts on fishers in Kubulau appeared to be more severe than in Levuka. This could be due to there being a greater proportion of fishers in the population at Kubulau which are dependent on fishing income (Marshall 2011). Levuka is geographically closer to Suva which means the respondents have greater access to formal employment (e.g. tuna industry) and purchasing power compared to Kubulau, possibly decreasing their reliance on fish. Similar trends of declining reliance on fresh fish have been observed throughout Fiji in both larger developed and smaller remote communities (Turner et al. 2007).

The majority of these fishers also believed they could not successfully change to another occupation apart from fishing to support their livelihoods. Occupational attachment and resource dependency can strongly influence an individual's ability to adapt after a disturbance due to a person being sensitive to losing income and identity from being unable to continue their occupation (Minnegal et al. 2003; Marshall et al. 2011). In Kubulau, respondents reported a decrease in the number of boats after cyclone Winston which is likely to have had flow-on effects on accessing fishing locations, the fishing equipment used, fishing effort and catches. Subsequently, greater effort to catch similar fish quantities was reported post-cyclone, decreasing the value for effort of fish catches of some respondents. Alternatively, with other food resources diminished as a result of cyclone damage this may have increased the value of fish and fishing effort of the respondents as a means to generate income. This may have changed the mindset of fishermen into selling more of their catches instead of giving them away due to an increased need to pay for their additional time (effort) put into fishing and possible repairs or replacements to infrastructure caused by cyclone Winston.

Similar to the cyclone impacts, perceptions of the status of fish between districts were variable with perceived increases in Kubulau and decreases in Levuka. However, it seems unusual that this trend is common across all popular target species of differing guilds (e.g. slow growing demersal carnivores and quick reproducing herbivores) apart from Siganids in Kubulau. Most Lethrinidae and Serranidae species are highly vulnerable to fishing being slow growing and having low fecundity (Russ and Alcala 1998; Hawkins and Roberts 2004). Studies have shown these highly valued demersal species are in relatively low abundance in Fiji (Jennings and Polunin 1996), tending to be in higher abundances in deeper water within MPAs where the fishing pressure is lowest (Goetze et al. 2011; Barrett et al. 2018). Surveyed communities appear to have a varying knowledge of fish stocks and the threats, processes and management strategies which can influence stocks. PHCs are seen as a popular measure for improving fish stocks largely due to their common use in Fijian traditional ecosystem management (Govan 2009). Further supporting this, community fisheries surveys after cyclone Winston show communities strongly believe that the management strategies in place before the cyclone would successfully help with recovery of natural ecosystems (Chaston Radway et al. 2016). Such management practices can be beneficial, but equally provide no benefits if PHCs are small and harvested too regularly (Goetze et al. 2016, 2018). Perceptions created by a large successful harvest could create false impressions that PHCs are successful by increasing catchability through altering fish behaviour and if not managed properly may not be sustainable (Goetze et al. 2017; Carvalho et al. 2019). Although there is a strong recognition amoung Fijians for MPAs and PHCs to conserve fish stocks for the future, Fijians use and value of ocean resources and observed lack of change in livelihoods puts communities at risk from impacts on fish communities which could jeopardise their livelihoods.

Previous ecological surveys between 2009 and 2014 have shown reefs in Kubulau to be healthier, containing higher coral cover, fish abundance and biomass compared to those in Levuka (Jupiter and Egli 2010; Jupiter et al. 2017). Compliance has also previously shown to be higher, and fishing pressure, poaching and population lower in Kubulau, which over time could be translating to the fish stock increases perceived in Kubulau (Jupiter et al. 2017; Goetze et al. 2018). Alternatively, a lack of compliance and higher poaching, fishing and population levels in Levuka could result in the perceived decreases of fish stocks. Surveys by Chaston Radway et al. (2016) show communities in Kubulau thought their fishing grounds were remaining very healthy and unchanged prior to cyclone Winston whereas this response was not as positive in Ovalau island (which encompasses Levuka District). Perceived increases in fish stocks could be linked to behavioural responses and increased abundances of fish which have been observed after cyclone disturbances (Letourneur et al. 1993; Naim et al. 1996) and were observed in situ after cyclone Winston (Chapter 3). However, socio-economic surveys were conducted 6 months after the ecological surveys and 9 months after the cyclone, and these short-term ecological responses would have diminished. It seems unlikely that all fish species and stocks have increased as perceived considering their relatively low abundance in our research and previous studies, vulnerability to fishing and status of the most popular food fishes in Fiji (Russ and Alcala 1998; Goetze et al. 2011; Goetze 2016; Barrett et al. 2018).

Responses to hypothetical fish status questions were more variable after the cyclone in both districts and in Kubulau compared to Levuka. Many of these changes were not significant, however, there was a more even spread across differing responses in regards to what management actions should be taken to increase fish stocks and hypothetical actions if fish stocks decreased. After multiple cyclone disturbances in Puerto Rico, fishers were shown to have greater concerns regarding climate change and disturbances affecting fisheries than prior to the cyclones (Seara et al. 2020). Perception differences between districts in our study could be explained by this cautious nature of respondents after cyclone Winston. Respondents in Levuka suffered greater damage compared to those in Kubulau in our surveys, and reported more severe damage to natural resources (coral reefs, mangroves and seagrass) in other post-cyclone surveys (Chaston Radway et al. 2016). This could correspond with the more variable responses to survey questions and hypothetical scenarios observed in Levuka compared with Kubulau. It should also be noted that a large proportion of these respondents in Levuka didn’t answer survey questions regarding perceptions in 2015, which could contribute to the variable results. Regardless of this, we didn’t observe a large proportion of respondents wanting to alter livelihood incomes (e.g. have more income sources or change income to a more stable source) or be tentative in stating fish stocks were increasing which would indicate greater caution as in other studies after a cyclone (Marshall et al. 2013; Seara et al. 2020).

In Fiji, indigenous communities use a risk-sharing network which can help to absorb damages caused by the disturbance across the whole community. This has shown to limit communiy perception changes and the use of natural resources in a more conservative way despite the belief that future cyclones will have severe negative impacts (Brown et al. 2018). Such lack of perception change could indicate limited resilience and adaptive capacity within communities, however this may not be true in Fijian communities.

2.7 Conclusion

Social factors including risk, adaptive capacity and vulnerability are influential factors in dictating how a community may be impacted by a natural disturbance, their recovery from impacts and livelihood impacts from future disturbances. Similar to other studies, a significant proportion of respondents engaged in fishing income for livelihoods, high consumption of fish and strong place attachment, puts surveyed communities at higher risk to climate related disturbances (Cinner et al. 2012; Marshall et al. 2013; Morzaria-Luna et al. 2014). Apart from the direct damage caused by cyclone Winston to agriculture, infrastructure and household items, minimal changes were observed in catch data and the perceptions towards fish stocks in our study nine months later. Respondents in these surveys seem to have a base level knowledge on fish stock management and ecosystem function considering their hypothetical actions and reasonings related to perceived changes in fish abundance. However, a lack of changes in perceptions after the cyclone did not show respondents being risk averse. These findings contradict the perception changes observed elsewhere (Marshall et al. 2013; Seara et al. 2020; Senimoli et al. 2020) and it is possible that the lack of changes in our study could indicate a lower level of adaptive capacity to future disturbances. Alternatively, the passing down of practical information about cyclone impacts orally may assist Fijian communities to be resilient to cyclone impacts and increase adaptive capacity (Brown et al. 2018). While there were some impacts on catch and fishing, these did not seem to translate to significant changes in fish consumption or other livelihood impacts in our study. This could be due to limited ecological impacts and rather infrastructure impacts from loss of boats and equipment. Although this research showed that respondents fished regularly for subsistence and income, we couldn’t determine the degree of reliance on this resource and other resources such as agriculture. Between the time that community fisheries surveys were completed (directly after cyclone Winston) (Chaston Radway et al. 2016) and our surveys, recovery in respondents' livelihoods had occurred which is a positive sign for the adaption of communities to future climate related disturbances. As shown by fishers in the Great Barrier Reef, having strong adaptive capacity can help mitigate the direct and indirect cyclone impacts in high risk, fishing dependent communities (Marshall et al. 2013). We are unsure of the exact level of adaptive capacity and sensitivity among Fijian communities in Kubulau and Levuka, however, given exposure to disturbance events is predicted to increase and their strong connections with coral reef ecosystems we believe that respondents are vulnerable to degradation of reefs and declines in ecosystem health. As such, we believe communities in Kubulau, which were more reliant on fishing appear to have higher vulnerability to future disturbances which may degrade coral reef ecosystem goods and services. Given that Fijian coastal communities regularly utilise the marine environment for food and income it is important that more research is collected to develop management strategies which can minimise and mitigate the impact of future cyclones on the people inhabiting these areas.

2.8 Acknowledgements

We are grateful to the chiefs and villagers in Kiobo and Navatu (Kubulau District), and Arovudi and Taviya (Levuka District) for access to villages and hospitality whilst completing surveys. Thanks to the Wildlife Conservation Society staff, particularly Margaret Fox, Epeli Loganimoce and Waisea Naisilisili for conducting surveys, cleaning data and for access to the survey data. This research was supported and funded by the John D. and Catherine T. MacArthur Foundation and the Wildlife Conservation Society.

Chapter 3

Responses of benthic habitat and fish to severe tropical cyclone Winston in Fiji

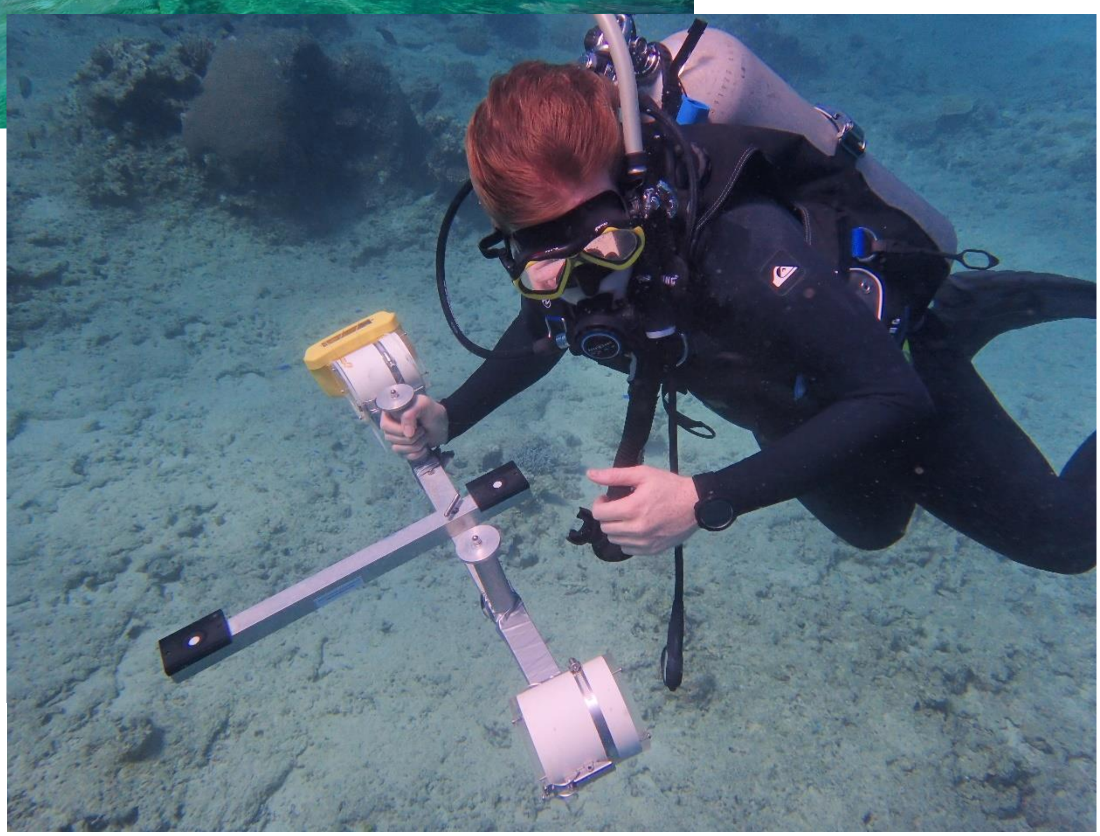


Photo 1: B. Price
Photo 2: S. Mangubhai/WCS

Preface: This chapter has been published in the journal Coral Reefs (https://doi.org/10.1007/s00338-021-02086-x) and has been formatted to the journal guidelines.

3.1 Abstract

Tropical cyclones can dramatically reduce coral cover, coral diversity and structural complexity, which can all cause flow-on effects to fish communities. In 2016, Fiji sustained extensive damage from one of the most severe cyclones recorded in the southern hemisphere (Category 5 cyclone Winston). We assessed the impacts of cyclone Winston on the coral reef habitat and fish assemblages in Kubulau and Levuka districts in Fiji. Wave modelling showed that cyclone-generated waves were substantially larger and persisted longer in Levuka than Kubulau. Damage to live corals was spatially variable and highest in Levuka with the extent of damage highly correlated to the exposure, height and duration of waves at each site. We recorded increases in macroalgae directly after the cyclone and increases in encrusting coralline algae two years after the cyclone. We did not detect many changes in the fish assemblage caused by cyclone Winston. Obligate corallivores, and species within this group, *Chaetodon baronessa* and *Labrichthys unilineatus,* were the only fish to show a decline post-cyclone, most likely caused by declining coral cover. We found that the modelling of cyclone wave dynamics explained the variation and damage to live corals better than proximity to the cyclone path, providing a useful tool to predict cyclone damage. Future climate models predict that more cyclones will reach the highest intensities. Understanding the impact this will have on vulnerable coastal communities that are dependent on marine resources and are protected from wave energy by reefs is essential for effective mitigation and adaptive management plans.

3.2 Introduction

Tropical cyclones are one of the most destructive natural disturbances of coral reef ecosystems

(Stoddart 1971; Harmelin-Vivien 1994). The extreme winds generated by cyclones can create large waves that can exert mechanical forces large enough to directly damage both individual corals (e.g. dislodgement, breakage) and the reef matrix (Done 1992), reducing the structural complexity of the reef (Alvarez-Filip et al. 2009). Heavy rainfall associated with cyclones can induce secondary impacts such as high nutrient runoff, freshwater flood plumes and high turbidity. This can create anoxic conditions and algal blooms, which impact live corals over an extended time period (Stoddart 1971; Harmelin-Vivien 1994). Repeated cyclone damage, especially when combined with other anthropogenic disturbances (e.g., land-based run-off), can be a major driver of coral community structure change and decline (De'ath et al. 2012).

Physical wave damage to coral communities from cyclones is spatially variable, especially at fine-scales (Done 1992; Harmelin-Vivien 1994). Processes which affect this spatial variability in damage include the magnitude of the wave climate, the spatial location of the cyclone relative to surrounding coral reefs and other wave blocking features like islands, and the structural vulnerability of the coral colonies themselves (coral size and shape). The magnitude of the wave climate that develops from a cyclone is determined by the combination of cyclone intensity, size and speed. Accordingly, large sized, intense and slow-moving cyclones have the greatest potential for damaging reefs (Puotinen et al. 2016). Cyclone intensity and distance alone are poor predictors of the potential for damage, as evidenced by major coral loss at reefs up to 850 km from a recent cyclone (Puotinen et al. 2020). For example, live corals located very close to the cyclone path can be undamaged because wave energy is lost upon interaction with shallow water features like reefs, islands and coastlines, creating a wave shadow beyond them (Massel and Done 1993). At a finer scale, reef depth, topography and reef profile cause variability in exposure across tens of metres. Finally, the vulnerability of coral colonies to wave damage is driven by factors that affect their size and shape. Larger coral colonies are generally easier to dislodge (Done 1992), while stream-lined colonies oriented in the direction of the flow are more resistant (Tunnicliffe 1981). Coral colonies that are more compact in shape are overall the least prone to dislodgement (Massel and Done 1993; Madin and Connolly 2006; Madin et al. 2014).

The history of disturbance and recovery in a particular location is important (Hubbard et al. 1991; Done 1992; Hughes and Connell 1999) because previous exposure to thermal stress, predation and disease can weaken coral skeletons and make them easier to break and dislodge (Madin et al. 2012; Cheal et al. 2017). Very recent damage may mean that few live corals are left to be damaged or that coral colony sizes are temporarily small and therefore more resistant to dislodgement and further damage (Done 1992). Coral reefs that have not been impacted by other recent disturbances are also likely to recover quicker due to higher initial coral cover. Local-scale variation in live coral exposure and vulnerability means that coral reef ecosystems in cyclone prone regions can be impacted differently by cyclones with similar characteristics, which may result in the level of damage within and between reefs varying significantly. This spatially variable damage can help with reef recovery through the provision of coral recruits post-cyclone from undamaged coral colonies (Beeden et al. 2015).

Compared to corals, cyclone impacts on coral reef fish assemblages are more variable, difficult to document and rarely result in direct mortality (Harmelin-Vivien 1994). Indirect or delayed impacts on reef fish are more commonly observed due to the strong positive relationship often detected between fish with live coral cover and its associated three-dimensional structural matrix (Emslie et al. 2014; Darling et al. 2017). When structural complexity levels are maintained, coarse-scale fish metrics remain stable at an assemblage level (Graham et al. 2006; Emslie et al. 2014). However, at finer scales the abundance of fishes such as planktivorous damselfish and corallivorous butterflyfish can decline significantly due to their reliance on live corals for shelter and food (Munday 2004; Pratchett et al. 2006; Ceccarelli et al. 2016). Hence, the impacts of cyclone disturbance on fish assemblages depends not only upon the level of habitat disturbance, but also on the composition of the fish assemblages themselves.

Severe cyclones can have serious implications for the food availability, security and income of coastal communities in tropical regions (Hunt 1999; Sulu et al. 2015). Due to its tropical marine climate, Fiji is exposed to regular severe storms and cyclones during the wet season (summer months) between November and April (Mangubhai et al. 2019). On the 20 February 2016, tropical cyclone Winston, a category 5 storm on the Saffir-Simpson scale with wind speeds up to 233 km/h and gusts to 306 km/h, passed between the two main islands of Fiji, Viti Levu and Vanua Levu (Fig. 3.1; Government of Fiji 2016). Cyclone Winston was one of the most destructive cyclones recorded to date in the southern hemisphere, causing widespread damage to coral reefs (Mangubhai 2016) and significant impacts to the livelihoods and food security of fisheries-dependent communities (Chaston Radway et al. 2016). An initial broad-scale assessment of benthic impacts after cyclone Winston reported extensive coral dislodgement, breakage and abrasion, as well as structural damage to the reef framework up to a depth of 20–30 m (Mangubhai 2016). Prior to cyclone Winston, Fiji regularly experienced storm and low intensity cyclone disturbances (average of top one-third of wave heights <4 m) (Fig. S1b, d). Apart from these disturbances, reefs around the study sites had been exposed to few natural disturbances since a large-scale bleaching event in 2000 (Cumming et al. 2002; Sykes and Morris 2009; Mangubhai et al. 2019).

Only two studies have investigated the impact of tropical cyclones on Fiji's coral reefs and both of these focused solely on immediate/short-term post-cyclone impacts to coral communities (Cooper 1966; Mangubhai 2016). In this study, we examined the impacts of cyclone Winston and the early recovery of coral reef communities and reef fish assemblages using datasets collected prior to cyclone Winston (Goetze et al. 2015, 2016, 2017; Goetze 2016) and, ~3 months and ~2 years after the cyclone. The objectives of the research were to: (a) quantify changes in benthic composition, live coral cover and structural complexity; (b) quantify changes in fish abundance and trophic structure; and (c) examine how changes in reef habitat features relate to changes in fish assemblages, after the cyclonic disturbance and during early recovery.

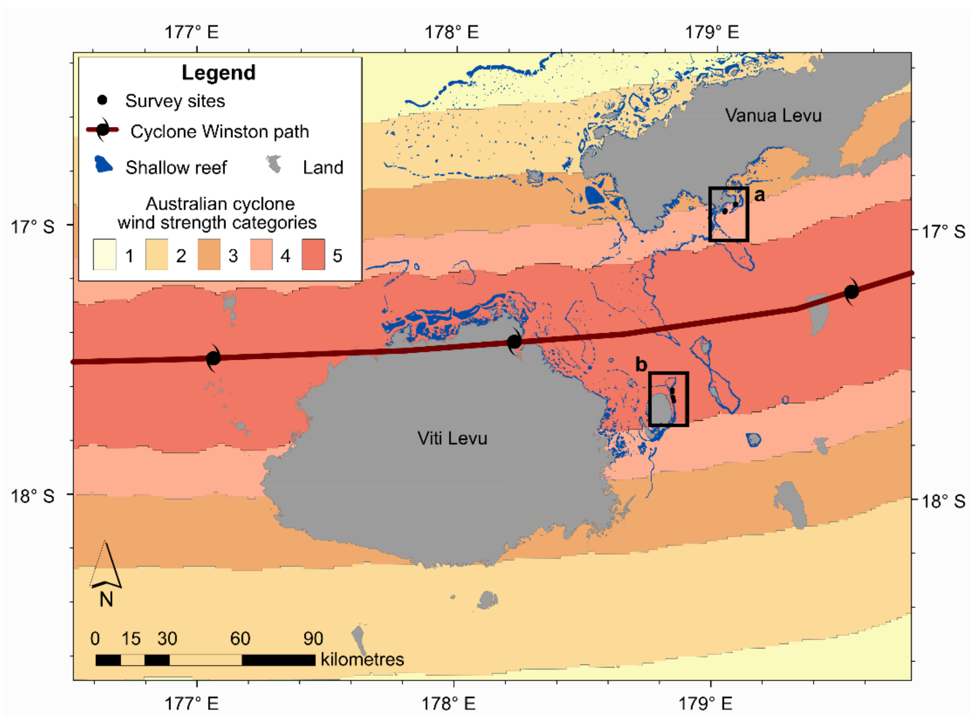


Fig 3. 1 The position of the study sites in Kubulau **a** and Levuka **b** districts, Fiji, relative to the path of tropical cyclone Winston. Australian cyclone wind categories modelled based on Puotinen et al. (2016) are overlaid to indicate the spatial extent of likely exposure to conditions likely to cause severe wave damage.

3.3 Methods

3.3.1 Study location and design

Surveys were completed on the reef slope (7–9 m depth) of inshore coral reefs, adjacent to the villages of Kiobo and Natokalau in Kubulau District (hereafter “Kubulau”) on the island of Vanua Levu and on the back reef (3–5 m depth) adjacent to the village of Nauouo in Levuka District (hereafter “Levuka”) on Ovalau Island in Fiji (Fig. 3.1). Four study sites were surveyed at each district (Fig. 3.2a, b) in areas exposed to moderate (Kubulau) and high (Levuka) levels of fishing pressure (Goetze et al. 2018).

At each site, six 50 x 5 m belt transects were completed and separated by 10 m to ensure independence of replicates. Sites were sampled twice before and twice after cyclone Winston (Fig. 3.2a, b). Pre-cyclone surveys were completed in October 2012 and September 2013 at Kubulau, and in October 2013 and 2014 in Levuka. Post-cyclone surveys were completed in May 2016 and 2018 for both districts.

3.3.2 Video sampling, analysis and calibration

Fish abundance and habitat composition were assessed using a diver operated stereo-video system (stereo-DOV), following Goetze et al. (2019). Two experienced stereo-DOV operators completed surveys each year, with one of these divers present across all years to ensure consistency in sampling technique. Throughout the surveys three types of cameras were used: Sony HDR CX12s in 2012, Canon HF G25s in 2013 and 2014 and GoPro Hero 3+ silver editions in 2016 and 2018, however, all imagery was captured with high-definition video (1920p-1080p). Stereo-DOV design followed Harvey and Shortis (1995) and Shortis and Harvey (1998). Stereo video systems were configured following Goetze et al. (2019), which allows transect size to be explicitly defined in post analysis of stereo-DOV footage and ensure that fish were within the transect (Harvey et al. 2004).

Stereo video footage was calibrated at the beginning and end of each survey using the program

CAL (http://www.seagis.com.au/bundle.html) and calibration files specific to the coinciding camera type and setup following published protocols (Harvey and Shortis 1998; Shortis and Harvey 1998). Paired video imagery (left and right cameras) was analysed in EventMeasure (http://www.seagis.com.au/event.html), following (Goetze et al. 2019). All fish seen in each video were identified to species level where possible or lumped to genus or family.

3.3.3 Wave modelling

Significant wave heights (Hs - average of the top one-third of wave heights) were taken from the National Oceanic and Atmospheric Administration (NOAA) WaveWatch III global hindcast dataset (Tolman 2009; http://polar.ncep.noaa.gov/waves/index2.shtml). From this dataset, the percent frequency that waves approached the sites from each of 16 compass directions and their magnitude was used with estimates of fetch to calculate relative wave energy and wave exposure. These were calculated separately for: i) routine wave conditions, and ii) during the passage of cyclone Winston at each of the sites in both survey districts (See Supplemental Materials 1 for the full wave modelling methods).

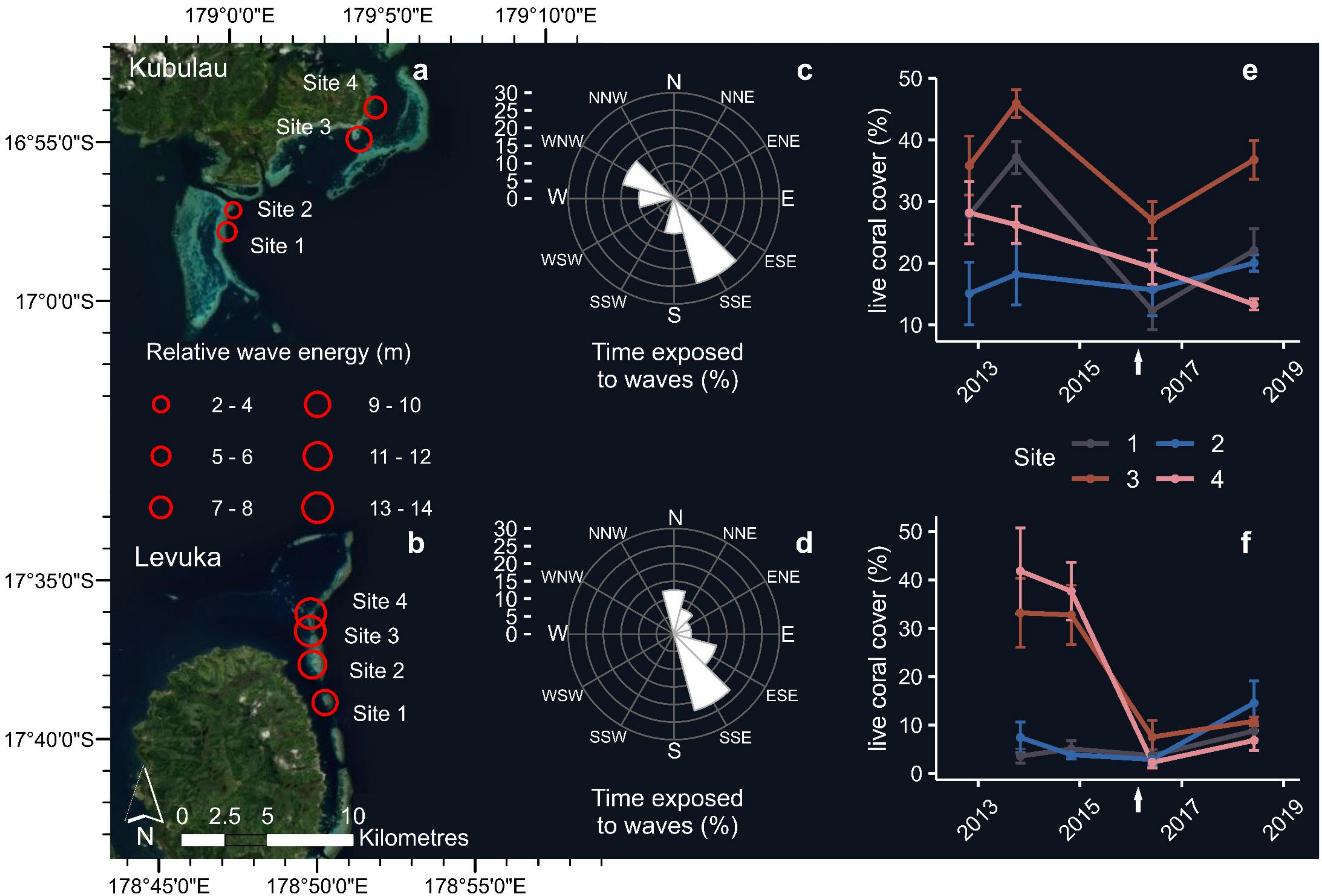
3.3.4 Coral reef habitat analysis

Benthic composition and reef structural complexity were assessed using the stereo-DOV footage in the program TransectMeasure (https://www.seagis.com.au/transect.html) at 20 intervals along each 50 m transect. At each interval, structural complexity was analysed over the entire field of view using the 6-point scale presented in (Polunin and Roberts 1993; Wilson et al. 2007). To determine benthic cover, a virtual quadrat of a set size (a sixth of the video frame) was placed in the bottom left or right corner (determined by the location of the reef slope) of the video frame at each interval (Fig. S2). Placement of the quadrat in this way ensured habitat was in close proximity to the camera for more accurate identification (Bennett et al. 2016). Within each quadrat, 5 random points were placed and the benthic cover under each point was identified.

Benthic cover was classified into the following broad benthic categories: stony corals, black/octocorals, macroalgae, consolidated substrate and unconsolidated substrate (derived from the CATAMI guide (Edwards 2013). Benthos was further identified to morphological form for corals and macroalgae, and into different substrate types (Table S1). Additionally, the health status (benthic condition) of stony corals (i.e. live, damaged, dead or bleached) was assessed to determine damage, which could be associated or coincide with a cyclone impact. Likewise, benthos identified as abiotic (e.g., rock, sand) was assessed for substrate condition (benthic condition) (i.e., substrate had no biota, silt covering, or benthic filamentous algae growth) (Table S1) which could indicate a cyclone impact in line with observations reported in previous studies (Bouchon et al. 1994; Naim et al. 1996; Wantiez et al. 2006).

3.3.5 Statistical analysis

All statistical analyses were completed using the PRIMER statistical analysis software, and the PERMANOVA+ add on to PRIMER (Anderson et al. 2008). Benthic cover changes were explored over time at survey sites at the three levels described previously; broad benthic categories, morphological form and benthic condition, with structural complexity also analysed. Similarly, fish abundance were also explored at three levels; family, functional group and species. Fish functional groups were assigned using diet and trophic level information obtained from Froese and Pauly (2019). Benthic variables that were auto correlated were not analysed further. Similarity percentages (SIMPER) analyses were completed to show which fish variables in each family, functional group and species level had the greatest contributions to the trends in the fish assemblage between years at each site (Clarke et al. 2014). The most influential fish variables (>5 % contribution) identified by these analyses were further explored in univariate analyses (Table S2).



179°0'0"E
179°5'0"E
179°10'0"E
16°55'0"S
17°0'0"S
Kubulau
a
Site 4
Site 3
Site 2
Site 1
Relative wave energy (m)
2 - 4
5 - 6
7 - 8
9 - 10
11 - 12
13 - 14
b
Levuka
17°35'0"S
17°40'0"S
Site 4
Site 3
Site 2
Site 1
N
0 2.5 5 10
Kilometres
178°45'0"E
178°50'0"E
178°55'0"E
c
d
N
NNE
ENE
E
ESE
SSE
S
SSW
WSW
W
WNW
NNW
0
5
10
15
20
25
30
Time exposed to waves (%)
e
f
live coral cover (%)
10
20
30
40
50
0
2013
2015
2017
2019
Site
1
2
3
4

Fig 3. 2 The effect of cyclone Winston on wave height and benthic cover at the study sites. **a,b** Illustrates the relative wave exposure x maximum significant wave height (Hs - average of the top one-third of wave heights) (m) during cyclone Winston at each site in **a** Kubulau and **b** Levuka districts. Relative wave energy is indicated by the size of the red circles. **c, d** Direction of the waves during cyclone Winston at each site in **c** Kubulau and **d** Levuka, the size of the wave rose indicates the percentage of time waves approached from that specific direction when the cyclone generated damaging seas (Hs ≥ 4 m for at least 1 hour). **e, f** Percentage cover of live stony coral across all survey years (2012–2014, 2016 and 2018) at each site in e Kubulau and f Levuka districts. The passing of cyclone Winston is indicated by the white arrow

Multivariate benthic and fish community data were visually screened with shade plots and transformed at a magnitude to reduce the dominance of very abundant species/variables during analyses. Multivariate habitat data was square root transformed and fish data fourth root transformed. A permutational analysis of variance (PERMANOVA) was completed using a three-factor design (*District*: fixed, 2 levels: Kubulau, Levuka; *Years*: nested in District, fixed, 5 levels: 2012, 2013, 2014, 2016, 2018; *Site*: fixed, 4 levels: 1-4) to test for differences within benthos and fish assemblages between years and between sites in each district. PERMANOVAs with 9999 permutations were completed on benthic and fish data at multi and univariate levels (Anderson et al. 2008), using a Bray-Curtis matrix for multivariate fish data and a Euclidean distance dissimilarity matrix on all univariate data and multivariate habitat data. Pairwise post-hoc tests were used to explore significant interactions or differences obtained from the PERMANOVA. When there were insufficient permutations (<100) to conduct a rigorous statistical test Monte Carlo bootstrapping was used to obtain an adjusted p-value (PMC)(Anderson et al. 2008). Due to the large number of analyses PERMANOVA and post-hoc test results including significant interactions and p-values are presented in Electronic Supplementary Materials 2 (Table S3–6). Multivariate data was centroided and presented graphically in PCO plots in Electronic Supplementary Materials 1.

The strength of the correlation between each variable in the three fish classification levels (family, functional group and species) and each variable in the benthic classification levels (broad benthic composition, morphological form and benthic condition) were explored. Those with the strongest correlations (R > |0.6|) were further explored using a linear regression in Minitab version 19.2020.1 (64-bit version).

3.4 Results

3.4.1 Wave data results

During cyclone Winston a maximum significant wave height of 14.37 m was estimated near Levuka. This was 30 standard deviations higher than the average routine significant wave height values of 0.94 m (±0.48 m SD) (Fig. S1c). At Kubulau, the maximum significant wave height estimated nearby was 9.39 m. This was 22 standard deviations higher than the average routine significant wave height values of 0.77 m (±0.43 m SD) (Fig. S1a). Exposure to cyclone wave energy varied amoungdistricts and sites, however, exposure was consistently higher in Levuka compared to Kubulau, where the wave energy was more variable among sites (Fig. 3.2a, b). Cyclone Winston tracked in an east to west direction, resulting in Kubulau sites being exposed to waves from a south-southeast and west-northwest direction, and sites in Levuka between north to south-southeast directions (Fig. 3.1, 3.2c, d). In Levuka, sites were exposed to significant wave heights of 9 m or more for substantially longer time periods (~8 hours) compared to sites in Kubulau (~ 1 hour) (Fig. S1). However, both districts were exposed to significant waves greater than 4 m (above threshold for damage to vulnerable coral colonies following Puotinen et al. (2016) for ~15 hours; Fig. 3.2a, b, Fig. S1).

3.4.2 Benthic composition

A PERMANOVA analysis found significant interactions (α=0.05) between year and site at all benthic classification levels (broad benthic categories, morphological form and benthic condition) suggesting that variation in habitat variables across years was dependent on district and site (Fig. S3-5; Table S3; Electronic Supplementary Materials 1, 2). A significant interaction between year and site was found for structural complexity, and for the benthic morphological form of encrusting coralline algae and corymbose, branching, staghorn and bottlebrush corals (Table S4). The sediment type; rubble and benthic condition; benthic filamentous algae growth, live stony coral and dead stony coral had significant interactions between year and site (Table S4). Significant variation across years was observedfor macroalgae (Table S4). The morphological forms; massive, encrusting, foliose, table, sub massive, columnar, digitate, tabulate, other octocorals and massive soft corals, and filamentous/turf and other algae were either too rare, or not impacted by the cyclone significantly and were not explored further (Table S4).

3.4.2.1 Habitat impacts – Levuka

In Levuka, live stony coral cover was significantly lower post-cyclone (2016 and 2018) at site 3 and site 4 when compared to pre-cyclone (2013 and 2014) levels (Fig. 3.2f, Table S5). Declines of live stony coral cover was primarily driven by significant declines in the most abundant coral morphologies (Fig. 3.3h, e, g; Table S5). There was significantly lower cover of corymbose coral post-cyclone (2016 and 2018) at site 3 and site 4 compared to pre-cyclone levels (2013 and 2014) (Fig. 3.3e, Table S5). Likewise, branching coral cover declined significantly at site 4 post-cyclone (Fig. 3.3h, Table S5). Staghorn coral cover had a declining trend at site 3 and 4 post-cyclone (2016, 2018), and was significantly lower post-cyclone compared to 2013 at site 3 and 2014 at site 4 (Fig. 3.3g, Table S5). At the same sites where live corals significantly declined, there was a decrease in the structural complexity of the coral reef (Fig. 3.3b, Table S5). At sites 3 and 4, structural complexity was significantly higher in 2013 than 2016, and in 2014 compared to post-cyclone (2016 and 2018). Site 4 also had significantly higher complexity in 2013 than in 2018.

Macroalgae was at higher levels post-cyclone, however, this was only significant at site 1–3 in 2018 compared to 2014 (pre-cyclone) and at sites 1 and 2 in 2016 compared to 2014 (Fig. 3.3c, Table S5). Benthic filamentous algae growth on bare substrate was also observed in Levuka (Fig. 3.3a, Table S5). At sites 3 and 4, the highest levels of algae growth occurred in 2016 (post-cyclone); however, only at site 4 were the levels significantly higher in 2016 compared to all other years.

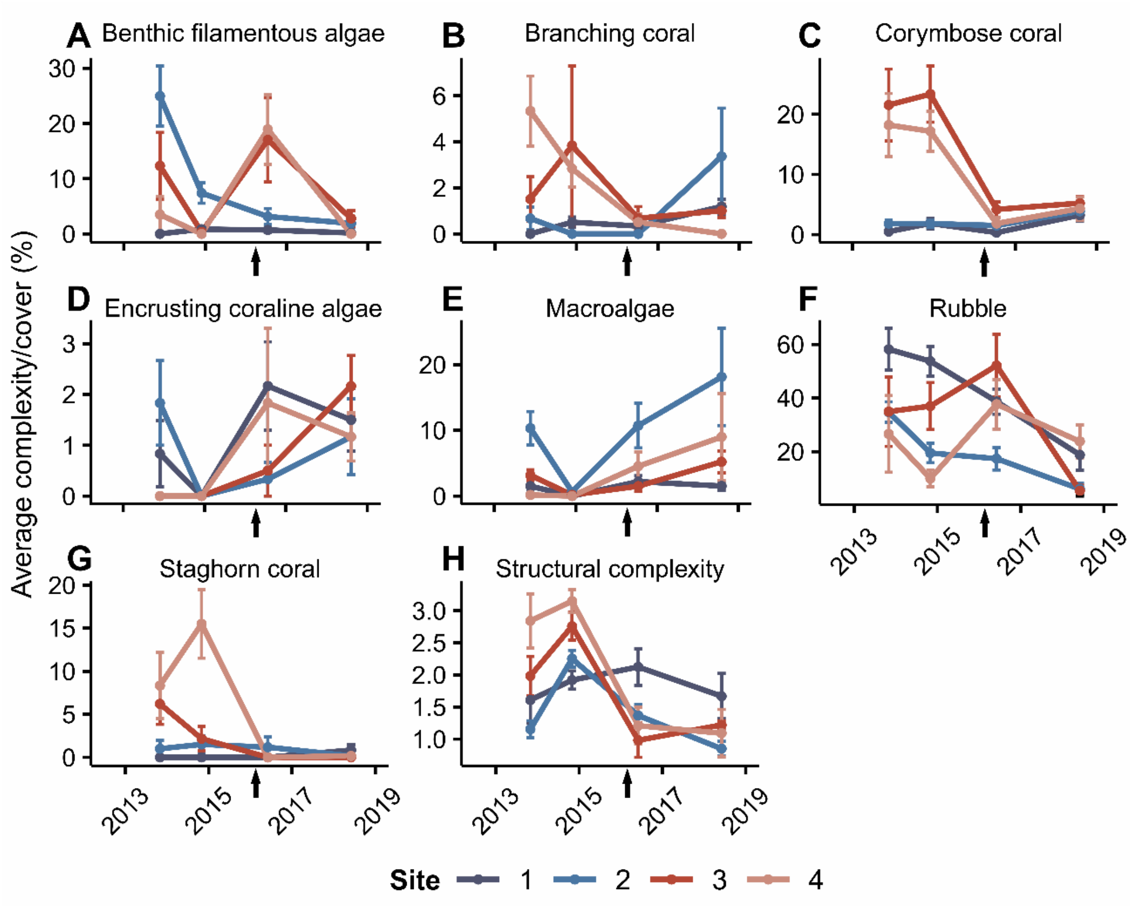


Fig 3. 3 Mean percentage cover (±SE) of cyclone impacted habitat variables in Levuka District **a** benthic filamentous algae, **c** macroalgae, d corymbose coral, e encrusting coralline algae, **f** rubble, **g** staghorn coral and **h** branching coral. **b** Mean structural complexity (± SE) of sites in Levuka District represented

on a 6pt scale (0 being flat substrate with few features and 5 being exceptional structural complexity, with numerous large holes and caves) (See link for full description of complexity scoring categories, https://github.com/TimLanglois/Habitat-annotation-of-forward-facing-benthic-imagery). The passing of cyclone Winston is indicated by the black arrow.

At sites 3 and 4 encrusting coralline algae cover was significantly higher in 2018 than pre-cyclone levels (2013 and 2014) (Fig. 3.3d, Table S5). At site 1 encrusting coralline algae was higher post-cyclone (2016 and 2018) compared to 2014. The cover of rubble substrate was highest in 2016 at sites 3 and 4 and was significantly higher than cover levels in 2018 at site 3 and 2014 at site 4 (Fig. 3.3f, Table S5). Rubble substrate levels continually declined at other sites and was significantly lower in 2018 compared to all other years.

3.4.2.2 Habitat impacts – Kubulau

In Kubulau, changes were observed at sites 1 and 3 that were indicative of a cyclone impact (Fig. 3.2e, 4, Table S5). At site 1 there was higher live stony coral cover in 2012 compared to 2016, and in 2013 compared to post-cyclone surveys (2016 and 2018) (Fig. 3.2e, Table S5). These changes were driven by lower cover of branching and staghorn corals in 2016 (post-cyclone) compared to pre-cyclone (2012 and 2013), and corymbose coral between 2016 and 2013 (Fig. 3.4e, f, h; Table S5). In 2018, staghorn coral cover was still lower than pre-cyclone (2012 and 2013) and corymbose lower than 2013 surveys, however, branching corals had increased in cover, similar to levels pre-cyclone.

At site 3 there was less live stony coral in 2013 compared to post cyclone (2016 and 2018) (Fig. 3.2e, Table S5), and accordingly, there was more dead coral in 2016 compared to pre-cyclone (2012 and 2013) (Fig. 3.4a, Table S5). Despite these changes, all coral morphologies at site 3 had similar coral cover pre- and post-cyclone. Bottlebrush coral cover at site 4 was significantly lower in 2018 than other years (Fig. 3.4d, Table S5). At all sites, no significant changes were observed in the structural complexity of the reef pre- or post-cyclone Winston (Fig. 3.4b, Table S5).

Macroalgae cover was higher in 2018 compared to all other years at sites 2 and 3 (Fig. 3.4c, Table S5). Macroalgae cover at site 1 was also higher in 2018 than 2016. These trends appear to be driven by encrusting coralline algae, which had higher cover in 2018 at sites 1-3 compared to all other years (Fig. 3.4i, Table S5). Rubble substrate cover only varied at sites 1 and 2 (Fig. 3.4g, Table S5). Site 1 had significantly higher rubble cover in 2016 compared to 2013 and 2018, whereas rubble at site 2 was significantly lower in 2018 compared to 2012.

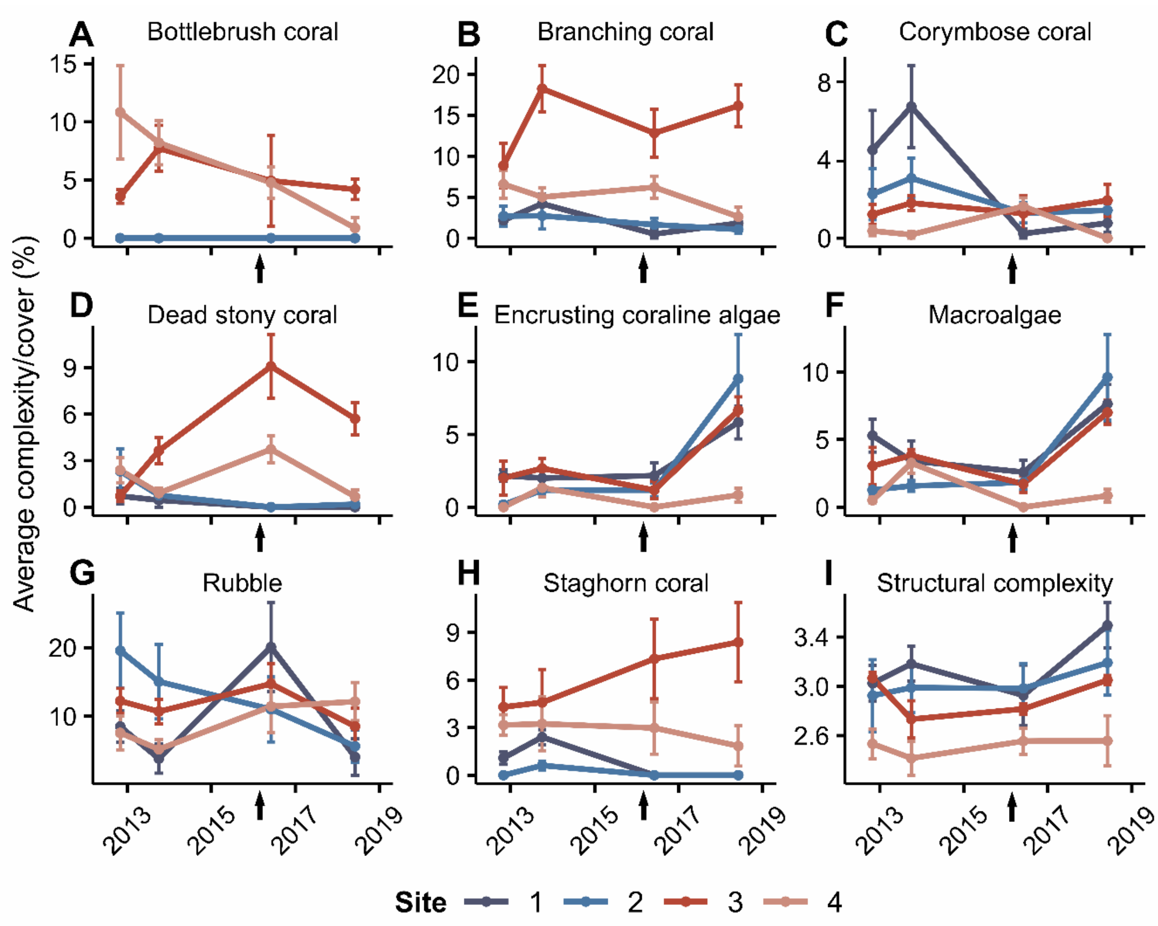


Fig 3. 4 Mean percentage cover (±SE) of cyclone impacted habitat variables in Kubulau District **a**dead stony coral, **c** macroalgae, **d** bottlebrush coral **e** branching coral, **f** corymbose coral, **g** rubble, **h** staghorn

coral and **i** encrusting coralline algae. **b** Mean structural complexity (± SE) of sites in Kubulau District represented on a 6pt scale (0 being flat substrate with few features and 5 being exceptional structural complexity, with numerous large holes and caves) (See link for full description of complexity scoring categories, https://github.com/TimLanglois/Habitat-annotation-of-forward-facing-benthic-imagery). The passing of cyclone Winston is indicated by the black arrow.

3.4.3 Fish assemblages

A PERMANOVA analysis found significant interactions (α=0.05) between year and site for all fish classification levels (family, functional group and species), suggesting that variation in fish metrics across years was dependent on district and site (Fig. S6-8; Table S3; Electronic Supplementary Materials 1, 2)). From each of the classification levels a SIMPER analysis selected the families; Acanthuridae, Pomacentridae, Scaridae and Labridae, functional groups; algae/invertebrate consumers, zooplanktivores, herbivores and invertebrate carnivores, and species; *Pomacentrus callainus, Pomacentrus maafu, Chromis ternatensis, Pomacentrus flavioculus*, *Ctenochaetus striatus*, *Amblyglyphidodon orbicularis, Chlorurus spilurus, Dascyllus reticulatus*, *Dascyllus aruanus*, *Pomacentrus coelestis*, *Pomacentrus nigromarginatus*, *Scarus schlegeli, Chrysiptera talboti* and *Chromis viridis,* as the most indicative of a cyclone impact (Table S2).

3.4.3.1 Fish impacts – Levuka

Acanthuridae were found in higher abundance in 2016 (post-cyclone) compared to all other years at site 1 and site 4 (Fig. 3.5a, Table S5). Acanthuridae were also in their highest abundance in 2016 at site 3, however, this abundance was only significantly higher than 2013 (pre-cyclone). Pomacentridae abundances at site 2 were higher in 2016 post-cyclone compared to pre-cyclone (2013 and 2014) (Fig. 3.5f, Table S5). Herbivore abundance was highest in 2016, however, was only significantly higher than 2013 and 2018 abundance (Fig. 3.5b, Table S5). The trends observed in herbivore and Acanthuridae abundance are driven by *C. striatus*. This species was significantly higher in abundance at site 1 in 2016 compared to pre-cyclone (2013 and 2014), and at site 4 in 2016 compared to all other years (Fig. 3.5c, Table S5). The abundance of other species also

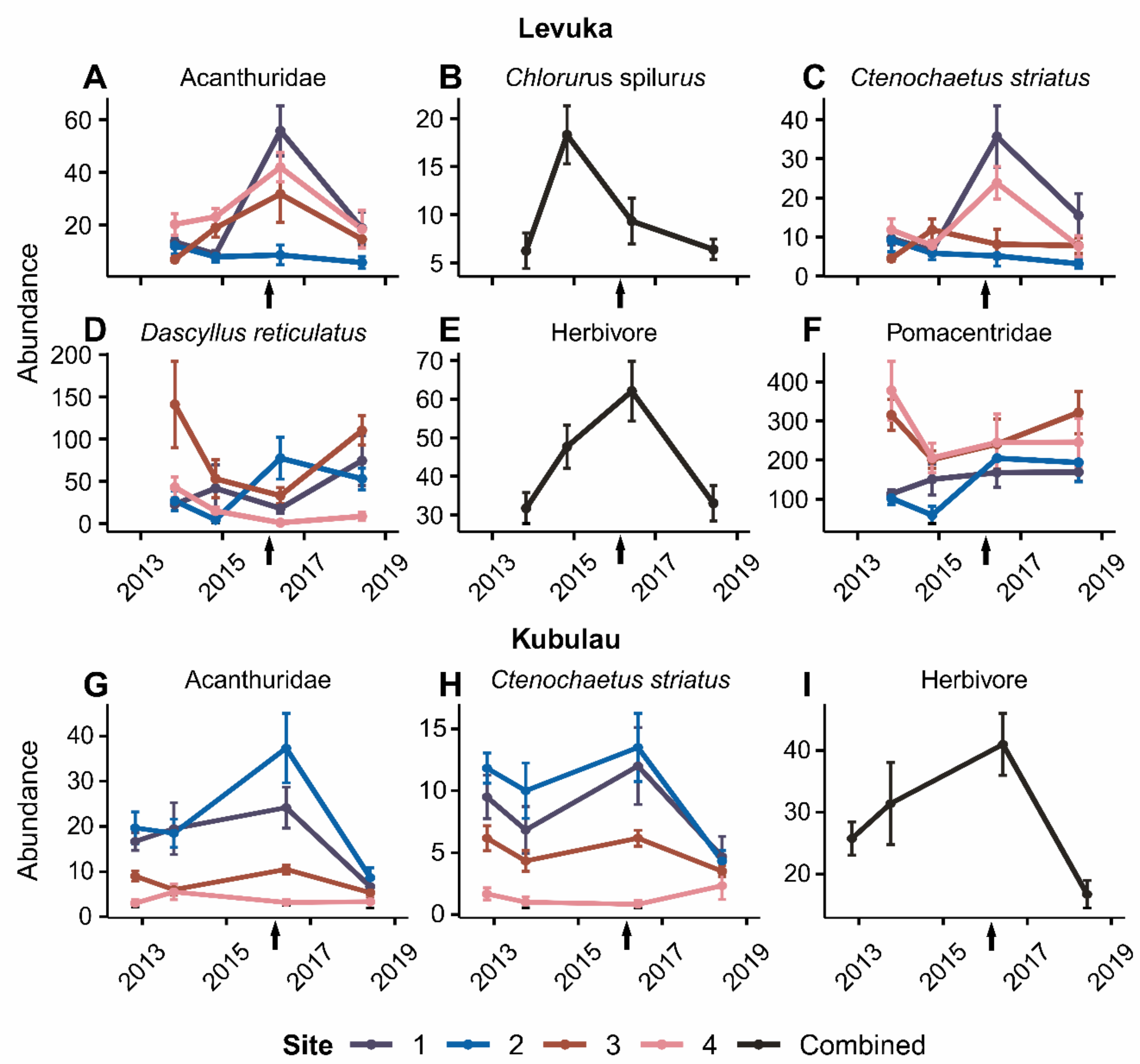


Fig 3. 5 Mean abundance (± SE) of possible cyclone impacted fish variables in Levuka District **a** Acanthuridae, **b** herbivore, **c** *Ctenochaetus striatus*, **d** *Dascyllus reticulatus*, **e** *Chlorurus spilurus* and **f** Pomacentridae, and Kubulau District **g** Acanthuridae, **h** herbivore and **i** *C. striatus*. The passing of cyclone Winston is indicated by the black arrow.

changed over time. *D. reticulatus* was higher in abundance pre-cyclone (2013 and 2014) compared to 2016 at site 4 (Fig. 3.5d, Table S5). *C. spilurus* was lower in abundance post-cyclone (2016 and 2018) compared to 2014 (pre-cyclone) (Fig. 3.5b, Table S6).

3.4.3.2 Fish impacts – Kubulau

In a similar pattern to Levuka, the family, Acanthuridae had a lower abundance in 2013 (pre-cyclone) at site 2 and 3 compared to 2016 (Post-cyclone) (Fig. 3.5g, Table S5). At site 2 Acanthuridae abundance was significantly lower in 2018 than all other years. Herbivore abundance was highest in 2016, with abundance significantly higher than 2012 and 2018 (Fig. 3.5h, Table S6). Similarly, to Acanthuridae, the species *C. striatus* had significantly lower abundance in 2018 at site 2, than all other years (Fig. 3.5i, Table S5).

3.4.4 Habitat and fish relationships

For most of the specific fish families, functional groups or species, correlation with the habitat variables was minimal. Obligate corallivores were one of the few species, which showed a strong relationship with habitat variables that had significant temporal changes (live stony coral cover, corymbose coral and staghorn coral). However, these relationships were only evident at sites in Levuka. Obligate corallivore abundance in Levuka was strongly positively correlated with live stony coral cover (R^2 = 0.583), Corymbose (R^2 = 0.370) and Staghorn cover (R^2 = 0.490) (Fig. 3.6e). These trends at Levuka were primarily driven by the two most abundant obligate corallivore species, *Chaetodon baronessa* and *Labrichthys unilineatus*. The abundances of both species had a strong relationship with live stony coral cover (Fig. 3.6a, c). While *L. unilineatus* also had a strong positive relationship with staghorn coral (R^2 = 0.582), and *C. baronessa* with corymbose coral (R^2 = 0.433).

A significant interaction between year and site was observed in obligate corallivore abundance (Table S4). Corallivore abundance was higher pre-cyclone (2013 and 2014) compared to post-cyclone (2016 and 2018) at site 4, and in 2018 compared to pre-cyclone at site 2 (Fig. 3.6f, Table S5). A significant interaction between year and site was observed in *L. unilineatus* and effect for the factor year for *C. baronessa* (Table S4). *L. unilineatus* abundance was higher in 2014 compared to all other years at site 4 (Fig. 3.6d, Table S5). *C. baronessa* had higher abundance in 2014 compared to post-cyclone (2016 and 2018) and in 2013 compared to 2018 (Fig. 3.6b, Table S6).

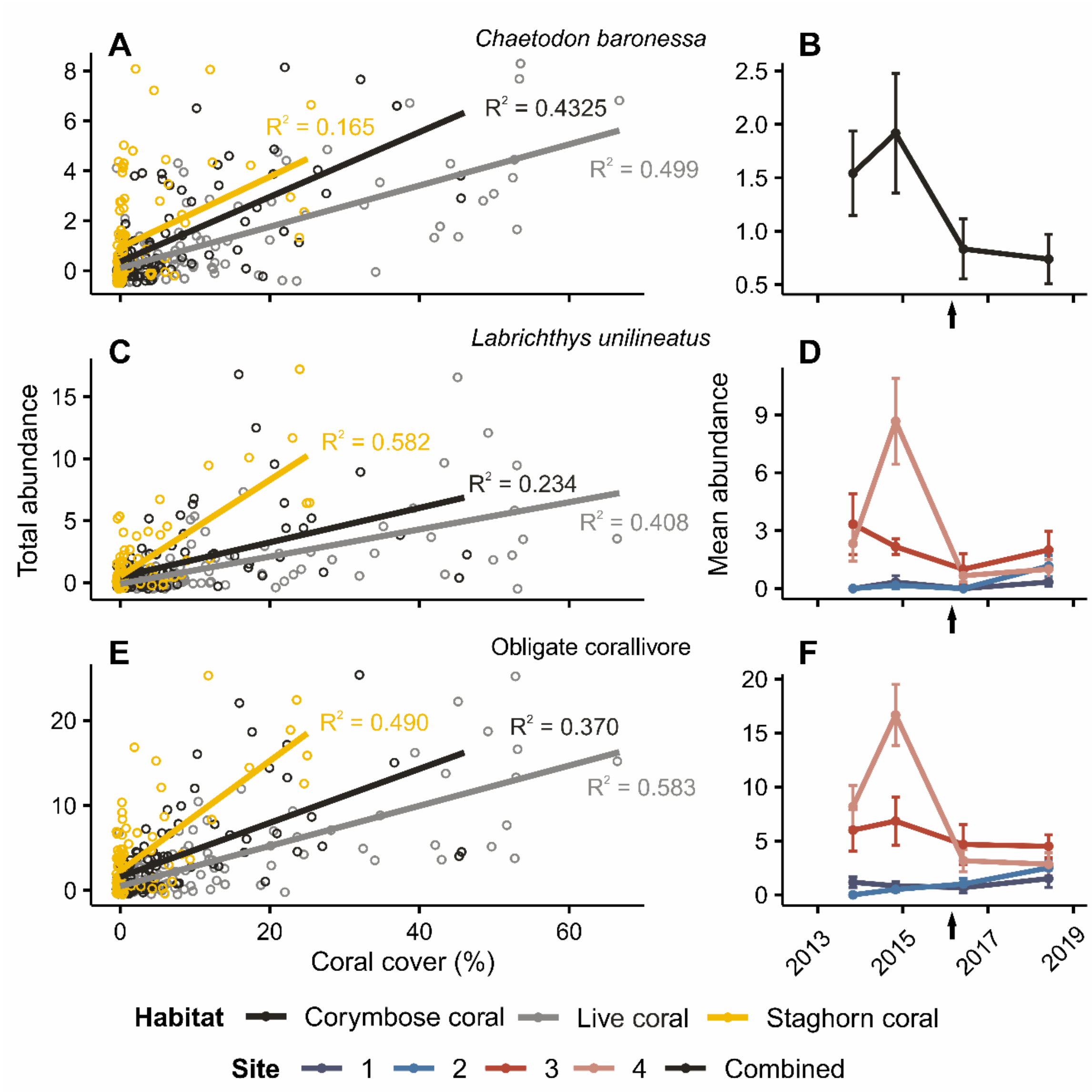


Fig 3. 6 Relationship between live stony coral, corymbose coral and staghorn coral cover with **a** *Chaetodon baronessa* **c** *Labrichthys unilineatus* and **e** obligate corallivore, abundance in Levuka District.

Mean abundance of **b** *Chaetodon baronessa* **d** *Labrichthys unilineatus* and **f** obligate corallivore across sites and years in Levuka District. Mean abundance for *C. baronessa* is a combined average for all sites. The black arrow indicates the occurrence of cyclone Winston.

3.5 Discussion

We found that live coral damage and loss of structural complexity from cyclone Winston was greatest at sites that were exposed to the largest and longest lasting waves. Losses from wave damage were the most prevalent for corymbose or branching varieties of *Acropora* species (branching, staghorn and bottlebrush). These were also the morphologies most commonly observed prior to cyclone Winston, and are also the most vulnerable to damage from cyclone waves (Madin and Connolly 2006; Madin et al. 2014) as well as other disturbances like crown-of-thorns starfish predation (De'ath and Moran 1998) and coral bleaching (Loya et al. 2001). They support a wide variety of juvenile and adult invertebrate and fish species in the form of shelter, food and settlement substrate (Wilson et al. 2008, 2010; Coker et al. 2014). Losses of these corals morphologies can cause large shifts in reef function and structure, and loss of species, whilst also contributing to widespread structural complexity declines associated with the breakdown of coral skeletons (Hughes 1994; Graham et al. 2006; Precht et al. 2010). Over time, repeated losses can lead to an assemblage structure dominated by slower growing, hydrodynamic resistant species (massive, sub massive) as has been observed for the Caribbean (Hughes 1994) and parts of the Great Barrier Reef (Hughes 1994; Fine et al. 2019).

A reduction in live coral cover often results in a loss of structural complexity (Alvarez-Filip et al. 2009). Indeed, we measured a decline in structural complexity at the most heavily impacted sites (3, 4) at Levuka where live coral skeletons were mostly turned to rubble. However, this decline in live coral cover did not occur at cyclone impacted sites in Kubulau along the fore reef. At the fore reef sites in Kubulau, structural complexity before cyclone Winston was predominantly formed from remnant reef structure which may provide an important substrate for corals to recruit to and refuge for many reef fauna (Graham and Nash 2013). Conversely, the mobile nature of rubble due to movement with regular winter storms may inhibit coral recruitment, settlement and survivorship, slowing down the rate of coral recovery (Dollar and Tribble 1993). Increases in the cover of coralline encrusting algae occurred at greater magnitude on fore reefs compared to back reef habitats. This could be due to more suitable reef slope habitat and greater availability of settlement substrate (rock and boulder). Increases in coralline encrusting algae have been observed after cyclones (Beeden et al. 2015) and may contribute towards reef recovery by helping new coral recruits to establish (Rogers 1993; Beeden et al. 2015).

Our study did not detect major changes to fish community composition in response to cyclone Winston. One reason for this could be the patchiness of damage to coral communities even at reefs which suffered significant losses of live coral cover and structural complexity. This patchiness leaves areas of undisturbed reef as refuge for fish post-cyclone that is critical to sustaining fish populations because live coral cover and structural complexity are often primary drivers in fish assemblage structure (Emslie et al. 2014; Darling et al. 2017; Richardson et al. 2017). Whereby, declines in complexity can cause major subsequent decreases in the abundance of many fish species (Harmelin-Vivien 1994; Syms and Jones 2000). When exposed to high wave energy, fish rarely suffer direct mortality, rather exhibiting behavioural changes including lack of schooling, benthic fish staying away from substrata, or movement to deeper or unimpacted areas (Tribble et al. 1982). Further, a number of fish species we observed are known to be habitat generalists (Pratchett et al. 2006), with the ability to move to take refuge in less impacted coral colonies or reefs (Tribble et al. 1982; Walsh 1983; Letourneur et al. 1993). Adding to this is the fact that fish such as schooling zooplanktivorous pomacentrids naturally fluctuate significantly in abundance over time (Lassig

1983; Munoz 2017).

As a group, obligate corallivore fish were the most impacted by cyclone Winston, likely due to their strong affiliation with live corals. Obligate corallivores are heavily reliant on live coral polyps for food, which predominantly make up their diet (Harmelin-Vivien and Bouchon-Navaro 1983). Such declines are common after significant live coral damage from large scale disturbances such as bleaching, crown-of-thorns starfish outbreaks, and cyclones (Munday 2004; Pratchett et al. 2006; Ceccarelli et al. 2016). There is little evidence to suggest that a decline in corallivores will result in trophic cascades or collapses in other fish groups after such events (Ceccarelli et al. 2016; Cheal et al. 2017). However, future assessment of reefs should monitor recovery and any delayed impacts to fish assemblages which may be driven by the substantial habitat loss or reduction in this functional group of fishes.

Cyclones can initiate extensive macroscopic algal blooms. We observed increases in benthic filamentous algae at several sites after cyclone Winston, as per previous studies (Harmelin-Vivien 1994; Naim et al. 1996). In the Caribbean, the similar algae blooms after large disturbances have persisted due to overfishing of herbivorous fishes, and as a result the ecosystem has shifted from an *Acropora* coral-dominated state to an algal-dominated system (Hughes 1994). The impact of such algal increases on fish assemblages has been mixed, showing large shifts in some studies (Wantiez et al. 2006; Friedlander and Beets 2008), but no changes in others (Bouchon et al. 1994; Naim et al. 1996). Herbivorous fish abundance increased after cyclone Winston, especially in Acanthuridae species such as *C. striatus* (feeding on detritus associated with turf algae). The overall fish abundance was also observed at higher levels *in situ* during 2016 surveys, two months after cyclone Winston (J. Goetze pers. comm.) indicating a positive cyclone impact. Conversely, *C. spilurus* was lower in abundance indicating a negative impact of the cyclone. Herbivorous fish in the family Acanthuridae and Scaridae are highly mobile and form schools, and unnatural schooling behaviour (large compact schools of juveniles and small unstable schools) in scarids has been observed after cyclones (Woodley et al. 1981; Wantiez et al. 2006). It is possible the abundance increases in herbivores observed here were partially explained by fish schooling whilst feeding on benthic filamentous algae blooms (Wantiez et al. 2006; Emslie et al. 2008).

Stereo-video techniques are typically used to collect data on changes in fish assemblages. However, this technique can also be used to assess composition in the underlying benthos and is a standard assessment approach in deep-water benthic surveys (Shortis et al. 2008; Williams et al. 2015). We used stereo-DOVs to quantify changes in habitat instead of the traditional downward facing methods. A previous study by Bennett et al. (2016) indicated that data from forward facing stereo-DOVs is comparable with data collected from the traditional method but can provide greater representation for structural complexity and estimates in cover of vertically growing species such as branching corals and canopy algae. Given the benthic data in this research was identified at higher taxonomic levels on survey sites containing structurally complex substrate and high proportions of branching coral cover suited the stereo-DOV technique. As such this technique can provide a useful tool to collect additional benthic data to capture habitat change during stereo-video surveys and monitoring for fish and other fauna.

Cyclone Winston had a significant impact on the coral reef communities near Fiji. The magnitude of the impact differed over a range of spatial scales as seen elsewhere for past events (Harmelin-Vivien 1994; Beeden et al. 2015; Ceccarelli et al. 2016). We found that the modelling of wave exposure, height and energy explained the variation and damage to reef habitat better than proximity to the cyclone path, providing a useful tool to predict the spatial distribution of cyclone damage. Wedemonstrate that the damage that was observed in this study to coral habitats was not associated with significant changes to the fish assemblage. Under a warming climate, researchers predict the likelihood that cyclones, which reach maximum intensity will increase, but are much less certain how the frequency, size and spatial distribution of cyclones will change around the world (Knutson et al. 2019). Preliminary work suggests that changes in intensity alone may shorten return intervals between damaging storms for many of the world's coral reef ecosystems (Puotinen et al. 2020), but much work remains to be done.

Many coral reefs in Fiji have remained relatively stable and shown fast recovery (5-10yrs) in coral cover after disturbance events such as bleaching or crown-of-thorns starfish outbreaks (Mangubhai et al. 2019), in comparison to reefs elsewhere 10-100yrs (Baker et al. 2008; De'ath et al. 2012). Whereas coral reefs usually take between 20-50yrs to fully recover from a severe cyclone disturbance (Harmelin-Vivien 1994). The remote nature (generally lower levels of anthropogenic impacts) and relatively quick recovery from historic disturbances (Mangubhai et al. 2019) suggests coral reefs in Fiji have a strong recovery potential to future large disturbances. Surveys in 2020 from Kubulau and other areas of Fiji which suffered large coral cover losses from cyclone Winston have shown promising signs of recovery, with high cover of *Acropora* species on previously damaged reefs (Wildlife Conservation Society, unpublished data).

How coral reefs will respond to the changing "behaviour" and intensity of cyclones combined with other anthropogenic stressors such as increasing sea surface temperatures and declining water quality remains uncertain. For example, recent modelling of a combination of cyclones and coral bleaching on the northern Great Barrier Reef predicted changes to the balance between hard coral, soft coral and algae in coral communities in response to shortening return intervals (Vercelloni et al. 2020). Such changes could have profound impacts for the ability of live corals to sustain coral reefs as hard coral dominated, and to continue to provide the ecosystem services upon, which much of humanity depends. With coastal communities in many parts of the world dependent on marine resources for an income and subsistence it is important that more research is undertaken to fully understand the potential impacts allowing governments in vulnerable countries to develop adaptive management and mitigation strategies.

3.6 Acknowledgements

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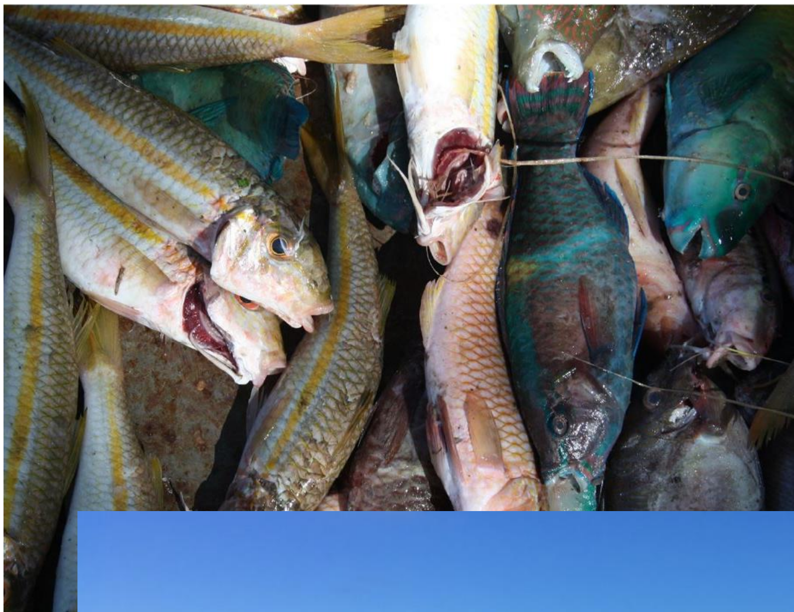

Chapter 4

General Discussion

Photo 1 & 3: S. Mangubhai/WCS
Photo 2: B. Price

4.1 Thesis Summary

The overarching motivations for this research were to understand how cyclones impact the ecology of a coral reef ecosystem and the social vulnerability of human coastal communities that live beside and depend upon them. I assessed the relationships of Fijian coastal communities to ocean resources and documented the impacts caused by cyclone Winston on these relationships and coral reef ecosystems. I used before and after social and ecological surveys to compare the ecological and socioeconomic impacts caused by cyclone Winston in Fiji. I found that cyclone Winston had a negative impact upon the livelihoods and economic wellbeing of the Fijian coastal communities. I also believe that these coastal communities are vulnerable to future cyclone events due to their dependence on natural resources, which reflects the ecological impacts on the coral reefs and reef structures. However, cyclone Winston did not have a significantly negative effect on fish assemblages or the community perception of the health of fish stocks.

In chapter 2, I assessed how communities used fish (e.g., to consume or sell), what their perceptions were on the status of fish stocks and hypothetical scenarios around fish declines and management strategies, generally and in relation to cyclone Winston (Fig. 4.2). This indicated that the communities surveyed utilised fish regularly for their daily subsistence needs, but also for income. Catches of fish at Kubulau did not appear to be impacted by cyclone Winston and that respondents perceived that fish stocks were increasing (Fig. 4.2). This has important insights into how Fijians might be impacted by future cyclones based on their high sensitivity to ocean degradation because of their dependence on natural resources. Given their reliance on fish, this raised further questions regarding the ecological impact on coral reefs and fish assemblages as a result of cyclone Winston (Fig. 4.2).

In chapter 3 I assessed cyclone Winston's impact on coral reefs and the associated fish assemblages (Fig. 4.2). Although some reefs were severely impacted, few cyclone related impacts were observed in the fish assemblage as a whole, in either functional groups or to most individual species. However, I did observe some declines in strongly associated obligate corallivore species (Fig. 4.2). Given the dependency of human coastal communities on fish, it is positive that the ecological impacts on fish assemblages from the cyclone were minimal. These minimal declines and impacts are also reflected in the fish catch data. Studying such ecological impacts is important in determining the ecological vulnerability of coral reef resources which strongly influences how sensitive and vulnerable Fijian communities are to future cyclone impacts (Fig 4.1). Ecological and socioeconomic systems are strongly linked being codependent on each other (Fig. 4.1; Marshall et al. 2009). Resource dependency (sensitivity) is a key determinant to calculating socioeconomic vulnerability (Fig. 4.1), with the results of chapter 2 indicating that respondents in Kubulau were most at risk to future disturbances. However, this can be deceiving given the absence of data on fishing catches and other, non-marine resource-dependent livelihoods, and the implemented government disaster relief in Levuka. The cyclone did cause significant damage to coral reef ecosystems, infrastructure, fishing equipment and the environment (Chapter 2, 3; Chaston Radway et al. 2016), but with a lack of catch data in Levuka impacts on fisheries cannot be quantified or compared to those observed in Kubulau. Likewise, the absence of data on the magnitude of ocean dependence among respondents (i.e., how much fish is consumed relative to other protein sources and how much income fishing provides relative to other income sources) limits the ability to draw direct conclusions on the level of sensitivity and adaptive capacity within communities to future ocean degradation.

A key component of determining social vulnerability to future cyclone disturbances is a coastal community's adaptive capacity (Fig. 4.1). The capacity to adapt from a given impact can be determined through mitigative responses (preparation, diversity of income and food), but also based on people's perceptions before and after a disturbance. Respondents perceived fish stocks were increasing after cyclone Winston, however this did not reflect the changes observed in ecological surveys (Chapter 3). This could be because a number of fish species which were preferred by respondents and influence their perceptions of fish stocks are large carnivorous (lethrinids and serranids) and pelagic species, which are not documented well/accurately on stereo-DOVs (Watson and Harvey 2007; Lindfield et al. 2014; Goetze et al. 2015). Opening of a Periodically Harvested Closure (PHCs) after cyclone Winston may have helped to compensate for destruction of other food sources (Crops, including taro, cassava, yam, banana and plantain),

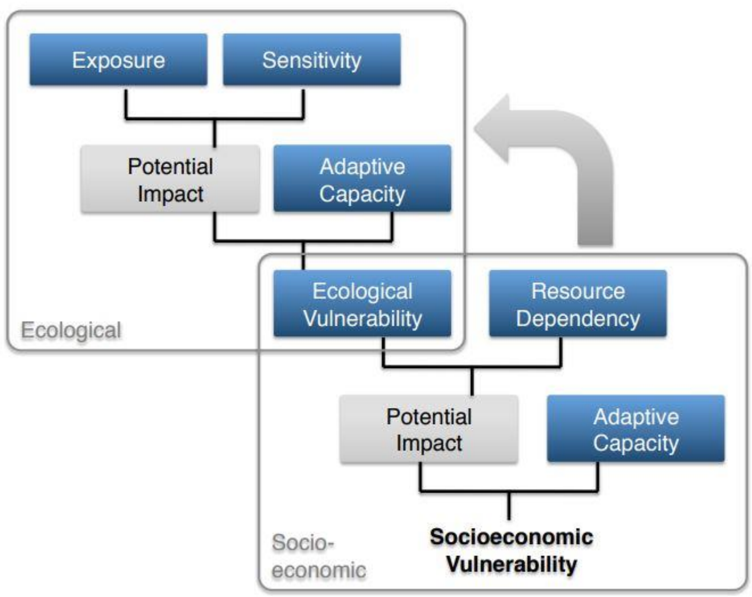

Fig 4. 1 A model showing the codependency and links between ecological and social systems used to assess vulnerability. Taken from Marshall et al. (2009)

but also may have influenced perceptions that fish stocks were increasing if large successful harvests occurred. However, surveys by Chaston Radway et al. (2016) directly after the cyclone indicated that communities were largely against opening PHCs for food or income. Variable perceptions of marine resources can also stem from decreasing use of the marine environment (reduced fishing, diving and consumption of fish) which has been observed in other parts of Fiji (Turner et al. 2007). Consequently, this can limit communities' awareness and perceptions on the health of an ecosystem and the impacts caused by natural disturbances such as cyclones (Turner et al. 2007), which could explain the variable and lack of response to perception-based reef health questions in Levuka particularly. However, despite the damage caused by cyclone Winston the respondent's perceptions on fish stock assessments, actions to hypothetical fish declines and ability to change livelihoods were not altered after cyclone Winston.

There was some adaptive capacity shown in response to a hypothetical decline in fish stocks, however this was limited to changing fishing locations and gear, which could be ineffective in situations (mass coral bleaching or crown of thorns starfish events) where entire coral reef ecosystems are impacted. Such perceptions and actions could be a method of coping to environmental change (Ferse et al.2014) or suggest that human communities in Fiji may have a low level of adaptive capacity, making them vulnerable to future disturbances. However, Indigenous Fijian communities have been shown to implement risk-sharing networks and have long practical oral histories on enduring cyclone disturbances (Brown et al. 2018) which exhibits adaptive capacity to assist with recovery. In studies on the Great Barrier Reef (GBR) it has been shown that human communities, even those exposed to a high potential risk associated with climate warming related disturbances, are not necessarily vulnerable to these if they can mitigate/improve their adaptive capacity (Marshall et al. 2013).

The high sensitivity suggests that communities in Kubulau and Levuka and possibly many other coastal communities around Fiji may have a high vulnerability to future coral reef degradation.

Scientists have predicted increases in the number of cyclones which reach maximum intensity, which could compound other degradation occurring in coral reef ecosystems (Cheal et al. 2017; Knutson et al. 2019). The cumulative impacts of these cyclone disturbances and other anthropogenic impacts (bleaching, overfishing, COTS) have caused ecosystem collapses in the Caribbean and major coral declines in the GBR (Hughes 1994; De'ath et al. 2012). Studies in these regions have shown the negative impacts that this can cause to ecosystem health which could have subsequent flow-on impacts on tourism and fisheries. Coastal communities throughout the tropical Pacific have a strong reliance on fish for livelihoods and subsistence and have commonly occurring cyclones and bleaching events (Pratchett et al. 2011; Mangubhai et al. 2019) making these communities sensitive and vulnerable to environmental degradation. Long historical records regarding impacts and recovery from cyclones passed down orally may assist Fijian communities to increase adaptive capacity to future cyclone events, although with changing marine environments this cannot be guaranteed. There are gaps in the knowledge surrounding resource use, infrastructure and income and food sources which will be important to be filled to more accurately determine resource dependency and adaptive capacity assist (Fig. 4.1). As such it is important that further research be implemented which investigates human community and coral reef recovery from cyclones to develop mitigation/adaptation strategies to ensure communities and their vulnerable livelihoods can be sustained in future (Fig. 4.2).

4.2 Research Limitations

Cyclone impacts are a difficult disturbance to study given the unpredictability in when and their magnitude. Consequently, the majority of cyclone impact studies have resulted by coincidence from baseline or long-term datasets. A big limitation and challenge with this research were the use of previously collected data, the availability and suitability of this data. All of the data in this research, with the exception of the 2018 ecological surveys, were collected as part of other research and monitoring with alternative research questions in mind. As a result, the experimental design was not optimised for a cyclone impact study. The limitations associated with the pre-collected data and other limitations are discussed in detail in the following sections (Fig. 4.2).

4.2.1 Socioeconomic suitability and availability of data

A large limitation in the data was the availability and replication, especially in the socio-economic surveys. Surveys conducted in 2015 had an alternate set of questions compared to those in 2016. Many of the questions were almost identical allowing for comparisons between years, however, some questions had slightly different wording or answer selections which lead to varying answers. This caused me to categorise data with similar responses together in order to compare surveys between each year. Furthering this, data collected in different survey years in each district had inconsistencies in the metrics used for fish data. In Kubulau, data was comparable with multiple catches being reported in either kilograms or whole fish in both years, however in Levuka all catches in 2015 were reported in Kgs and 2016 in whole fish. With no comparable units in catches for Levuka this data had to be omitted.

The socio-economic surveys were further limited through collection of data in only two villages in each District (Kubulau and Levuka). This was mainly due to these villages being the only suitable communities linked to the ecological sites in which there was previously collected data.

Population sample size can vary significantly with small populations residing in many of the communities, which is further reduced if a large proportion of the village does not want to partake in surveys or answer certain questions. This was the case in some of our surveys, where a number of respondents did not answer or were unsure for certain questions. A population of people can also show large variations in preferences and responses given differing cultural, religious and social influences. For example, one village might be heavily reliant on ocean resources and fish which makes up 90% of their diet, whereas the neighboring village depends on agriculture.

Ultimately, having a robust baseline dataset with questions that are consistent between years combined with greater community replication could have accounted for variability and non-responses leading to stronger patterns particularly in hypothetical perceptions about fish stocks and resource management.

4.2.2 Ecological spatial and temporal data limitations

It has been reported in other studies that fish move to deeper water prior to a cyclone by detecting atmospheric pressure changes and after a cyclone to deeper or undamaged reefs to seek refuge from the storm and its damages (Tribble et al. 1982; Munks et al. 2015). My study detected variable changes in fish communities with inconsistent increases of some species at particular sites. Data collected prior to the cyclone was generated from surveys on shallow fore and back reefs ecosystems. Consequently, it did not provide the opportunity to quantify any possible movement or changes in fish abundance as a result of movement between habitats and areas of varying damage. Having greater spatial replication and sites at differing water depths and habitat types (fore reefs, reef slope, reef crest, back reefs) may have allowed the quantification of some of this variability and detection of trends in fish assemblages. In the ecological surveys there was lots of temporal variability in the fish assemblages, which resulted in few cyclone related impacts being detected. With the inclusion of further temporal data, the separation of cyclone impacts from natural variation may have been possible.

4.2.3 Ecological survey technique

Stereo diver operated video (Stereo-DOV) is becoming a commonly used survey technique due to its ability to sample shallow water fish assemblages, measure the length of fish and review identifications and abundances (Goetze et al. 2019). There are biases associated with the technique, where larger predatory species and targeted food fish are known to be wary and avoid the cameras due to diver presence and SCUBA noise (Watson and Harvey 2007; Lindfield et al. 2014). A combination of survey techniques including Stereo-DOV and BRUV (baited remote underwater video) have been shown to be more effective in determining the abundance of the entire fish assemblage (Schramm et al. 2020). The inclusion of BRUV data would have helped to give more accurate abundances of predatory species (Cappo et al. 2004; Harvey et al. 2007) and impacts caused from the cyclone, which would have strengthened the research given the strong reliance upon fish resources for community livelihoods and subsistence. BRUV footage was collected prior to the cyclone at some of the research sites as part of other studies (Goetze et al. 2011, 2015), however, did not have suitable temporal or spatial replication to be used in this research to detect cyclone impacts. Although not the ideal sampling technique for surveying habitat, stereo-DOVs have been shown to give accurate habitat identifications allowing the detection of disturbances and impact on a system (Bennett et al. 2016). The use of traditional coral survey techniques is unlikely to have changed the results in terms of overall damage to habitat, however, would have given greater power to identify habitat at lower taxonomic levels and detect changes at these levels.

4.3 Future Research

Although cyclone impacts on coral reefs are reasonably well understood, research on the impacts on fish is variable and contradictory. As shown in my research there were limited cyclone related impacts on fish assemblages (Fig. 4.2). Research documenting the impacts of cyclone disturbances on fish assemblage are limited globally (Harmelin-Vivien 1994). Considering the value of fish for tourism, recreation, income and most importantly as food, this reiterates the need and importance of research into how fish are impacted by cyclones and subsequent spatially variable damage to habitat. Further research into how fish behave directly before, during and after a cyclone through the use of live camera feeds, telemetry tracking and software determining fish movement trajectories (Bolden 2001; Spampinato et al. 2014; Castelo et al. 2020) may help to quantify cyclone associated impacts and distinguish these from the diverging fish responses currently known. These factors can influence where fish may move or what they may do to minimize impacts after a cyclone which could help in focusing sampling efforts on these areas of refuge or damage allowing impacts in fish assemblages to be quantified and subsequent effects to fisheries calculated. Likewise, modelling of waves created by the cyclone could help in future research where resources (funding and time) can be focused on determining reef ecosystem impacts in areas of high population density, in threatened reef ecosystems, heavily used fishing grounds or where the most severe cyclone damage occurred.

Various types of marine spatial closures including MPAs are used extensively in Fiji as a method to increase fish stocks and conservation of numerous marine organisms and coral reef habitat. These spatial closures may help with resilience of coral reef ecosystems and help to increase recovery after cyclone impacts. Similar spatial closures have been observed to influence recovery after other disturbances (e.g bleaching) in the GBR (Hughes et al. 2007; Mellin et al. 2016). Similarly, the preservation of herbivores after severe habitat destruction has also been observed in assisting recovery of coral reefs after a disturbance (Hughes et al. 2007). Building upon this knowledge could help in exploring future ways to mitigate damage improving ecological adaptive capacity after a cyclone.

Cyclone impact studies to date have primarily involved underwater visual census type methods to assess damage and change. These methods have long been used for assessing the abundance, diversity and size of reef fishes (English et al. 1997), but their reliability and repeatability have been questioned (Harvey et al. 2001, 2004; Watson et al. 2010; Holmes et al. 2013). Combining Stereo-DOV and socio-economic surveys in conjunction with wave modelling and stereo-BRUVs will help to expand on the current knowledge base of cyclone impacts which currently exist creating a more robust and comprehensive knowledgebase. Using a suite of complementary approaches will be critical in determining the flow-on effects of cyclone impacts on coral reef ecosystems and fish assemblages and on livelihoods and the subsistence needs of many coastal communities worldwide.

Building a greater understanding of all these ecological and social impacts, and the interactions between disturbances, will help to create a stronger understanding when undertaking planning for the mitigation of and recovery from cyclones impacts. Socio-ecological systems are dynamic; Fijian communities rely on the goods and services provided by coral reef ecosystems, however by using these resources the communities can directly affect the health and fish stocks within these ecosystems. These relationships will be important to understand given the predicted increases in maximum intensity cyclones and possible changes in cyclone behaviour (frequency, size, timing and location), which could increase the number of Fijian communities affected by future cyclones. As such, establishing alternative or supplementary sources for subsistence and livelihoods in addition to coral reef-related resources as well as determining vulnerability and other missing socio-ecological components will be critical for adaptation of Fijian communities and preservation of coral reef ecosystems in future (Fig. 4.2).

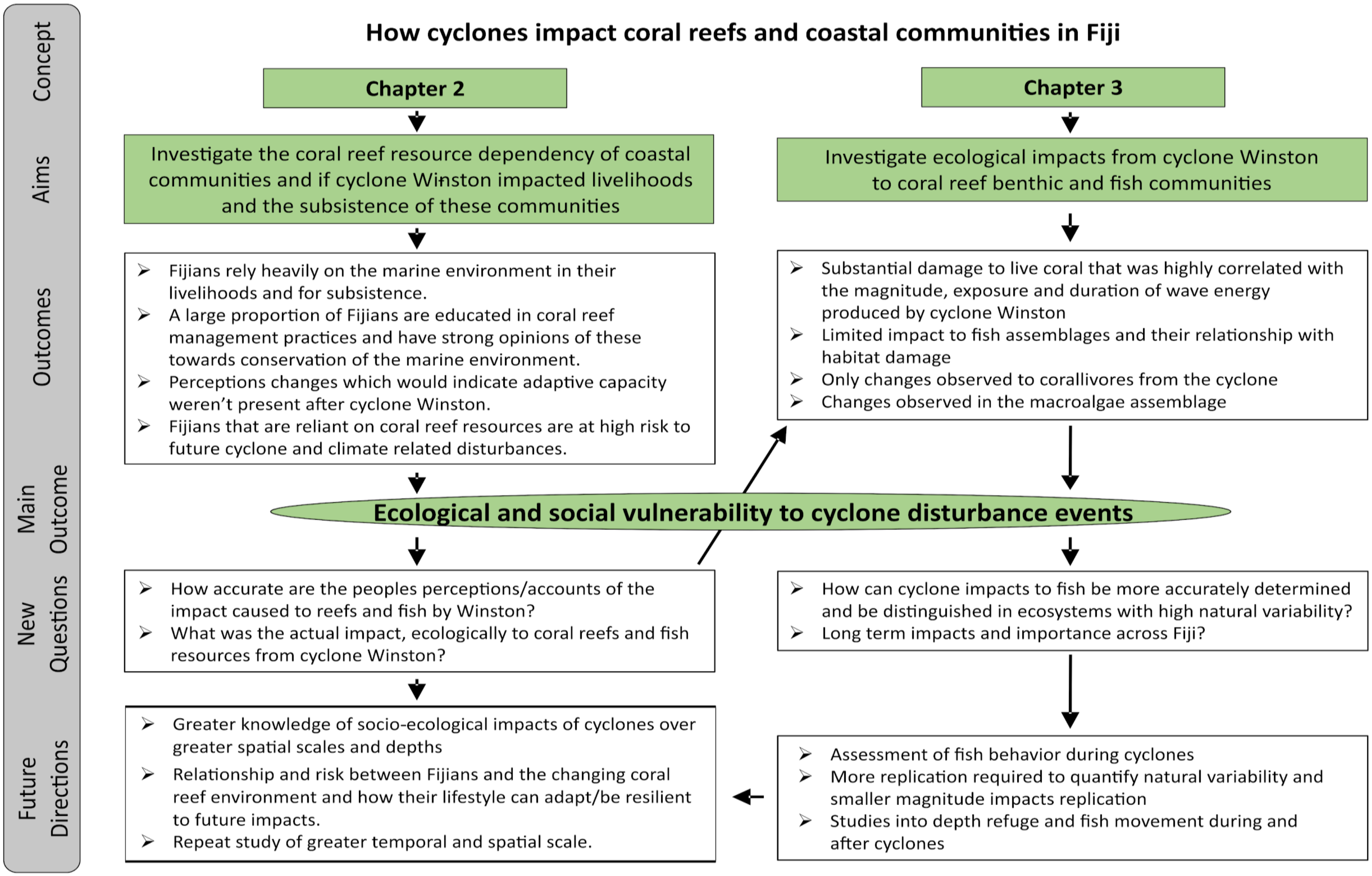

Fig 4. 2 Flow diagram describing the outcomes of the thesis highlighting future questions and directions in researching cyclone impacts.

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Every reasonable effort has been made to acknowledge the owners of copyright material. I would be pleased to hear from any copyright owner who has been omitted or incorrectly acknowledged.

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Appendix

1.1 Copyright Statement

Chapter 2: Unpublished. Prepared for Journal Submission

To Whom It May Concern I, Brae Price, contributed to the conceptualisation of this study, analysed the data, and wrote and edited the following manuscript:

Price, B. A., Harvey, E. S., Saunders, B. J., Goetze, J. S. and Mangubhai, S. Socioeconomic assessment of ocean reliance and community fisheries in the Kubulau and Levuka districts, Fiji.

BP Brae Price

I, as a co-author, endorse that the level of contribution stated above is appropriate and correct.

Dr Ben Saunders

Prof Euan Harvey

Dr Jordan Goetze

Dr Sangeeta Mangubhai

Chapter 3: Published in the journal Coral Reefs Journal. As first author, permission is automatically granted to use this article in this thesis.

To Whom It May Concern I, Brae Price, contributed to the conceptualisation of this study and data collection, analysed the data, and wrote and edited the following manuscript:

Price, B.A., Harvey, E.S., Mangubhai, S. et al. Responses of benthic habitat and fish to severe tropical cyclone Winston in Fiji. Coral Reefs (2021).

Brae Price

I, as a co-author, endorse that the level of contribution stated above is appropriate and correct.

Dr Ben Saunders

Prof Euan Harvey

Dr Jordan Goetze

Dr Marji Puotinen

Dr Sangeeta Mangubhai

1.2 Supplemental Material -Data – Chapter 3

Wave Modelling Methods

To evaluate wave conditions during cyclone Winston at the study sites, we extracted significant wave height (Hs - average of the top one-third of wave heights) and direction in the vicinity of the study sites from the NOAA WaveWatch III global hindcast dataset (Tolman, 2009 downloaded at: http://polar.ncep.noaa.gov/waves/index2.shtml). We did this for both districts (Ovalau -17.5°S, 179°E; and Kubulau - 17°S, 179°E) at a spatial resolution of 0.5° and a temporal resolution of 1 hour for the time series January 2013 - September 2019. From these, we calculated maximum Hs during Winston as well as the duration in hours that Hs exceeded thresholds for each of 4, 5, 6, 7, 8 and 9 m. We also calculated the average Hs over the entire time series, and the percent frequency that waves approached from each of 16 compass directions during: i) cyclone Winston, where Hs >= 4m, and ii) the entire time series.

Relative wave exposure during cyclone Winston

The Wave Watch 3 data estimates wave heights over a broad area, but waves transform and decay upon interaction with shallow water obstacles like land and reefs. Thus, it is important to consider how exposed each site was to the waves Winston generated in their vicinity. We generated quantitative estimates of relative wave exposure (RWE) at each sampling site using a 'Generic model for estimating relative wave exposure' (Pepper and Puotinen 2009; Hill et al. 2010). Distances to the nearest wave blocking obstacle every 7.5 degrees around each site (fetch) were weighted by the relative frequency at which waves approached the site from each of 16 equidistant compass directions as calculated from the WaveWatch III data. These distances were then weighted by their percent frequency and summed and normalised to the maximum possible summed distances (at a site 100% exposed in all directions) to create a dimensionless index of relative wave exposure during cyclone Winston (RWE_TC) as per Underwood et al (2018, 2019). A second index was calculated to adjust for differing wave magnitude between the two groups of sites by multiplying the relative wave exposure value by the maximum modelled Hs value (RWE_times_maxHs).

We defined wave blocking obstacles based on the coastlines (Ministry of Lands & Mineral Resources, Fiji) and millenium reefs (Serge Andrefouet) GIS datasets. For the former, we assumed land completely blocked wave energy. For the latter, we assumed that the categories ‘land’ and ‘aquatic land features’ completely blocked wave energy. At low tide, very shallow reef features such as ’faro reef flat’, ‘immature reef flat’, ‘main land’, ‘pass reef flat’, ‘reef flat’ and ‘subtidal reef flat’ would dissipate considerable wave energy. However, NOAA data (NOAA 2016) indicated that the tide would have been almost at peak levels (~ 1.35 m) at the time Winston crossed near the sites. Thus, we assumed that fore reefs and back reefs would be exposed to similar magnitudes of wave energy, particularly given the large significant wave heights (up to 14.35 m for the southerly sites and 9.43 m for the northerly sites – noting that Hs provides an average of wave height of the top one-third highest waves; so maximum wave heights would be much higher than this).

Relative wave exposure over the entire time series

Typical relative wave exposure can be an important driver of coral community structure and thus vulnerability to wave damage. We thus estimated RWE over the entire time series, weighting the fetch lines by the long-term percent frequencies of waves from the 16 compass directions. In this case, it is likely that reef flat associated features would act as wave obstacles, so we used fetch lines that assumed this. We then calculated a further index to adjust for different wave magnitudes between the sites by multiplying the routine RWE value (RWE_routine) by the average Hs (RWE_times_avgHs).

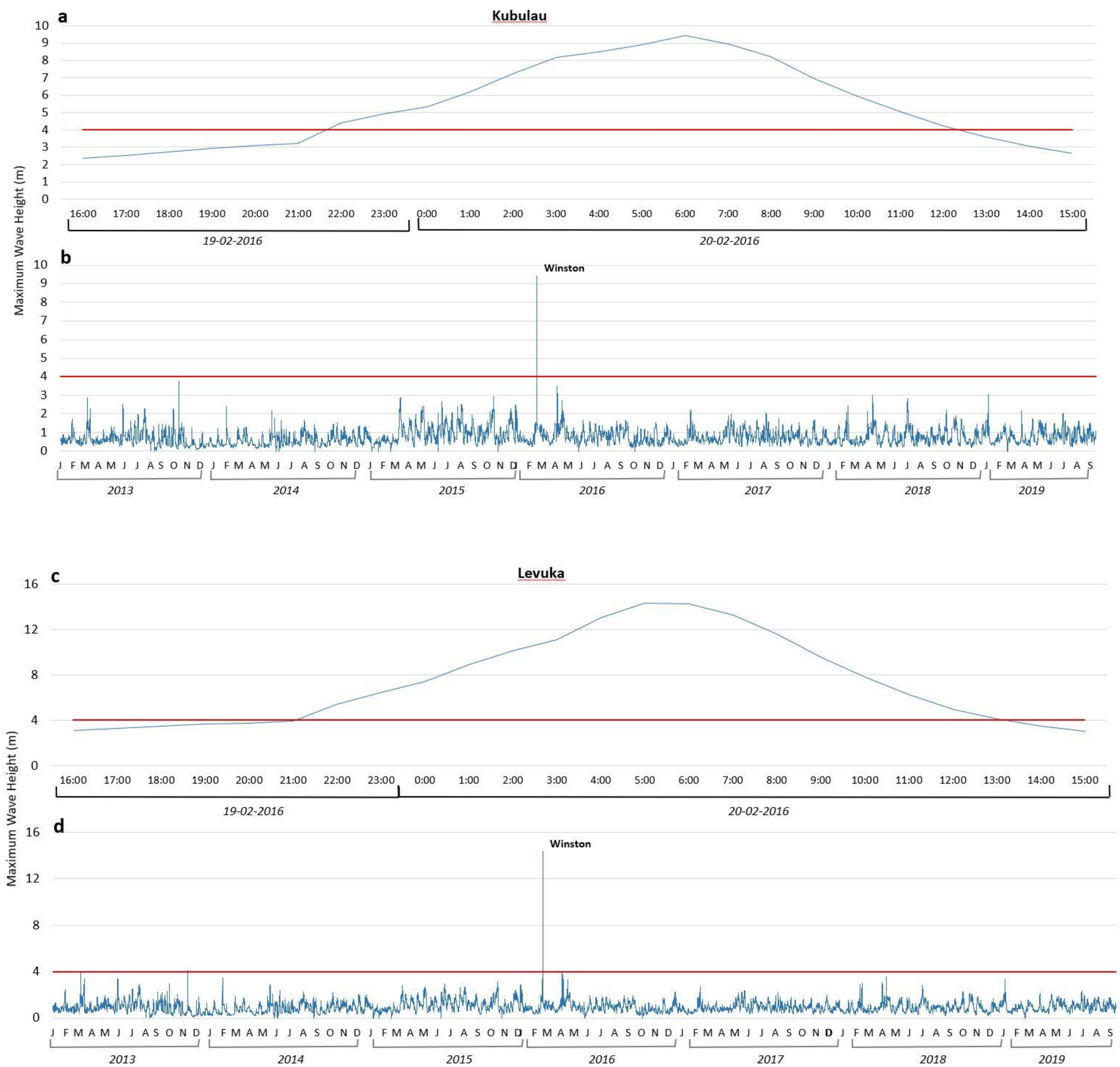

Fig. S1 Hourly sea state as indicated by significant wave height (Hs: average height of the top one-third of waves, in metres) between 2013 and 2019 in **b** Kubulau, **d** Levuka, and during the passage of cyclone Winston (1600, 19/02/2016 - 1500, 20/02/2016) at **a** Kubulau and **c** Levuka. The red line indicates an Hs threshold (≥4m) at which most vulnerable coral colonies are expected to sustain severe damage (Puotinen et al 2016).

The greatest damage from cyclone Winston could be expected to be found at those sites highly exposed during the cyclone but normally very sheltered. To identify these, we subtracted the cyclone exposure from the routine exposure. Negative values of this index mean the site was more exposed during Winston than under routine conditions. Positive values mean the site was more exposed under routine conditions than during the cyclone. Presumably the most severe damage should be found at sites with the highest negative values.

Fig. S2 Screenshot from the habitat analysis using footage from the left camera in the Stereo-DOV setup. The screenshot shows the virtual quadrat (a sixth of the video frame) with 5 randomly placed habitat identification points at 1 of the 20 equally spaced intervals along each transect.

Table S1: Categorisation of all the broad benthic, morphological and health/substrate condition variables used to classify habitat.

Broad benthic	Morphological	Health/Substrate condition
Stony corals	Branching	Bleached
Stony corals	Branching	Live
Stony corals	Branching	Damage
Stony corals	Branching	Dead
Stony corals	Digitate	Bleached
Stony corals	Digitate	Live
Stony corals	Digitate	Damage
Stony corals	Digitate	Dead
Stony corals	Encrusting	Bleached
Stony corals	Encrusting	Live
Stony corals	Encrusting	Damage
Stony corals	Encrusting	Dead
Stony corals	Foliose / plate	Bleached
Stony corals	Foliose / plate	Live
Stony corals	Foliose / plate	Damage
Stony corals	Foliose / plate	Dead
Stony corals	Massive	Bleached
Stony corals	Massive	Live
Stony corals	Massive	Damage
Stony corals	Massive	Dead
Stony corals	Sub-massive	Bleached
Stony corals	Sub-massive	Live
Stony corals	Sub-massive	Damage
Stony corals	Sub-massive	Dead
Stony corals	Tabulate	Bleached
Stony corals	Tabulate	Live
Stony corals	Tabulate	Damage
Stony corals	Tabulate	Dead
Stony corals	Bottlebrush	Bleached
Stony corals	Bottlebrush	Live
Stony corals	Bottlebrush	Damage
Stony corals	Bottlebrush	Dead
Stony corals	Columnar	Bleached
Stony corals	Columnar	Live
Stony corals	Columnar	Damage
Stony corals	Columnar	Dead
Stony corals	Branching table	Bleached
Stony corals	Branching table	Live
Stony corals	Branching table	Damage
Stony corals	Branching table	Dead
Stony corals	Corymbose	Bleached
Stony corals	Corymbose	Live

Stony corals	Corymbose	Damage
Stony corals	Corymbose	Dead
Stony corals	Staghorn	Bleached
Stony corals	Staghorn	Live
Stony corals	Staghorn	Damage
Stony corals	Staghorn	Dead
Octocoral/Black	Massive soft corals	-
Octocoral/Black	Massive soft corals	-
Octocoral/Black	Other	-
Octocoral/Black	Other	-
Macroalgae	Encrusting coralline algae	-
Macroalgae	Filamentous/turf	-
Macroalgae	Other	-
Consolidated	Rock	Benthic filamentous algae
Consolidated	Rock	Silt covering
Consolidated	Rock	No biota
Unconsolidated	Rubble	Benthic filamentous algae
Unconsolidated	Rubble	Silt covering
Unconsolidated	Rubble	No biota
Unconsolidated	Sand	Benthic filamentous algae
Unconsolidated	Sand	No biota
Open Water	-	-
Unknown	-	-

Table S2: Simper analyses results indicating the species, families or functional groups which have a >5% contribution to the temporal variation at each of the sites in Kubulau and Levuka districts. SIM/SD shows how a species is consistent within transects, Contrib.% shows the contribution in percentage of a individual species, family or functional group to the Groups average similarity (Group Av. Sim.) and Cum.% is the accumulative contribution (%) of multiple fish species, family or functional group to Group Av. Sim.

	Kubulau				**Levuka**			
	Site 1							
Assemblage	Group Av. Sim.	41.54			Group Av. Sim.	38.4		
		Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
	Pomacentrus callainus	1.58	37.47	37.47	*Dascyllus reticulatus*	0.69	16.81	16.81
	Pomacentrus flavioculus	1.5	14.3	51.77	*Pomacentrus callainus*	1.24	13.06	29.87
	Ctenochaetus striatus	1.46	8.64	60.41	*Ctenochaetus striatus*	1.19	11.54	41.42
					Pomacentrus coelestis	0.44	10.71	52.13
					Chlorurus spilurus	1.02	7.19	59.32
	Site 2							

Group Av. Sim.	43.78			Group Av. Sim.	42.55		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Pomacentrus callainus	2.05	26.73	26.73	*Dascyllus aruanus*	1.21	29.11	29.11
Ctenochaetus striatus	1.04	11.23	37.96	*Dascyllus reticulatus*	0.92	18.76	47.87
Pomacentrus flavioculus	2.17	9.19	47.15				
Chrysiptera talboti	1.08	5.83	52.98				
Chlorurus spilurus	1.12	5.77	58.75				

Site 3

Group Av. Sim.	51.02			Group Av. Sim.	38.03		
Species	Sim/SD	Contrib.%	Cum.%	Species	Sim/SD	Contrib.%	Cum.%
Chromis ternatensis	1.29	23.79	23.79	*Dascyllus reticulatus*	1.27	31.93	31.93
Pomacentrus maafu	1.69	21.84	45.63	*Pomacentrus callainus*	1.08	11.21	43.14
Amblyglyphidodon orbicularis	2.34	8.61	54.24	*Chromis viridis*	0.51	8.86	52
Pomacentrus nigromarginatus	2.13	5.61	59.85	*Dascyllus aruanus*	0.75	6.8	58.8
				Chromis ternatensis	0.86	6.6	65.4

Site 4

Group Av. Sim.	30.4			Group Av. Sim.	38.24		
Species	Sim/SD	Contrib.%	Cum.%	Species	Sim/SD	Contrib.%	Cum.%
Pomacentrus moluccensis	1.01	36.66	36.66	*Chromis viridis*	0.67	13.79	13.79
Chromis ternatensis	0.31	11.24	47.9	*Pomacentrus coelestis*	0.35	13.14	26.93
Scarus schlegeli	0.75	6.14	54.04	*Chromis ternatensis*	0.4	9.27	36.2
Dascyllus aruanus	0.59	5.41	59.44	*Dascyllus aruanus*	0.6	8.04	44.24
Amblyglyphidodon orbicularis	0.69	5.36	64.8	*Ctenochaetus striatus*	1.14	6.12	50.36
				Dascyllus reticulatus	0.74	5.67	56.03
				Chlorurus sordidus	0.87	5.55	61.58

Family

Site 1

Group Av. Sim.	60.85			Group Av. Sim.	70.22		
Family	Sim/SD	Contrib.%	Cum.%	Family	Sim/SD	Contrib.%	Cum.%
Pomacentridae	2.2	60.23	60.23	Pomacentridae	3.75	68.59	68.59
Acanthuridae	1.64	12.42	72.65	Acanthuridae	0.98	10.12	78.7

Site 2

Group Av. Sim.	65.02			Group Av. Sim.	62.13		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Pomacentridae	2.37	61.2	61.2	Pomacentridae	2.35	66.9	66.9
Acanthuridae	1.37	13.37	74.57	Labridae	2.14	9.99	76.89

Site 3							
Group Av. Sim.	70.21			Group Av. Sim.	66.69		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Pomacentridae	4.28	77.62	77.62	Pomacentridae	2.78	79.76	79.76
Site 4							
Group Av. Sim. 48.62				Group Av. Sim. 64.05			
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Pomacentridae	1.95	63.16	63.16	Pomacentridae	3.03	69.7	69.7
Scaridae	1	14.19	77.35	Labridae	1.81	8.57	78.27
Functional Group							
Site 1							
Group Av. Sim.	64.11			Group Av. Sim.	65.81		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Algae/invertebrate consumer	2.16	42.67	42.67	Zooplanktivore	1.93	39.94	39.94
Herbivore	1.8	24.85	67.52	Herbivore	1.75	22.7	62.64
Zooplanktivore	1.34	15.43	82.95	Algae/invertebrate consumer	1.9	20.78	83.42
Site 2							
Group Av. Sim.	66.33			Group Av. Sim.	64.52		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Algae/invertebrate consumer	2.72	32.89	32.89	Zooplanktivore	2.27	52.15	52.15
Zooplanktivore	1.29	25.48	58.37	Herbivore	1.71	17.12	69.26
Herbivore	1.52	24.62	83	Invertebrate carnivore	3.27	16.2	85.47
Site 3							
Group Av. Sim.	72.88			Group Av. Sim.	67.91		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Zooplanktivore	3.17	49.95	49.95	Zooplanktivore	2.41	67.53	67.53
Algae/invertebrate consumer	2.97	30.67	80.62	Algae/invertebrate consumer	1.33	11.64	79.17
Site 4							
Group Av. Sim.	48.25			Group Av. Sim.	63.62		
	Sim/SD	Contrib.%	Cum.%		Sim/SD	Contrib.%	Cum.%
Algae/invertebrate consumer	1.41	32.39	32.39	Zooplanktivore	1.74	55.62	55.62
Zooplanktivore	0.93	25.72	58.11	Herbivore	1.49	16.26	71.89
Herbivore	1.2	22.56	80.68				

Table S3: PERMANOVA Results examining the multivariate habitat composition at broad benthic, morphological and health/substrate condition classification levels and fish assemblages at family, functional group and species classification levels in response to factors Location (Lo), Year (Ye) and Site (Si).

Habitat - (square root transformation)					**Fish - (fourth root transformation)**			
	Broad benthic				**Family**			
Source	*df*	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	688.28	98.037	**<0.001**	1	9173.8	26.002	**<0.001**
Si	3	113.27	16.134	**<0.001**	3	1567.1	4.4417	**<0.001**
Ye(Lo)	6	36.631	5.2177	**<0.001**	6	1633.8	4.631	**<0.001**
LoxSi	3	77.787	11.08	**<0.001**	3	2861	8.1093	**<0.001**
Ye(Lo)xSi	18	17.037	2.4267	**<0.001**	18	633.46	1.7955	**<0.001**
Res	159	7.0206			159	352.81		
Total	190				190			
	Morphological				**Functional group**			
Source	*df*	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	45206	79.054	**<0.001**	1	8165.1	45.81	**<0.001**
Si	3	6655.7	11.639	**<0.001**	3	1121.3	6.2912	**<0.001**
Ye(Lo)	6	3221.1	5.6328	**<0.001**	6	913.08	5.1228	**<0.001**
LoxSi	3	6651.8	11.632	**<0.001**	3	1587.1	8.9041	**<0.001**
Ye(Lo)xSi	18	1450.6	2.5367	**<0.001**	18	345.75	1.9398	**<0.001**
Res	159	571.84			159	178.24		
Total	190				190			
	Benthic condition				**Species**			
Source	*df*	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	318.82	79.727	**<0.001**	1	67299	51.977	**<0.001**
Si	3	46.721	11.684	**<0.001**	3	11284	8.7147	**<0.001**
Ye(Lo)	6	31.628	7.9092	**<0.001**	6	5517	4.261	**<0.001**
LoxSi	3	46.501	11.629	**<0.001**	3	12026	9.2878	**<0.001**
Ye(Lo)xSi	18	18.436	4.6103	**<0.001**	18	2616	2.0205	**<0.001**
Res	159	3.9989			159	1294.8		
Total	190				190			

Bold value indicates a significant P > 0.05

Table S4: PERMANOVA Results examining the univariate habitat and fish variables in response to factors Location (Lo), Year (Ye) and Site (Si) at broad benthic, morphological and health/substrate condition classification levels in habitat, and family, functional group and species classification levels in fish.

Habitat

Broad benthic

Source	Macroalgae				Octocoral			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	44.237	1.5841	0.2181	1	1530.4	137.27	**<0.001**
Si	3	192.47	6.892	**<0.001**	3	456.6	40.957	**<0.001**
Ye(Lo)	6	185.59	6.6459	**<0.001**	6	10.628	0.95336	0.4617
LoxSi	3	223.65	8.0087	**<0.001**	3	412.54	37.005	**<0.001**
Ye(Lo)xSi	18	40.543	1.4518	0.1073	18	11.791	1.0577	0.404
Residual	159	27.926			159	11.148		
Total	190				190			

Source	Sponge				Structural complexity			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	16.855	37.465	**<0.001**	1	62.23	211.24	**<0.001**
Si	3	1.1914	2.6482	0.0518	3	0.66389	2.2536	0.0847
Ye(Lo)	6	0.7566	1.6818	0.1199	6	4.1704	14.157	**<0.001**
LoxSi	3	0.87913	1.9541	0.1242	3	2.9976	10.175	**<0.001**
Ye(Lo)xSi	18	0.55263	1.2284	0.2442	18	0.91738	3.1141	**<0.001**
Residual	159	0.44988			159	0.29459		
Total	190				190			

Morphological

Source	Branching coral				Corymbose coral			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	950.5	75.27	**<0.001**	1	1274.9	55.783	**<0.001**
Si	3	437.02	34.607	**<0.001**	3	329.97	14.438	**<0.001**
Ye(Lo)	6	21.511	1.7034	0.1268	6	256.43	11.22	**<0.001**
LoxSi	3	324.62	25.707	**<0.001**	3	546.78	23.925	**<0.001**
Ye(Lo)xSi	18	26.584	2.1052	**0.0073**	18	103.5	4.5289	**<0.001**
Residual	159	12.628			159	22.854		
Total	190				190			

Source	Staghorn coral				Bottlebrush coral			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*

Source	df	MS	Pseudo-F	P(perm)	df	MS	Pseudo-F	P(perm)
Lo	1	1.5639	0.12084	0.7355	1	115.09	7.5158	**0.0059**
Si	3	220.25	17.018	**<0.001**	3	152.85	9.982	**<0.001**
Ye(Lo)	6	67.022	5.1787	**<0.001**	6	19.331	1.2624	0.2755
LoxSi	3	109.16	8.4347	**<0.001**	3	125.53	8.1978	**<0.001**
Ye(Lo)xSi	18	47.628	3.6802	**<0.001**	18	29.935	1.9549	**0.0173**
Residual	159	12.942			159	15.313		
Total	190				190			

Source	**Massive coral**				**Foliose/plate coral**			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	611.45	58.465	**<0.001**	1	83.701	18.942	**<0.001**
Si	3	11.254	1.0761	0.3654	3	18.449	4.1752	**0.0044**
Ye(Lo)	6	3.7648	0.35998	0.912	6	4.1902	0.94827	0.4686
LoxSi	3	20.58	1.9678	0.12	3	7.6237	1.7253	0.1606
Ye(Lo)xSi	18	7.7823	0.74412	0.7709	18	3.6628	0.8289	0.6824
Residual	159	10.458			159	4.4188		
Total	190				190			

Source	**Massive octocoral**				**Turf algae**			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	1561.5	137.55	**<0.001**	1	18.883	3.1553	0.0734
Si	3	407.49	35.895	**<0.001**	3	5.7483	0.96054	0.43
Ye(Lo)	6	12.294	1.083	0.3752	6	10.2	1.7045	0.1085
LoxSi	3	430.77	37.946	**<0.001**	3	15.103	2.5237	0.0516
Ye(Lo)xSi	18	8.4325	0.7428	0.7723	18	8.0308	1.3419	0.1376
Residual	159	11.352			159	5.9845		
Total	190				190			

Source	**Rubble**				**Encrusting coralline algae**			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	17266	81.903	**<0.001**	1	116.77	28.147	**<0.001**
Si	3	990.15	4.6969	**0.0037**	3	20.151	4.8573	**0.0033**
Ye(Lo)	6	1610.6	7.6398	**<0.001**	6	59.099	14.245	**<0.001**
LoxSi	3	1489.1	7.0637	**<0.001**	3	17.616	4.2462	**0.0059**
Ye(Lo)xSi	18	516.13	2.4483	**0.0014**	18	9.4208	2.2708	**0.0033**
Residual	159	210.81			159	4.1486		
Total	190				190			

Benthic condition

Source	**Dead stony coral**	**Live coral**

Source	df	MS	Pseudo-F	P(perm)	df	MS	Pseudo-F	P(perm)
Lo	1	12.249	2.7944	0.0959	1	5929.4	67.818	**<0.001**
Si	3	75.594	17.245	**<0.001**	3	2587.1	29.59	**<0.001**
Ye(Lo)	6	11.446	2.6112	**0.0201**	6	1187.3	13.579	**<0.001**
LoxSi	3	35.966	8.2049	**<0.001**	3	889.52	10.174	**<0.001**
Ye(Lo)xSi	18	19.11	4.3596	**<0.001**	18	463.99	5.3069	**<0.001**
Residual	159	4.3835			159	87.432		
Total	190				190			

Source	**Benthic filamentous algae**			
	df	MS	*Pseudo-F*	*P(perm)*
Lo	1	1329.7	37.125	**<0.001**
Si	3	137.95	3.8517	**0.0087**
Ye(Lo)	6	281.87	7.8698	**<0.001**
LoxSi	3	243.47	6.7978	**<0.001**
Ye(Lo)xSi	18	164.53	4.5937	**<0.001**
Residual	159	35.817		
Total	190			

Fish

Family

Source	**Acanthuridae**				**Pomacentridae**			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	2223.3	20.602	**<0.001**	1	3.51E+05	40.581	**<0.001**
Si	3	544.08	5.0417	**0.0021**	3	1.52E+05	17.629	**<0.001**
Ye(Lo)	6	1598.8	14.816	**<0.001**	6	62273	7.2019	**<0.001**
LoxSi	3	2464.3	22.835	**<0.001**	3	79376	9.1798	**<0.001**
Ye(Lo)xSi	18	365.87	3.3903	**<0.001**	18	16388	1.8953	**0.0175**
Residual	159	107.92			159	8646.8		
Total	190				190			

Source	**Labridae**				**Scaridae**			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	4643.8	32.54	**<0.001**	1	899.18	3.5719	0.0584
Si	3	1892.5	13.261	**<0.001**	3	306.56	1.2178	0.3075
Ye(Lo)	6	848.24	5.9438	**<0.001**	6	724.11	2.8765	**0.0093**
LoxSi	3	490.39	3.4363	**0.0167**	3	807.65	3.2083	**0.0197**
Ye(Lo)xSi	18	135.35	0.94846	0.5246	18	343.06	1.3628	0.1456
Residual	159	142.71			159	251.74		
Total	190				190			

Functional group

Source	Algae/Invertebrate consumer				Invertebrate carnivore			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	21659	25.289	**<0.001**	1	11513	100.57	**<0.001**
Si	3	10870	12.692	**<0.001**	3	240.19	2.0981	0.0994
Ye(Lo)	6	14277	16.67	**<0.001**	6	922.23	8.0559	**<0.001**
LoxSi	3	6947	8.1115	**<0.001**	3	579.6	5.0629	**0.0013**
Ye(Lo)xSi	18	1979.4	2.3113	**0.0034**	18	97.552	0.85214	0.6468
Residual	159	856.44			159	114.48		
Total	190				190			

Source	Obligate corallivore				Herbivores			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	34.973	4.0316	**0.0465**	1	10378	19.816	**<0.001**
Si	3	127.17	14.659	**<0.001**	3	1338.1	2.555	0.052
Ye(Lo)	6	61.05	7.0376	**<0.001**	6	3719.1	7.1012	**<0.001**
LoxSi	3	145.3	16.75	**<0.001**	3	5082.5	9.7046	**<0.001**
Ye(Lo)xSi	18	35.195	4.0571	**<0.001**	18	740.95	1.4148	0.123
Residual	159	8.6748			159	523.72		
Total	190				190			

Source	Zooplanktivore			
	df	MS	*Pseudo-F*	*P(perm)*
Lo	1	4.71E+05	45.161	**<0.001**
Si	3	1.65E+05	15.776	**<0.001**
Ye(Lo)	6	38587	3.7006	**0.0017**
LoxSi	3	65075	6.241	**<0.001**
Ye(Lo)xSi	18	22232	2.1322	**0.0077**
Residual	159	10427		
Total	190			

Species

Source	***Pomacentrus maafu***				***Ctenochaetus striatus***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	7979.1	72.781	**<0.001**	1	1061.2	26.266	**<0.001**
Si	3	6720.1	61.297	**<0.001**	3	356.62	8.8266	**<0.001**
Ye(Lo)	6	2037.7	18.587	**<0.001**	6	332.54	8.2305	**<0.001**
LoxSi	3	3829	34.926	**<0.001**	3	555.74	13.755	**<0.001**
Ye(Lo)xSi	18	766.18	6.9887	**<0.001**	18	161.52	3.9977	**<0.001**

Residual	159	109.63			159	40.403		
Total	190				190			

Source	***Pomacentrus coelestis***				***Dascyllus reticulatus***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	64797	22.309	**<0.001**	1	81430	66.914	**<0.001**
Si	3	6243.7	2.1496	0.0957	3	11254	9.2481	**<0.001**
Ye(Lo)	6	9131.3	3.1438	**0.0058**	6	3566.7	2.9309	**0.0078**
LoxSi	3	10269	3.5356	**0.0124**	3	7854.6	6.4544	**<0.001**
Ye(Lo)xSi	18	2025.9	0.6975	0.822	18	3386	2.7824	**<0.001**
Residual	159	2904.5			159	1216.9		
Total	190				190			

Source	***Dascyllus aruanus***				***Chlorurus spilurus***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	16737	86.662	**<0.001**	1	1534	23.877	**<0.001**
Si	3	1759.1	9.1085	**<0.001**	3	183.14	2.8506	**0.0339**
Ye(Lo)	6	228.18	1.1815	0.319	6	417.31	6.4955	**<0.001**
LoxSi	3	2323.1	12.029	**<0.001**	3	348.05	5.4174	**0.0013**
Ye(Lo)xSi	18	769.74	3.9857	**<0.001**	18	67.295	1.0474	0.4091
Residual	159	193.13			159	64.247		
Total	190				190			

Source	***Chromis ternatensis***				***Chromis virdis***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	4216.8	2.6633	0.104	1	34844	28.948	**<0.001**
Si	3	23136	14.612	**<0.001**	3	9080.6	7.5441	**<0.001**
Ye(Lo)	6	7032.3	4.4415	**<0.001**	6	1617.4	1.3437	0.238
LoxSi	3	9918	6.2641	**<0.001**	3	8564.2	7.115	**<0.001**
Ye(Lo)xSi	18	5820.8	3.6763	**<0.001**	18	1670.4	1.3878	0.1373
Residual	159	1583.3			159	1203.7		
Total	190				190			

Source	***Pomacentrus flavioculus***				***Pomacentrus callainus***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	1888.3	107.88	**<0.001**	1	1408.2	3.3707	0.0709
Si	3	597.06	34.111	**<0.001**	3	3711.3	8.8835	**<0.001**
Ye(Lo)	6	149.27	8.5284	**<0.001**	6	2453.1	5.8717	**<0.001**
LoxSi	3	483.09	27.6	**<0.001**	3	8617	20.626	**<0.001**
Ye(Lo)xSi	18	57.343	3.2761	**<0.001**	18	814.26	1.949	**0.0169**

Residual	159	17.503			159	417.78		
Total	190				190			

Source	***Amblyglyphidodon orbicularis***				***Chaetodon baronessa***			
	df	MS	*Pseudo-F*	*P(perm)*	*df*	MS	*Pseudo-F*	*P(perm)*
Lo	1	1746	78.147	**<0.001**	1	1.2921	0.67221	0.4071
Si	3	858.32	38.416	**<0.001**	3	48.773	25.373	**<0.001**
Ye(Lo)	6	144	6.4452	**<0.001**	6	8.209	4.2706	**<0.001**
LoxSi	3	848.88	37.994	**<0.001**	3	4.5591	2.3718	0.0731
Ye(Lo)xSi	18	99.687	4.4617	**<0.001**	18	2.2794	1.1858	0.2803
Residual	159	22.343			159	1.9222		
Total	190				190			

Source	***Labrichthys unilineatus***			
	df	MS	*Pseudo-F*	*P(perm)*
Lo	1	41.925	16.933	**<0.001**
Si	3	18.927	7.6447	**<0.001**
Ye(Lo)	6	15.699	6.3406	**<0.001**
LoxSi	3	32.768	13.235	**<0.001**
Ye(Lo)xSi	18	11.573	4.6742	**<0.001**
Residual	159	2.4759		
Total	190			

Bold value indicates a significant P > 0.05

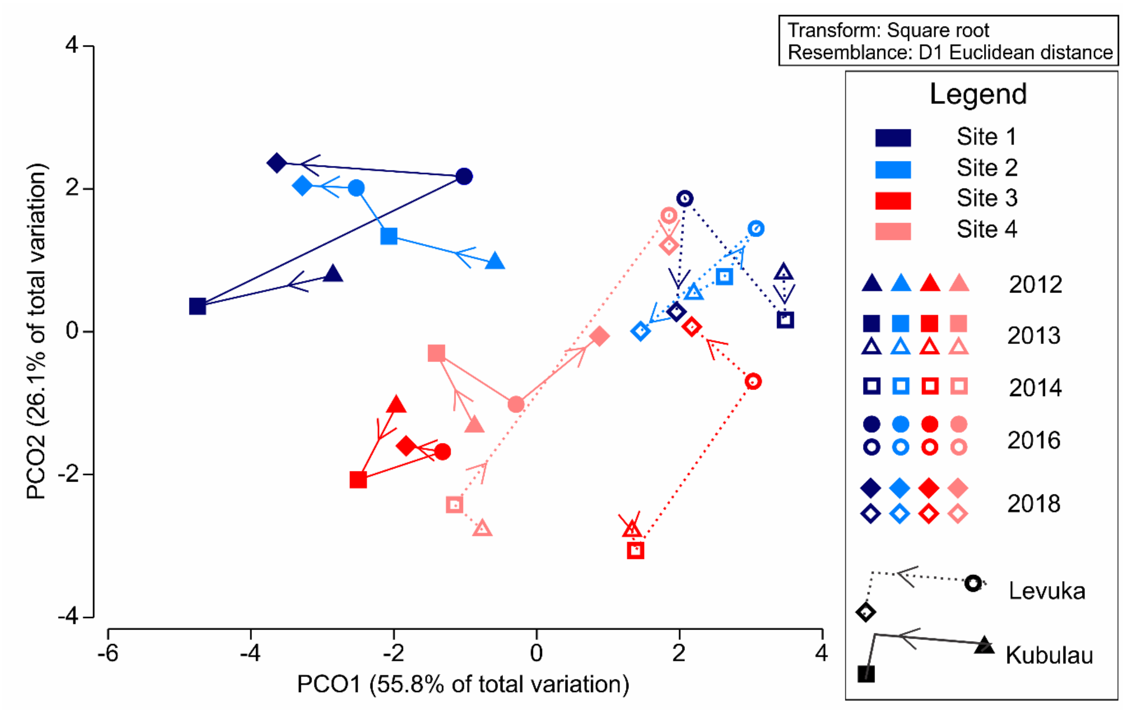

Fig. S3 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the composition of habitat at the broad benthic level across different sites in Kubulau and Levuka. Centroided ordinations are based on a square root transformation and Euclidean distance resemblance matrix

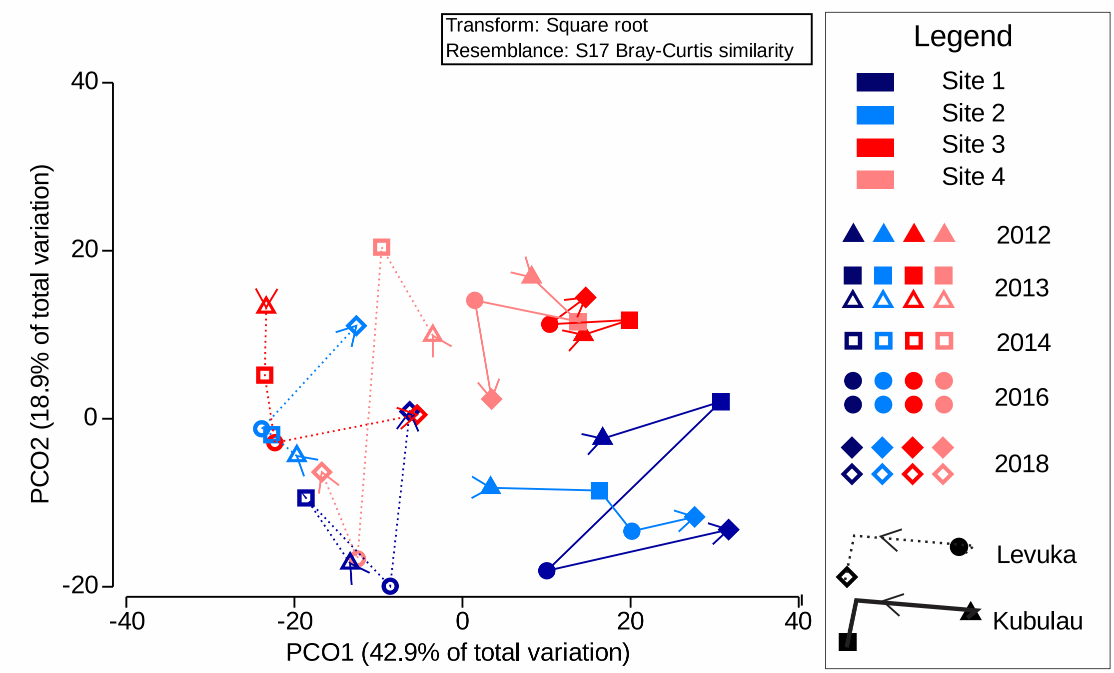

Fig. S4 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the composition of habitat at the morphological level across different sites in Kubulau and Levuka. Centroided ordinations are based on a square root transformation and Euclidean distance resemblance matrix

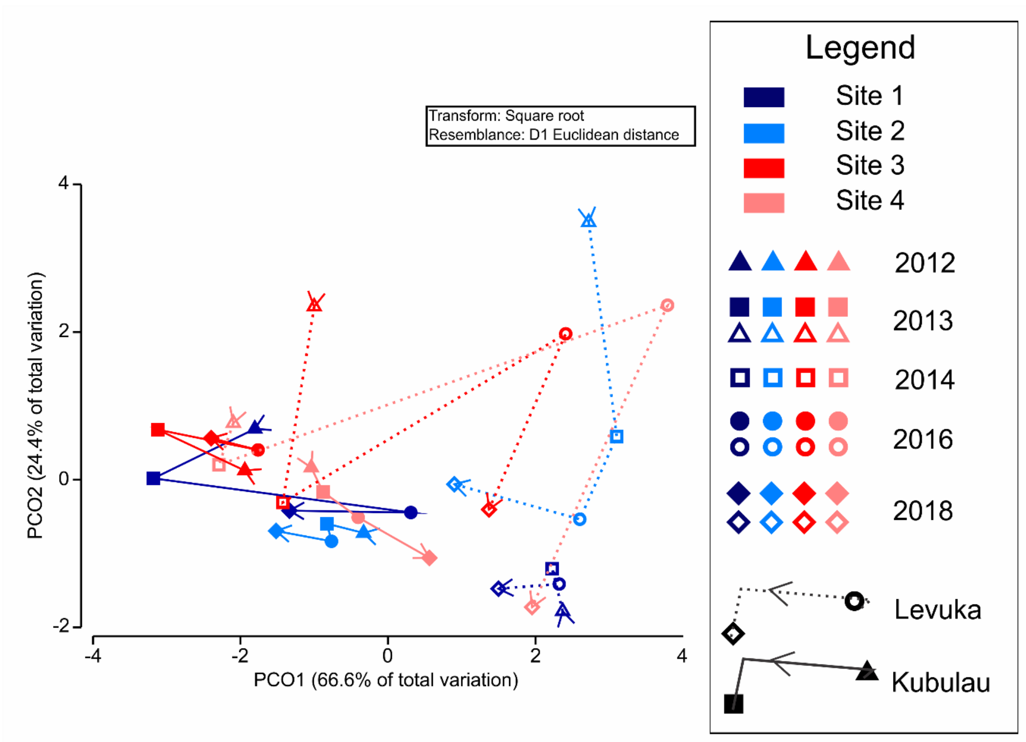

Fig. S5 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the composition of habitat at the benthic condition level across different sites in Kubulau and Levuka. Centroided ordinations are based on a square root transformation and Euclidean distance resemblance matrix

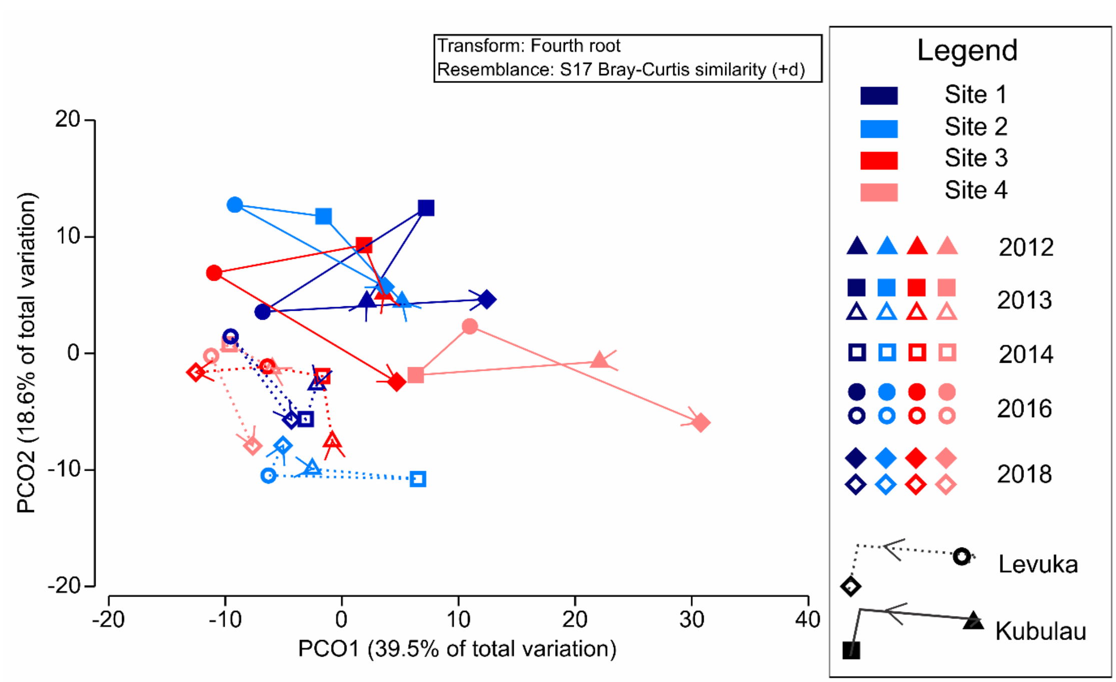

Fig. S6 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the assemblage of fish at family level across different sites in Kubulau and Levuka. Centroided ordinations are based on a fourth root transformation and Bray Curtis resemblance matrix

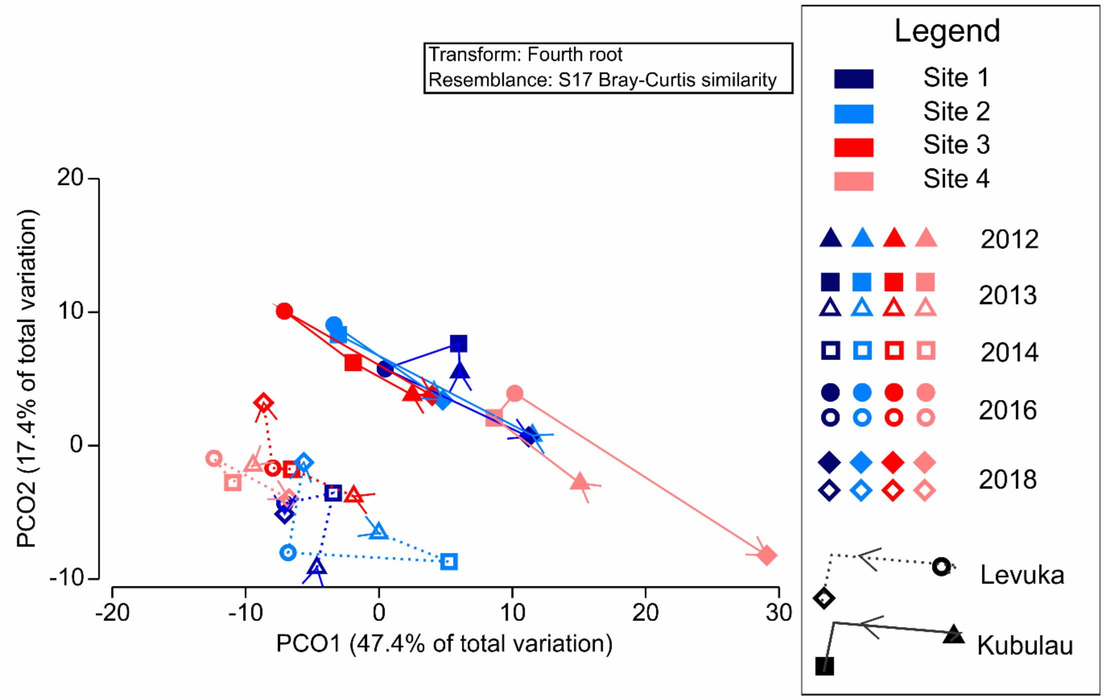

Fig. S7 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the assemblage of fish at functional group level across different sites in Kubulau and Levuka. Centroided ordinations are based on a fourth root transformation and Bray Curtis resemblance matrix

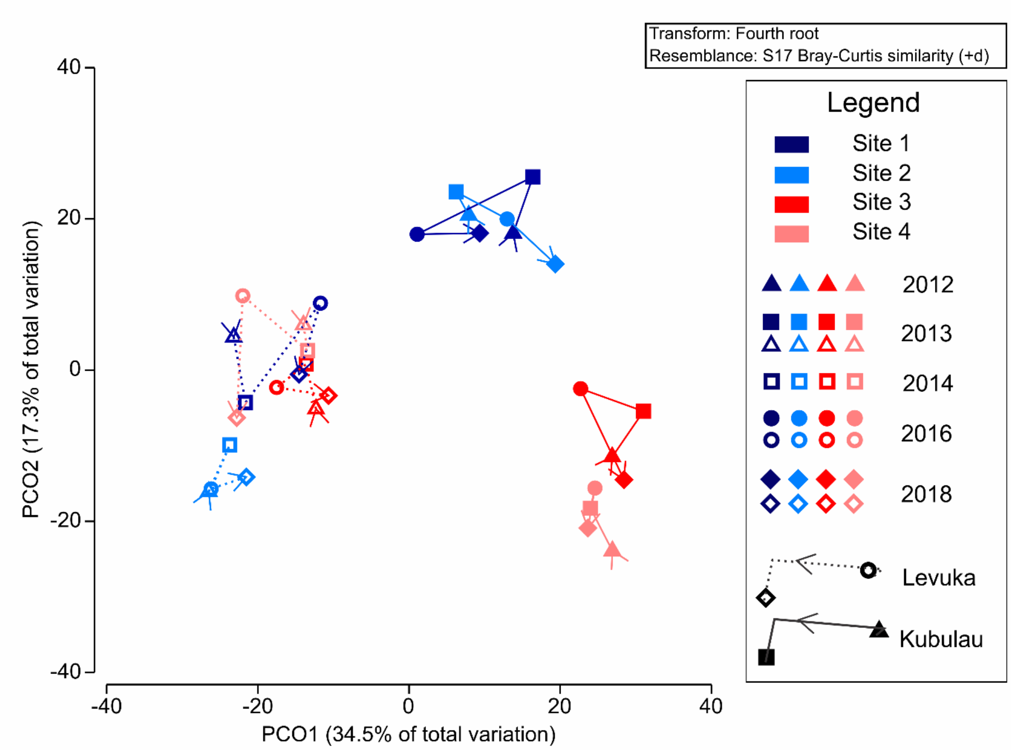

Fig. S8 Centroided Principle Coordinate Ordination (PCO) plot showing temporal changes in the assemblage of fish at species level across different sites in Kubulau and Levuka. Centroided ordinations are based on a fourth root transformation and Bray Curtis resemblance matrix