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Over a decade monitoring Fiji's seagrass condition demonstrates resilience to anthropogenic pressures and extreme climate events

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ABSTRACT

Seagrass are an important marine ecosystem of the Fiji Islands. We confirm six seagrass species from the archipelago and defined five broad categories of seagrass habitat. We report, with high confidence, seagrass meadows covering 59.19 km^2 of Fiji's shallow water habitats from literature and this study. Long-term monitoring of seagrass abundance, species composition, and seed banks at eight sentinel sites, found no long-term trends. Examination of key attributes that affect seagrass resilience identified meadows as predominately enduring and dominated by opportunistic species which had moderate physiological resistance, and high recovery capacity. We examined threats to Fiji's seagrass meadows from extreme climatic events and anthropogenic activities using a suite of indicators, identifying water quality as a major pressure. Based on these findings, we assessed existing protections in Fiji afforded to seagrass and their services. This understanding will help to better manage for seagrass resilience and focus future seagrass research in Fiji.

1. Introduction

Seagrasses are marine flowering plants that grow in the intertidal and shallow subtidal marine waters of sheltered near-shore environments throughout the Fiji Islands (McKenzie and Yoshida, 2007). As a foundation species for marine biodiversity, seagrasses (locally known as *veivutia* or *co ni waitui*) play a supporting role in fisheries production and contribute significantly to the wellbeing of Fijians through their provision of food and a source of livelihoods (Butler, 1983; Choy, 1982; Cullen-Unsworth and Unsworth, 2013; Cullen-Unsworth et al., 2014; Richards et al., 1994). Seagrasses play a critical role in coastal ecosystem dynamics, such as coastal protection by stabilizing sediments and sediment accretion (Gacia et al., 2003; Madsen et al., 2001). Seagrasses also produce natural biocides and improve water quality by controlling pathogenic bacteria to the benefit of humans, fishes, and marine invertebrates such as coral (Lamb et al., 2017). Nutrient cycling in seagrass meadows makes them one of the most economically valuable ecosystems in the world (Costanza et al., 1997), and the retention of carbon within their sediments contributes significantly to Blue Carbon sequestration (Duarte and Krause-Jensen, 2017; Fourqurean et al., 2012; Macreadie et al., 2017; Unsworth et al., 2012).

Fiji's seagrasses are also a significant resource for green turtles in the central south Pacific region (Craig et al., 2004; Piovano et al., 2020) and the primary food for the occasional dugong (Hill-Lewenilovo et al., 2018). These non-reef habitats are particularly important to the maintenance and regeneration of populations of reef fish such as Emperor fish (*Lethrinus* spp) (Cullen-Unsworth et al., 2014; Richards et al., 1994; Unsworth et al., 2009), with much of the connectivity in reef ecosystems dependant on intact and healthy non-reef habitats (Waycott et al., 2011). In addition, the incorporation of carbon within seagrass tissues can affect local pH and increase calcification of coral reefs, thereby mitigating the effects of ocean acidification affecting coral reefs (Fourqurean et al., 2012; Unsworth et al., 2012). The ecosystem services provided by seagrasses therefore make them a high conservation priority (Cullen-Unsworth and Unsworth, 2013; Unsworth et al., 2019).

Despite being economically valuable (Costanza et al., 1997; Costanza et al., 2014), little is known of the status of Fiji's seagrass resources, which are likely under increasing threats from anthropogenic activities and global climate change (Waycott et al., 2009; Waycott et al., 2011). Local threats include coastal development, inappropriate methods of solid waste disposal, sewage pollution, and siltation of coastal areas as a result of agriculture, forestry and mining runoff (McKenzie and Yoshida, 2007; Singh, 2019; Vuki et al., 2000). These pressures are further exacerbated by global pressures related to climate change, such as increasing cyclone incidence/strength and alterations to rainfall, temperature and light levels (Cullen-Unsworth and

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Unsworth, 2013; Waycott et al., 2011). As a result of these pressures, the resilience of seagrass ecosystems is becoming compromised, which is likely to result in the loss of Fiji's seagrass habitats estimated to reach < 5% by the year 2035 and between 5 and 20% by 2100 (Waycott et al., 2011).

To understand the current state and condition of seagrass in the Fiji Islands, we first conducted various assessment and monitoring activities to contextualise the diversity and dynamics of seagrasses and their habitats. We updated the list of species and their locations through extensive literature and herbarium searches, and field assessments. We also provide the most up-to-date review of seagrass spatial extent, and include additional mapping at a number of locations. We used long-term monitoring data to establish a baseline understanding, identify long-term trends, and used seagrass leaf tissue nutrient and isotopic ratios coupled with human population statistics and climate data to identify anthropogenic threats. Finally, to understand resilience state we examined the attributes of seagrass which support its ability to resist stressors and capacity to recover from large scale disturbances.

2. Methods

2.1. Study area and environmental pressures

The Republic of Fiji (the Fiji Islands) is an archipelago of 322 islands (excluding atolls and reefs) in the South Pacific Ocean, of which 106 are permanently inhabited (Vuki et al., 2000). The Fiji Islands are situated between 15° and 22°S latitude and 174°E and 177°W longitude (Fig. 1). The two largest islands, Viti Levu (10,386 km^2) and Vanua Levu (5535 km^2), together comprise 87% of the total land area. In 2017, Fiji's population was 884,887, with 81% living on Viti Levu and an annual growth rate of 0.6% (FBoS, 2018).

Fiji's climate is warm and tropical year-round, with average annual air temperature ranges from 20.8–30.7 °C and average annual sea surface temperature ranges from 26.2–30.5 °C (ABoM, 2019a). Fiji has two different oceanic tropical climates and is dominated by "Af" (cf "Am") according to the Köppen-Geiger climate classification i.e. all 12 months have average precipitation of at least 60 mm (Peel et al., 2007). Rainfall in Fiji is highly variable and mainly influenced by the island topography and the prevailing south-east trade winds (Kumar et al., 2014). Nevertheless, the islands generally experience a dry season from May–June to October and a wet season from November to April–May (FMS, 2015). This seasonal difference is largely associated with the movement of the South Pacific Convergence Zone (SPCZ) which fluctuates northeast and southwest being closest to Fiji in the wet season (Salinger et al., 1995). On Viti Levu, the long-term average annual rainfall is higher on the eastern side than on the western; 2984 mm at Laucala Bay (Suva) and 1861 mm at Nadi, respectively (Kumar et al., 2014). River flooding occurs almost every wet season and occasionally in the dry season during La Niña events. Major floods tend to be associated with severe weather events, such as tropical depressions and cyclones which bring high intensity rainfall. Located in the tropical cyclone belt, Fiji experiences 2.7 cyclones on average annually (1969–2017), generally occurring from November to April, and characterized by damaging winds, rain and storm surges (ABoM, 2019b; ABoM and CSIRO, 2014). Interannual variability in the number of tropical cyclones impacting Fiji is large, ranging from zero in 1994/95 to six in 1979/80, 1992/93 and 2015/16 (ABoM, 2019b).

Environmental pressures that can influence the Fijian seagrass community included climate related changes and deteriorating water quality. Climate data (including air temperature, rainfall and sunshine hours) and water temperature data over the monitoring period 2002–2017 were provided courtesy of the Fiji Meteorological Service. Tropical cyclone data and tracks were courtesy of the Southern Hemisphere Tropical Cyclone Data Portal (https://bit.ly/3bXReN5). Water quality datasets which we could access were limited by location (e.g. only covering Laucala Bay and Tagaqe) and did not cover the duration of the monitoring period (e.g. only available prior to 2007, with the exception of 2011–2012 in Laucala Bay). Overall, accessible water quality datasets were inadequate to investigate trends in relation to seagrass status and condition, and we therefore relied on surrogate indicators (e.g. seagrass leaf tissue nutrients, epiphyte cover) for assessing the water quality conditions.

2.2. Seagrass diversity and meadow spatial extent

Observations and field data were collected to create a seagrass baseline checklist at a number of locations across the Fiji Islands. Seagrass species were identified as per Waycott et al. (2004). Additional information on seagrass species reported from the Fiji Islands was sourced from the following: Seagrass-Watch Virtual Herbarium (SWVH [not an official acronym]), Cairns, Australia; South Pacific Regional Herbarium (SUVA), University of South Pacific, Suva, Fiji; Herbarium Pacificum (BISH), Bernice Pauahi Bishop Museum, Honolulu, Hawai'i; National Herbarium Nederland - Rijksherbarium, Leiden (L), Naturalis Biodiversity Center, Netherlands; Smithsonian Institution (US), U.S.A. District of Columbia. Washington; Herbarium of the Royal Botanic Gardens, Kew (K), Richmond, England; British Museum (Natural History) (BM), London, England; Laboratoire de phanérogamie (Muséum national d'histoire naturelle) (P), Paris, France; New Zealand Virtual Herbarium (NZVH [not an official acronym]), New Zealand National Herbarium Network; literature (e.g., den Hartog, 1970; Parham, 1972; Skelton and South, 2006; Smith, 1979); content analysis of photographs, using the freely accessible photo-sharing website Flickr (Richards and Friess, 2015); and the contributory citizen science and citizen engagement program SeagrassSpotter (Jones et al., 2018b).

An inventory of seagrass meadow extent throughout the Fiji Islands was compiled from published literature and supplemented with field surveys. Field survey methodology followed globally standardised protocols (detailed in McKenzie et al. (2003, 2001)). Mapping of the meadow landscape (including patches and scars) at locations was conducted using a handheld GPS on foot (accuracy ± 3 m). Where the seagrass landscape tended to grade from dense continuous cover to no cover over a continuum that included small patches and shoots of decreasing density, the meadow edge was delineated where there was a gap with the distance of more than 3 m (i.e. accuracy of the GPS). Mapping was conducted using ESRI®ArcMap™ 10.4.1 (Environmental Systems Research Institute, ArcGIS™ Desktop 10.4.1).

2.3. Seagrass condition and long-term monitoring

Monitoring of seagrass meadow condition in the Fiji Islands commenced from July 2002 as part of the Seagrass-Watch global seagrass observing network (McKenzie et al., 2003). Monitoring locations included Ovalau (Cawaci), the southern shores of Viti Levu (Nasese, Tagaqe, Cuvu Harbour, Natadola and Denarau), and Rotuma (Maka Bay) (Fig. 1); which are adjacent to some of the highest population centres in the Fiji Islands.

At each location, 1–2 sites (5.5 ha, permanently marked with GPS) (Table 1), were assessed by a professional scientist or trained observer competent in the monitoring protocols. These sentinel sites represented the seagrass population within a meadow and the unit of measure (quadrat) was not anchored to the substrate between sampling events; so the probability of repeatedly sampling the same shoot or ramet was unlikely. In the centre of each site, observers visually estimated seagrass percentage cover and species composition within 33 quadrats (50 cm × 50 cm), placed every 5 m along three 50 m transects, located 25 m apart. Seagrass abundance (percent cover) was visually estimated as the fraction of the seabed (substrate) obscured by the seagrass species leaves when submerged and viewed from above. To improve resolution and allow greater differentiation at very low percentage covers (e.g. < 3%), shoot counts based on global species density maxima were used (for example, 1 pair of *Halophila ovalis* leaves in a quadrat = 0.1%;

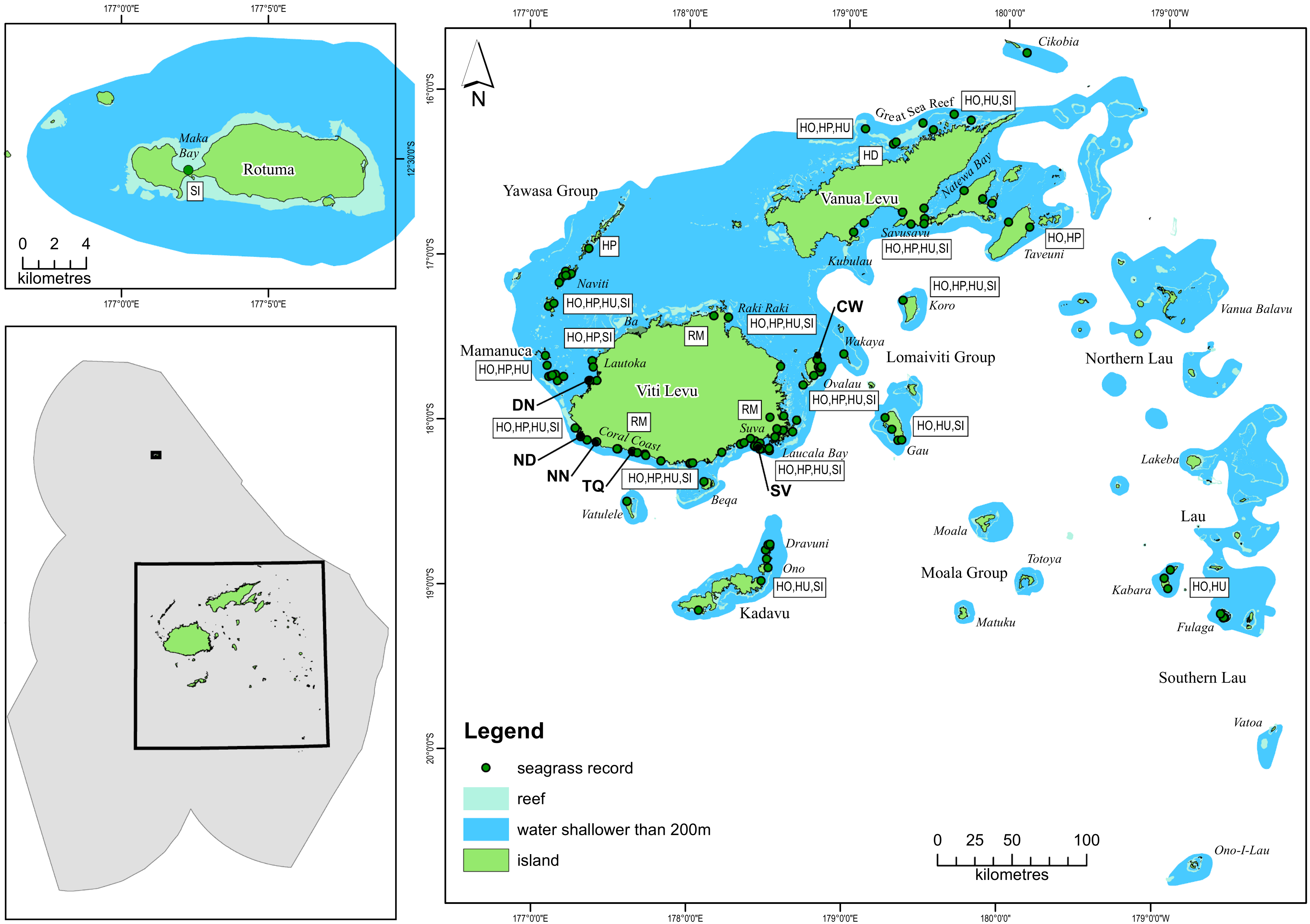

Fig. 1. Map showing locations where seagrass (including species) has been reported from around the Fiji Islands. Long-term monitoring locations are shown: CW = Cawaci, Ovalau; DN = Denarau; ND = Natadola; NN = Cuvu Harbour, Nadroga Navosa; SV = Nasese, Laucala Bay (Suva); TQ = Tagaqe, Coral Coast. HD = *Halophila decipiens*, HO = *Halophila ovalis*, HP = *Halodule pinifolia*, HU = *Halodule uninervis*, RM = *Ruppia maritima* L. var. *pacifica*, SI = *Syringodium isoetifolium*. For sources, see supplementary data (Table S1).

Table 1

Description of long-term (2002–2017) sentinel seagrass monitoring sites in the Fiji Islands, including: depth, type of habitat, population and households within 5 km, and conservation status. Depth is metres below Mean Sea Level and lower littoral sites only exposed to air at the lowest of low tides. Population and household data courtesy Fiji Bureau of Statistics, Government of Fiji. Inshore and coastal areas of Fiji, while owned by the state, are divided into 410 *qoliqoli* areas under community jurisdiction and stewardship. Some communities have implemented Local Marine Management Areas (LMMA), within which tabu (no take) areas may be declared/agreed. Conservation status courtesy UNEP-WCMC and IUCN (2020).

Location	Site	Position	Depth (m bMSL)	Habitat	Population (5 km radius)	Households (5 km radius)	Conservation status
Nasese, Laucala Bay (Suva)	SV1	18.16257°S 178.44326°E	0.22	Intertidal, coastal sand flat in sheltered bay.	57,141	9527	Uninfluenced by LMMA or *tabu* areas.
	SV2	18.16134°S 178.44428°E	0.22				
Cawaci, Ovalau	CW1	17.63303°S 178.81461°E	0.43	Lower littoral fringing reef flat, in partially sheltered bay.	3371	591	Tikina Levuka (*Arovudi/Levuka Vakaviti/Naqaliduna/Nauouo/Nukutocia/Rukuruku/Taviya/Vagadaci/Vatukalo/Waitovu*).
	CW2	17.63462°S 178.81570°E	0.40				
Tagaqe, Coral Coast	TQ1	18.19715°S 177.64968°E	0.44	Lower littoral fringing reef flat.	1885	359	Within *tabu* area of Korolevu-i-wai LMMA (*Namada/Votua/Vatuolalai/Tagaqe*).
Cuvu Harbour, Nadroga Navosa	NN2	18.13849°S 177.42288°E	0.82	Lower littoral sand bank, in Yanuca Channel, north of Nalovo Creek mouth.	7705	1441	Tikina Cuvu LMMA (*Rukurukulevu/Cuvu/Sila/Tore/Naevuevu/Yadua*).
Natadola	ND1	18.10733°S 177.32007°E	0.35	Intertidal fringing reef flat, in partially sheltered bay.	4672	908	*Qoliqolis* uninfluenced by LMMA or *tabu* areas.
Denarau	DN1	17.76588°S 177.37818°E	0.68	Lower littoral coastal sand flat, in Nadi Bay.	10,050	1919	*Qoliqolis* uninfluenced by LMMA or *tabu* areas.

1 shoot/ramet of *Halodule uninervis* in a quadrat = 0.2%). Seagrass species were further categorised according to their life history traits and growth strategies, and classified into colonising, opportunistic or persistent as broadly defined by Kilminster et al. (2015).

Epiphyte and macroalgae cover were measured by estimating the total percentage of leaf surface area (both sides, all species pooled) covered by epiphytic algae and percentage of quadrat area covered by macroalgae (algae not attached to seagrass leaves). From June 2007, *Halodule* seed density (seed bank) measures were conducted at Cawaci (CW) and Nasese (SV) sites. Seeds banks were sampled by sieving (2 mm mesh) 30 cores (50 mm diameter, 100 mm depth) of sediment collected across each site and counting the seeds retained.

Additional information collected from each quadrat included the presence of herbivory (e.g. evidence of grazing or excavating) and visual/tactile estimation of sediment grain size composition (0–2 cm below the sediment/water interface). Details of the Seagrass-Watch monitoring protocols are described in McKenzie et al. (2003, 2000). All monitoring data included in this study underwent standardised and accepted Quality Assurance-Quality Control (QAQC) procedures to ensure data accuracy (McKenzie and Yoshida, 2012).

Leaf tissue nutrient content was assessed as seagrass are passive indicators of $\delta^{15}N$ enrichment by integrating the signature of their environment over time throughout their growth cycle. The various sources of nitrogen pollution to coastal ecosystems often have distinguishable $^{15}N/^{14}N$ ratios (Heaton, 1986), and in regions subject to anthropogenic inputs of nitrogen, levels in the $\delta^{15}N$ signature can be used to identify the source and distribution of the nitrogen (Costanzo, 2001). Very low (~0‰) or negative values of $\delta^{15}N$ can indicate nitrogen sourced from nitrogen fixation (Owens, 1988; Peterson and Fry, 1987), which can supply one third to one half of seagrass demand (O'Donohue et al., 1991). Moderate values indicate internal sources from remineralisation (Owens, 1988; Peterson and Fry, 1987) and higher values (> 3‰) can indicate anthropogenic sources (e.g. sewage (Costanzo et al., 2001; Jones et al., 2018a) or from fertilizer (Udy et al., 1999)).

In July 2014, *Halodule* spp. leaf tissue nutrient content was measured by randomly harvesting three handfuls of shoots from each long-term monitoring site. In the laboratory, avoiding the older chlorotic leaves, leaf material was scraped free of epiphytes and oven dried at 60 °C to weight constancy. Dried biomass samples of leaves were then homogenised by milling to fine powders prior to nutrient analysis. Milled leaf samples were sent to Chemcentre (a NATA certified laboratory in Western Australia) for analysis. Nitrogen and phosphorus were extracted using a standardised selenium Kjeldahl digest and the concentrations determined with an automatic analyser. Percent C was determined using atomic absorption. Elemental ratios (C:N:P) were then calculated on a mole:mole basis using atomic weights (i.e. C = 12, N = 14, P = 31). A subset of each ground tissue sample was sent to UC Davis Stable Isotope Facility (Davis, CA, USA) for $\delta^{15}N$ and $\delta^{13}C$ analysis. The samples were weighed into tin capsules and combusted by elemental analyser (ANCA-SL, SerCon Limited, Crewe, UK) and isotope ratios determined by continuous flow isotope ratio mass spectrometry (20–22 IRMS, SerCon Limited, Crewe, UK).

2.4. Data analysis

To examine the long-term trends in seagrass condition, we restricted our analysis to include only sites assessed more than 3 repeated observation events, over a period greater than 3 years. This resulted in the exclusion of ad hoc assessments conducted at sites in Rotuma and Cuvu Harbour (Nadroga Navosa).

Prior to all analysis, data exploration protocols included checks for spatial autocorrelation, collinearity, zero inflation (of percent cover data), normality (Shapiro-Wilk test) and homogeneity of variances (Cochrans Test).

Generalised additive mixed effects models (GAMMs) were fitted to seagrass cover to identify the presence and consistency of trends, using the “mgcv” (Wood, 2006; Wood, 2014) package in R 3.4.3 (R Core Team, 2014). GAMMs (Wood, 2006) were used to decompose the irregularly spaced time series into its trend cycles and periodic components. Percent cover data models were fitted using a quasibinomial distribution due to the proportional (bound between 0 and 1) nature of the data. These models include random effects to the quadrat level to provide the maximum resolution for modelling. For locations with replicate sites, two separate models were produced. Firstly, an overall model with the sites pooled and secondly a model including 2 different smoothers for the individual sites.

Trend analysis was conducted to determine if there was a significant trend (reduction or increase) in seagrass abundance (percent cover) at a particular site (averaged by sampling event) over all time periods. A Mann-Kendall test was performed using the “trend” package in R 3.2.1 (R Core Team, 2014). Mann-Kendall is a common non-parametric test used to detect overall trends over time. The measure of the ranked correlation is the Kendall's tau coefficient (Kendall-τ), which is the proportion of up-movements against time vs the proportion of down-

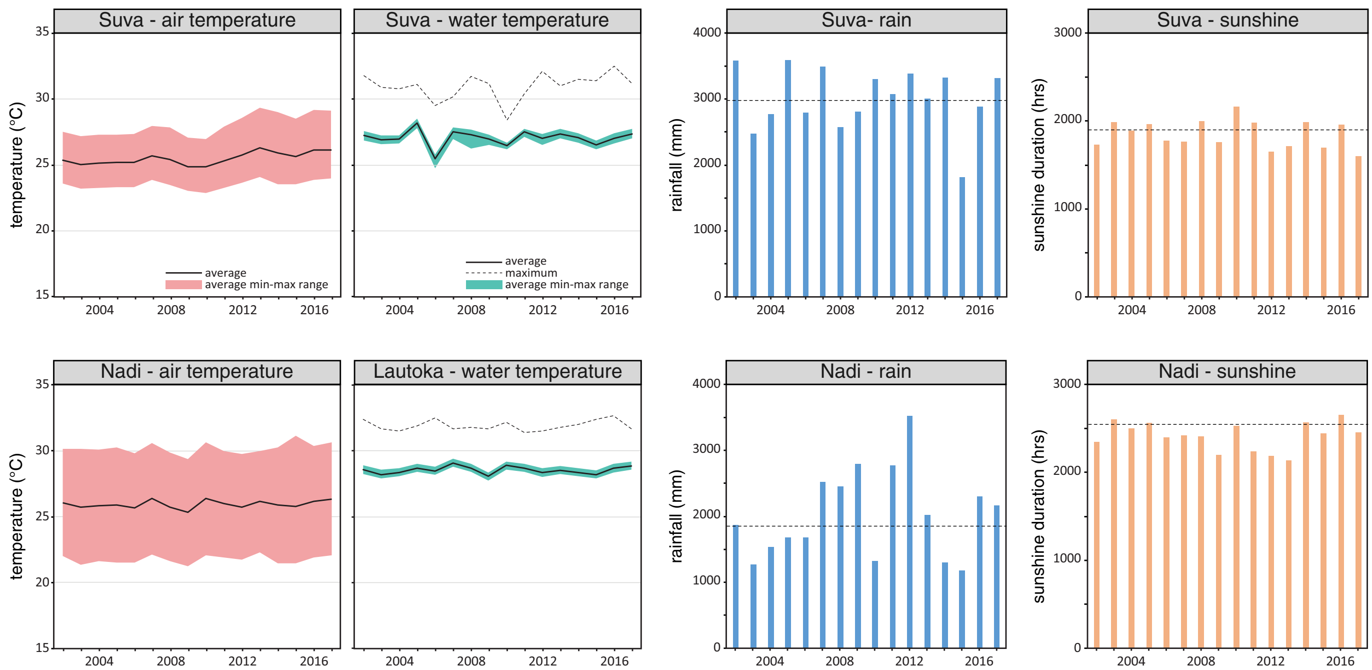

Fig. 2. Annual air temperature (°C), water temperature (°C), total rainfall (mm) and total sunshine duration (hrs) reported from Laucala Bay (Suva), on the eastern side of Viti Levu, and Nadi airport (water temperature from Lautoka) on the western side (data courtesy Fiji Meteorological Service). Dashed lines in rainfall and sunshine panels are the long-term averages (1942–2018). Sunshine duration is the period for which the direct solar irradiance exceeds 120 W m^{-2}.

movements, looking at all possible pairwise time-differences. As the test assumes independence between observations, data was checked for autocorrelation. As autocorrelation was found to be not significant across the dataset, no adjustment was required.

3. Results

3.1. Environmental pressures

Air and water temperatures at Nadi, on the western side of Viti Levu, were slightly warmer during the 2002–2017 monitoring period than those recorded at Laucala Bay (Suva) on the eastern side. The 2002–2017 monitoring period included the warmest years nationally since 1959. The warmest year on record at Nadi was 2007, followed by 2010 and 2017 (Fig. 2), whereas at Laucala Bay (Suva) the warmest year was 2013, followed by 2016 and 2017 (Fig. 2). Overall, Suva and Nadi air temperatures were slightly above long-term averages (Suva = 25.281 °C, Nadi = 25.1 °C) with a maximum temperature of 35.2 °C recorded in Laucala Bay on 11 February 2014 and 33.9 °C at Nadi on 12 March 2010. Maximum water temperatures were generally above 30 °C, but no extreme temperatures (e.g. > 35 °C) occurred during the monitoring period.

Annual rainfall across Viti Levu was above average for over half the 2002–2017 monitoring period (Fig. 2). The wettest year on the west (Nadi) was 2012 (Fig. 2), a consequence of two slow moving tropical depressions causing very heavy rain early in the year. On the east (Suva), the wettest year was 2005 (Fig. 2) with above average rainfall experienced for approximately half the year.

At Nadi, only 4 out of the 16 years recorded above-average bright sunshine hours during the monitoring period; the year with the greatest number of bright sunshine hours was 2016 (Fig. 2). At Laucala Bay on the eastern side, 7 of the 16 monitoring years recorded above average bright sunshine hours; the year of greatest sunshine duration was 2010 (Fig. 2).

A total of 8 tropical cyclones (TC) passed within 50 km of long-term monitoring locations over the 2002–2017 monitoring period. The sentinel seagrass locations impacted the greatest were Cawaci (CW) on Ovalau, Lomaiviti Group (6 cyclones, TC Lola-Jan05, TC Gene-Jan08, TC Cyril-Feb12, TC Kofi-Feb14, TC Winston-Feb16, TC Amos-Apr16), and Denarau (DN), north-western Viti Levu (5 cyclones, TC Gene-Jan08, TC Mick-Dec09, TC Evan-Dec12, TC Kofi-Feb14, TC Winston-Feb16). Locations on southern Viti Levu were less impacted, with three cyclones passing within 50 km of both Nadroga Navosa (NN) (TC Gene-Jan08, TC Mick-Dec09, TC Evan-Dec12) and Natadola (ND) (TC Gene-Jan08, TC Evan-Dec12, TC Kofi-Feb14), and only one impacting both Tagaqe (TQ) and Nasese, Suva (SV) (TCMick-Dec09). TC Winston in 2016 was the strongest tropical storm ever to affect Fiji and also one of the strongest to occur in the Southern Hemisphere. TC Winston entered Fiji waters as a Category 5 storm on the morning of February 20th, moving in a westerly then west-southwest direction at about 15 knots, making landfall on the northeast coast of Viti Levu at about 7 am (Fig. 3). TC Winston exited Viti Levu just north of Lautoka at around 9.30 pm and took a westerly direction before exiting out of Fiji Waters by 3 am on February 21st (Fig. 3). TC Winston broke all previous national records of maximum sustained winds and gusts at a land based station in Fiji, with sustained winds of up to 232 km/h and gusts of up to 306 km/h recorded (Fiji Meteorological Service, 2017). The very destructive winds from TC Winston only impacted CW and DN long-term monitoring sites; while all other sites were impacted to a lesser degree by destructive storm force winds (Fig. 3). During 2016, when TC Winston impacted the region, annual average and maximum air temperatures throughout the year were above the long-term average, while sea surface temperatures and total bright sunshine hours were near normal (Fig. 2).

3.2. Seagrass species, habitats and extent

Six seagrass species, from three families (Hydrocharitaceae, Cymodoceaceae and Ruppiaceae), were confirmed from across 146 localities in the Fiji Islands (Fig. 1, Table S1). These include: *Halodule pinifolia* (Miki) den Hartog; *Halodule uninervis* (Forsskål) Ascherson in Boissier; *Halophila ovalis* R. Brown; *Halophila decipiens* Ostenfeld; *Syringodium isoetifolium* (Ascherson) Dandy; and *Ruppia maritima* Linnaeus var. *pacifica* H. St. John & Fosberg.

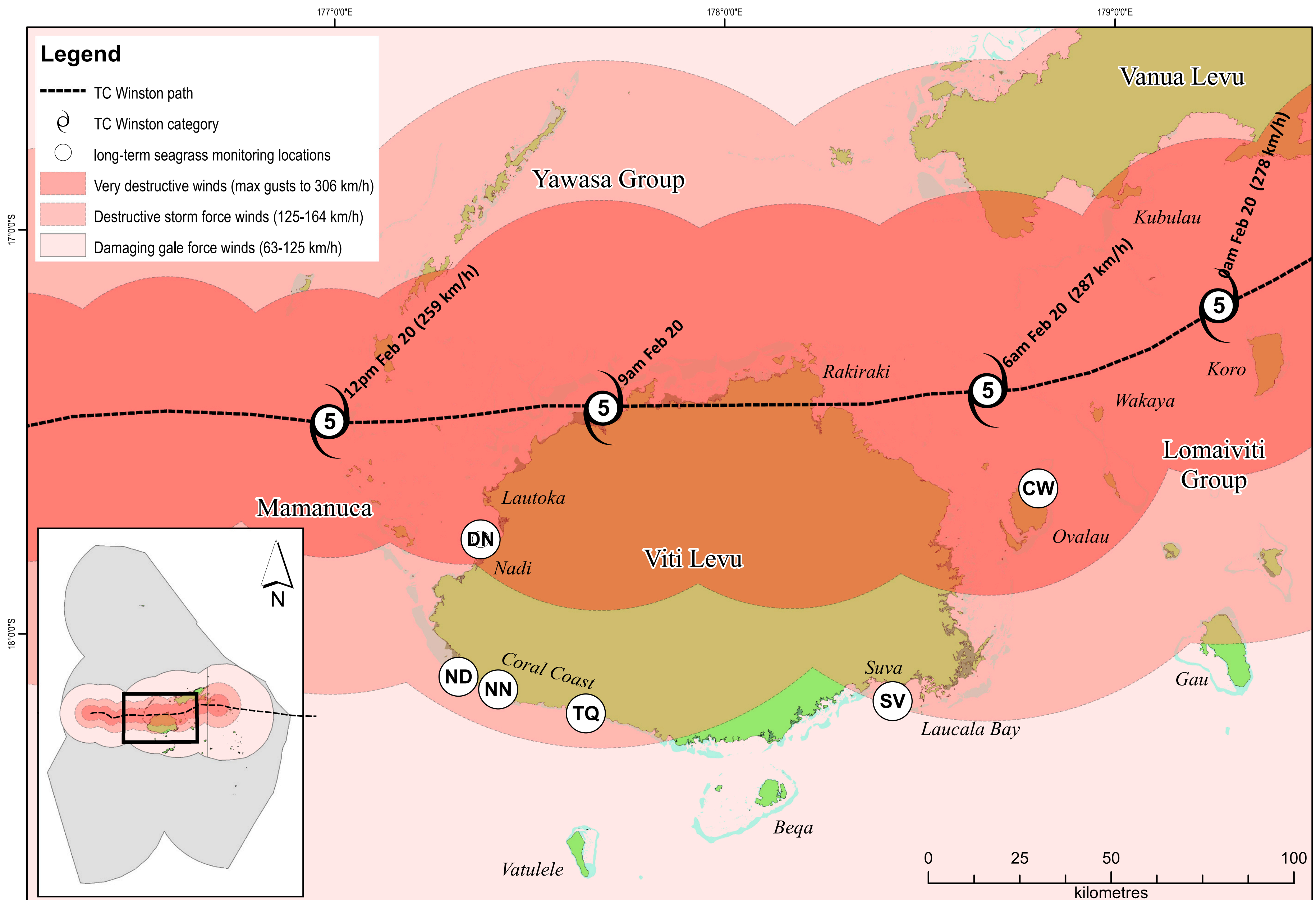

Fig. 3. Path of Tropical Cyclone Winston across the Fiji Islands in February 2016, showing category and area of wind strength. Long-term seagrass monitoring locations: CW = Cawaci, Ovalau; DN = Denarau; ND = Natadola; NN = Cuvu Harbour, Nadroga Navosa; SV = Nasese, Laucala Bay (Suva); TQ = Tagaqe, Coral Coast. Cyclone path, category and wind strength data courtesy Fiji Meteorological Service, 2016.

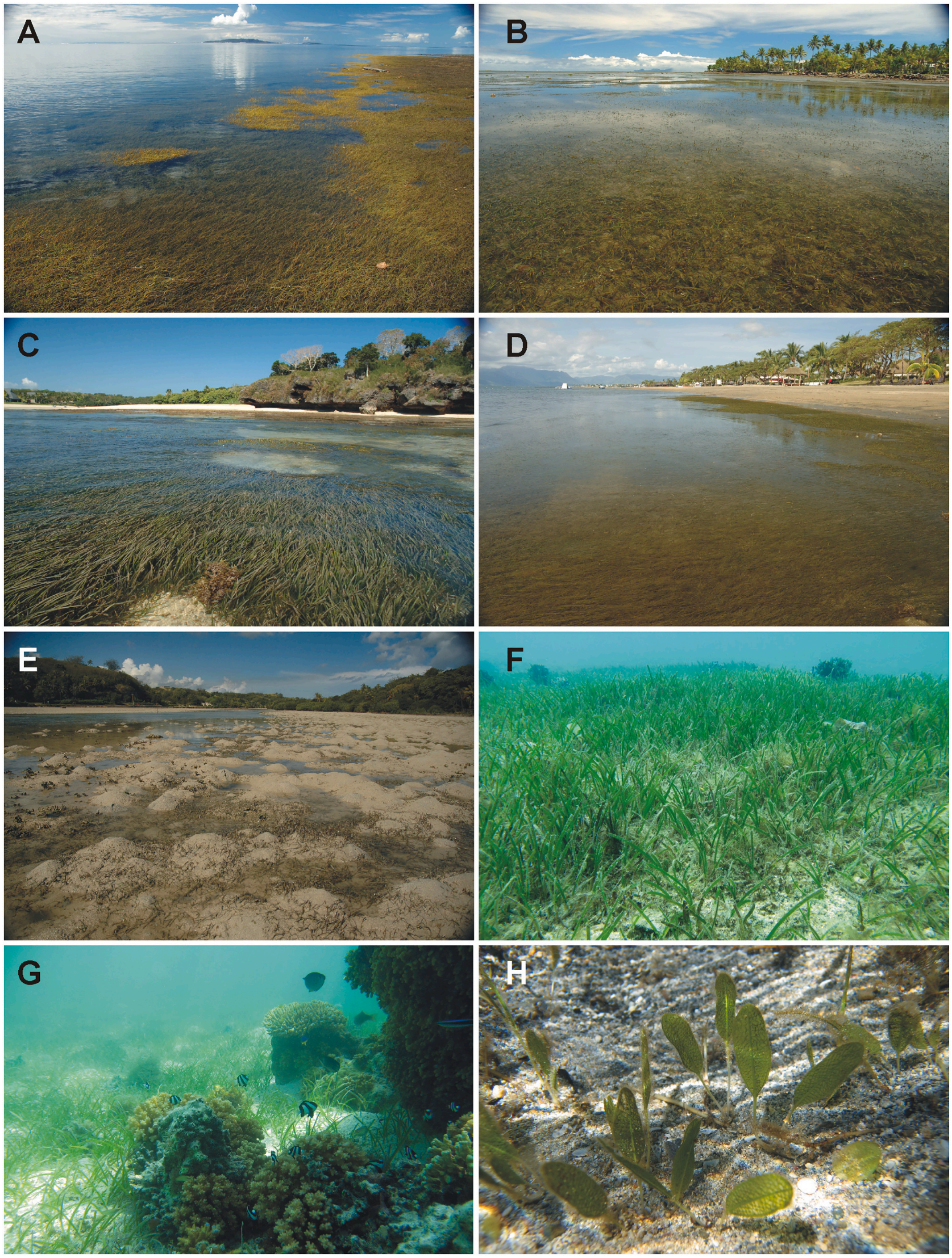

Fig. 4. Seagrass meadows in the Fiji islands occur in a variety of habitats: A *Syringodium isoetifolium* with *Halodule uninervis* meadow, Cawaci, July 2014; B mixed *Halodule uninervis/Halodule pinifolia* meadow, Nasese, Suva, March 2010; C *Halodule uninervis* meadow, Natadola, August 2011; D mixed *Halodule pinifolia/Syringodium isoetifolium/Halophila ovalis* meadow, Denarau, January 2007; E *Halodule uninervis/Halophila ovalis*, Nadroga Navosa, January 2007; F *Halodule uninervis* dominated meadows, Caqalai, August 2011; G mixed *Halodule uninervis/Halophila ovalis* and *Syringodium isoetifolium* meadow, Levuka reef, January 2007; H *Halophila ovalis* with bullations (blisters or pucker-like structures) present on the leaf blades, Tagaqe, May 2006.

The earliest record of a seagrass from the Fiji Islands were *Halophila ovalis* (bullate and smooth leaf), *Syringodium isoetifolium* and *Halodule pinifolia*, from near Bau (Viti Levu) in 1874 (Table S1), and the most recent addition to the species list was *Halophila decipiens* off Mali Passage (Great Sea Reef), approximately 130 years later in 2004 (Table S1).

Seagrasses are found in a range of habitats across the Fiji Islands including: estuarine; barrier and patch reefs; island fringing reefs; bays and lagoons; and deepwater (> 10 m) (Fig. 4). *Halodule pinifolia* is generally found in the high intertidal to upper subtidal areas of sheltered bays, reef platforms and in high energy locations. *Halodule pinifolia* often forms homogenous patches or occasionally intermixes with other seagrass species including the closely related *Halodule uninervis*. *Halodule uninervis* is found from intertidal to 6 m, in sheltered or exposed coral reefs, on shallow sand/mud banks, where it often forms dense meadows or is patchy and intermixed with other seagrass species (viz. *Syringodium isoetifolium*, or *Halophila* spp.). *Halophila ovalis* is the most eurybathymetric and eurythermic of all seagrasses in Fiji and extends from the intertidal to 10-12 m deep, occurring from estuarine to deep water habitats. *Halophila ovalis* forms dense meadows in some locations, but is frequently encountered in small patches. It tolerates a wide variety of substrata from fine mud/sand to coarse sand, mixed sand/rubble or large boulders with sand patches. *Syringodium isoetifolium* is usually found in the shallow subtidal reef areas (1–6 m depth), with some meadows occasionally exposed during extreme low tide on reef flats. *Syringodium isoetifolium* is also the only seagrass species reported from Rotuma. *Ruppia maritima* only occurs in estuarine habitats in Viti Levu and is reported from brackish water pools or along the banks of the Rewa, Penang and Sigatoka Rivers (Table S1). *Halophila decipiens* is a recent addition to the seagrass inventory in Fiji. It occurs from in waters > 6 m depth and has only been found in sparse patches growing in the fine mud/sand substratum along the reef channels of Cakaulevu Reef, northern Vanua Levu (Table S1). The records of *Halophila decipiens* from Dravuni (Kadavu) between 1992 and 1997 cannot be verified, but are most likely *Halophila ovalis* (Table S1).

The area of seagrass meadows mapped with high confidence in Fiji covers 59.19 km^2 (Table 2). The most expansive meadows occur within sheltered bays (e.g. Laucala Bay, Viti Levu), on broad fringing reef habitats (e.g. Kubulau, Vanua Levu) or within shallow lagoons bordered by barrier reefs (e.g. Great Astrolabe Reef, Kadavu). On fringing reef habitats (e.g. Coral Coast and Mamanuca Islands, Viti Levu; Lau Group), seagrass often occur mixed with a diversity of benthos, such as macroalgae and coral, in a complex mosaic of habitats from the shore to reef crest.

3.3. Seagrass condition & trend at sentinel sites

3.3.1. Seagrass cover, species composition and seed banks

All the seagrass meadows within which sentinel monitoring sites were established were classified as enduring, as they have all been present for durations greater than five years (sensu Kilminster et al., 2015). Results from monitoring between 2002 and 2017 indicates changes in seagrass abundance were variable among sites, changing seasonally and between years (Fig. S1). The seagrass meadows at Cawaci (CW), on Ovalau, fluctuated the most since monitoring was established in 2002, with abundances increasing for short periods in 2006–2007 and 2014, before subsequently returning to long-term averages (Fig. 5). In 2016, sentinel sites at CW, SV, ND and DN were assessed two months' post TC Winston's impact on the Fiji Islands, and although some minor losses were observed, total seagrass abundances remained close to long-term averages. Overall, despite fluctuations in abundances between years, no long-term trend was evident for any site (Fig. 5, Table 3).

With the exception of Nadroga Navosa (NN), seagrass meadows across Fiji within which sentinel sites were assessed were dominated by opportunistic species of seagrass (Fig. 6). The sentinel site at NN2, located adjacent to Nalovo Creek in Yanuca Channel, between Yanuca Island (Shangri-la Fijian Resort) and Rukurukulevu village, was composed predominately of the colonising species *Halophila ovalis* (Fig. 6). The composition of colonising species at other sentinel sites fluctuated slightly between years, but was generally below a tenth of the total composition. All sites assessed in the two months after TC Winston in 2016, had marginal increases in the composition of colonising species, however this declined within 12 months at CW and ND (Fig. 6).

Halodule seed banks were assessed at CW and SV sentinel sites between 2007 and 2017. A persistent seed bank occurred at all sites throughout the monitoring period, however seed bank densities were highly variable between years (Fig. 7). The maximum seed bank recorded was 22,918 seeds m^{-2} at CW2 (21 April 2016).

3.3.2. Epiphytic and macroalgae

Epiphytic algae occurred on seagrass leaves across all habitats and sites, and was predominately filamentous greens and reds (e.g.

Table 2
Spatial extent of seagrass mapped with high confidence around the Fiji Islands. Asterix identifies meadows which include long-term sentinel monitoring sites.

Island Group and Location	Description of benthos	Area (km^2)	Source
Viti Levu			
Laucala Bay	Seagrass	0.508	Roelfsema and Phinn, 2010
	Algae/seagrass	0.023	Roelfsema and Phinn, 2010
	Seagrass/sand/rubble	0.425	Roelfsema and Phinn, 2010
Nasese, Suva*	Seagrass	0.176	This study; Chand, 2019
Nukubuco	Seagrass	1.514	Koshy, 2001; Chand, 2019
Nawanada	Seagrass	0.771	Chand, 2019
Sosoikula	Seagrass	0.922	Chand, 2019
Navakavu	Seagrass	0.204	Phinn et al., 2012; Roelfsema and Phinn, 2010
	Algae/seagrass	0.106	Phinn et al., 2012; Roelfsema and Phinn, 2010
	Seagrass/sand/rubble	0.297	Phinn et al., 2012; Roelfsema and Phinn, 2010
Coral Coast	Seagrass	0.340	de Mazières, 2008
	Macroalgae/seagrass	0.120	de Mazières, 2008
Nadroga Navosa*	Seagrass	0.033	This study
Tagaqe*	Seagrass	0.016	This study
Natadola*	Seagrass	0.060	This study
Denarau*	Seagrass	0.379	This study
Mamanuca Islands	Sand with sparse algae & seagrass	6.460	Harborne et al., 2001
Ba Province	Seagrass	0.981	Dadhich and Nadaoka, 2012
Kadavu			
Kadavu	Seagrass	8.681	Roelfsema et al., 2013
	Seagrass - Sed	5.779	Roelfsema et al., 2013
	Seagrass/Algae Rubble Sed	1.886	Roelfsema et al., 2013
	Sed rubble seagrass/algae	3.365	Roelfsema et al., 2013
Dravuni Island	Seagrass (*Syringodium*)	0.089	Nojima and Mukai, 1991
Vanua Levu			
Kubulau	Seagrass/algae rubble sed	9.634	Roelfsema et al., 2013
	Seagrass sed	0.335	Roelfsema et al., 2013
	Sed seagrass/algae	2.740	Roelfsema et al., 2013
Lomaiviti group			
Cawaci, Ovalau*	Seagrass	0.041	This study
Lau group			
Totoya, Matuka, Moala, Fulaga, Kabara, Nayau, Vanua Vatu, Tuvuca, Cicia, Mago, Vanua Balavu	Dense seagrass	13.3	Bruckner, 2016
TOTAL		**59.19**	

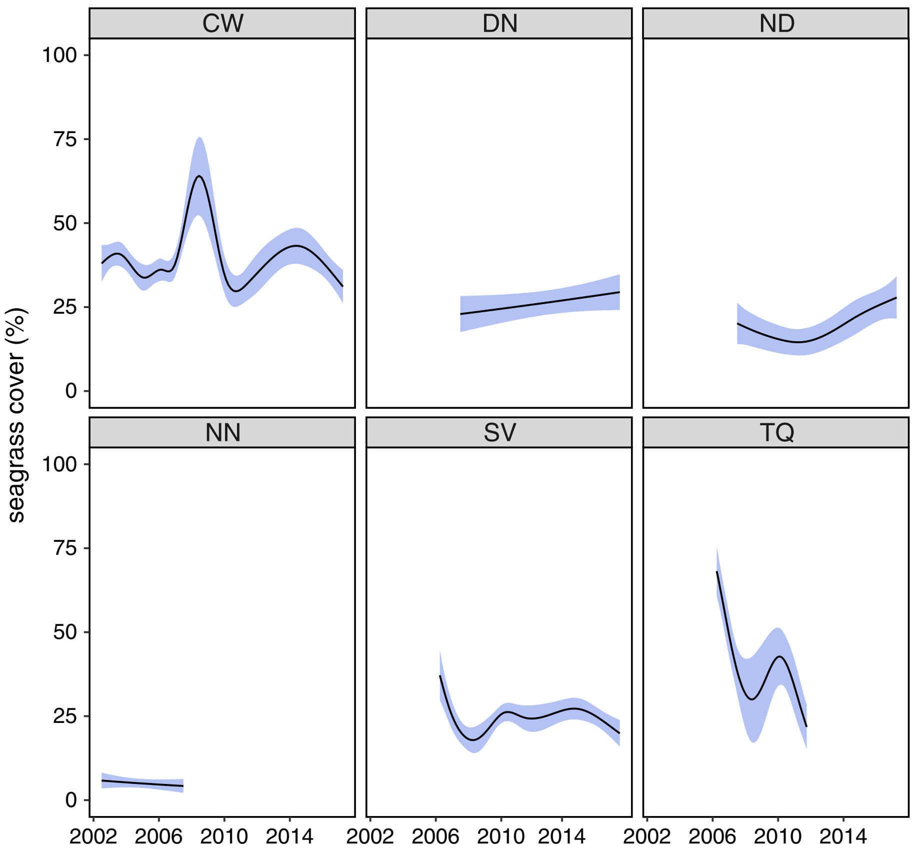

Fig. 5. Trends in seagrass abundance (% cover) represented by a GAMM plot for each long-term monitoring location: CW = Cawaci, Ovalau; DN = Denarau; ND = Natadola; NN = Cuvu Harbour, Nadroga Navosa; SV = Nasese, Laucala Bay (Suva); TQ = Tagaqe, Coral Coast. Trends are solid lines with shaded areas defining 95% confidence intervals of those trends.

Table 3

Results of MannKendall analysis to assess if there was a significant trend (decline or increase) over time in seagrass abundance (percent cover). The reported output of the tests performed are Kendall's tau coefficient (Kendall-τ), the two-sided *p*-value (significant at $\alpha = 0.05$ in bold), the Sen's slope (showing the sign and strength of the trend) and the long-term trend.

Site	First year	Last year	n	Kendall-τ	*p* (2-sided)	Sen's slope	Trend
CW1	2002	2017	20	0.041	0.8337	0.106	No trend
CW2	2002	2017	20	−0.006	1	−0.054	No trend
DN1	2007	2017	6	0.333	0.4524	2.161	No trend
ND1	2007	2017	6	0.467	0.2597	1.586	No trend
NN2	2002	2007	8	−0.214	0.5362	−0.335	No trend
SV1	2006	2017	12	−0.308	0.1606	−0.801	No trend
SV2	2007	2017	10	0.212	0.3727	0.707	No trend
TQ1	2006	2011	5	−0.8	0.0864	−11.223	No trend

Enteromorpha, *Audouinella*, *Ceramium*). The cover/abundance of epiphytes varied greatly between years, and periods of absence were rare (Fig. S2). Over the monitoring period, epiphytic algae were greater on seagrass leaves at coastal than reef habitats (32.9 ± 3.3% and 23.3 ± 4.9%, respectively). The greatest increase in the cover of epiphytes over the monitoring period occurred at SV sites in the coastal meadow at Nasese (Laucala Bay), where abundances more than doubled between 2002 and 2017 (GLMM, $p = 3.25e^{-11}$) (Fig. S2).

Macroalgae occurred at all sentinel sites, fluctuating both within and between years since monitoring was established (Fig. S2). Macroalgae at coastal habitats generally consisted of filamentous green algae (e.g. *Enteromorpha*), while on coral reefs it also included *Gracilaria*, *Halimeda*, *Caulerpa*, *Cladophora*, and *Sargassum*. Macroalgae abundances were generally low (< 5%), however occasionally reached > 25% average cover (Fig. S2). Macroalgae were most abundant between 2002 and 2010, and slightly higher at reef than coastal habitats (8.1 ± 1.7% and 3.1 ± 0.8%, respectively) over the long-term (Fig. S2).

3.3.3. *Seagrass tissue nutrients*

Leaf molar C:N ratios of the foundation seagrass *Halodule* spp. were above the global median of 20 at reef habitats (CW and ND), but below 20 at coastal intertidal habitats (DN and SV); indicating an elevation in the availability of nitrogen relative to the rate at which the leaves are growing and incorporating carbon at the coastal sites (Fig. 8). This, taken together with higher epiphyte cover and isotopically depleted $\delta^{13}C$ at coastal sites, indicated that increased availability of N is likely to be the principal cause of the low C:N ratios (Fig. 8). The less negative (isotopically depleted) $\delta^{13}C$ at DN and SV suggests sufficient light for photosynthesis; which is expected as all meadows are either intertidal or lower littoral (Table 1). The $\delta^{15}N$ values in the *Halodule* leaf tissue at the coastal habitats were particularly higher at Laucala Bay (SV), suggesting the primary source of N was influenced by anthropogenic N sources such as septic and possibly treated sewage (Fig. 8). The high $\delta^{15}N$ at Natadola (ND) similarly suggests some level of anthropogenic N sources (Fig. 8), while the lower $\delta^{15}N$ values at other sites suggest diverse sources of nitrogen affecting nitrogen availability.

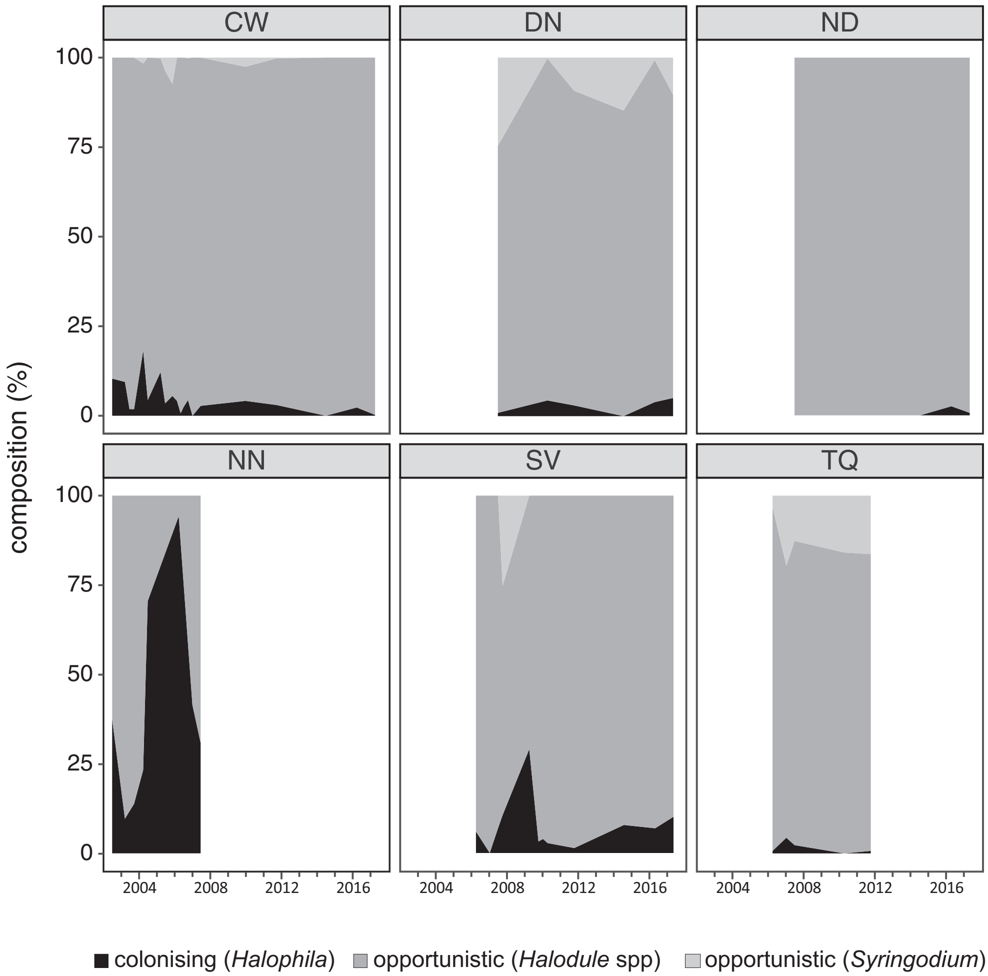

Fig. 6. Change in composition of seagrass species groups to total cover over the life of the long-term monitoring in the Fiji Islands: CW = Cawaci, Ovalau; DN = Denarau; ND = Natadola; NN = Cuvu Harbour, Nadroga Navosa; SV = Nasese, Laucala Bay (Suva); TQ = Tagaqe, Coral Coast. Species groups includes: Opportunistic = *Halodule uninervis*, *Halodule pinifolia* and *Syringodium isoetifolium*; and colonising = *Halophila ovalis*.

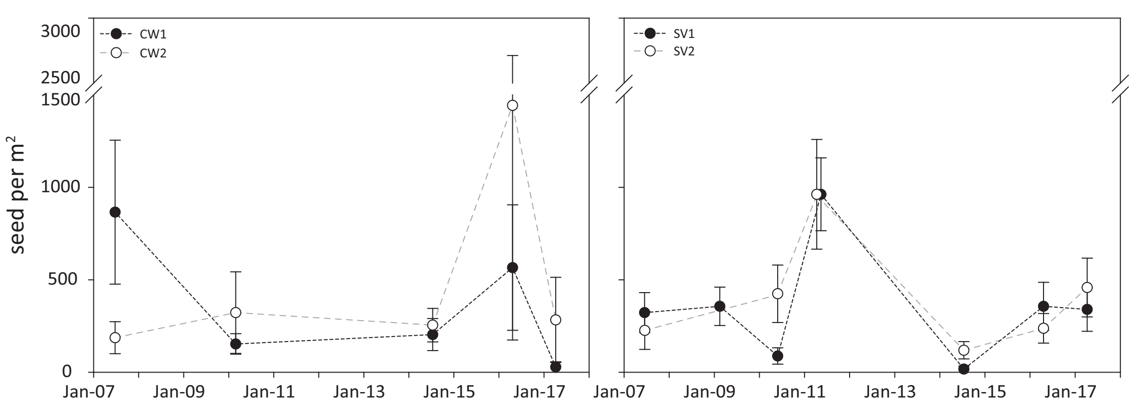

Fig. 7. Changes in *Halodule* spp. seed banks (average ± SE) between 2007 and 2017 at Ovalau (CW = Cawaci) and Viti Levu (SV = Nasese, Laucala Bay (Suva)) long-term monitoring sites.

4. Discussion

Six species of seagrass, from 4 genera, are reported from the Fiji Islands. The most widely distributed species throughout the Fiji Islands were *Halodule pinifolia* and *Halodule uninervis*, followed by *Halophila ovalis* and *Syringodium isoetifolium*, respectively. The rarest species were *Ruppia maritima* and *Halophila decipiens*. All the seagrass species within Fiji waters have an Indo-Pacific distribution. The bullate form of *Halophila ovalis* was previous recognised as the subspecies *Halophila ovalis* ssp. *bullosa* (McMillan and Bridges, 1982) endemic to Fiji, Tonga, and Samoa (Skelton and South, 2006; Tuiwawa et al., 2013), however, recent independent morphological and molecular barcoding approaches confirmed the Fijian *Halophila ovalis* and *Halophila ovalis* ssp. *bullosa* are conspecific (Singh et al., 2019, 2020). Similarly, molecular studies have shown that *Halophila minor* (incl. *Halophila ovata*), which has been reported from the Fiji Islands (Green and Short, 2003), is

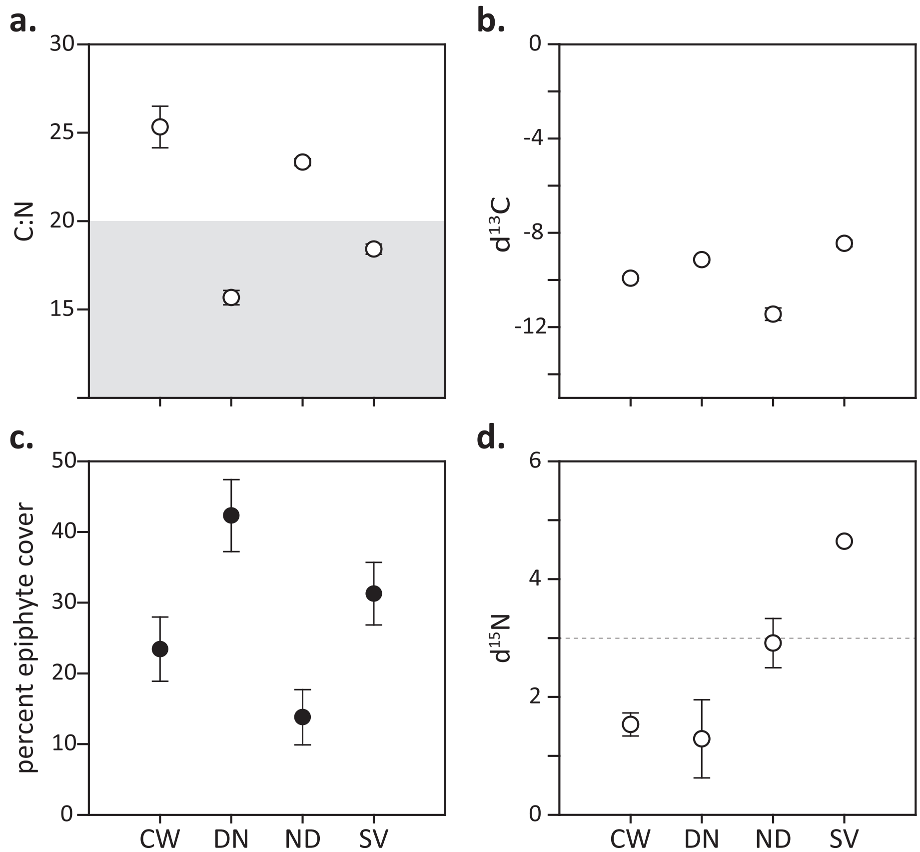

Fig. 8. *Halodule* spp. leaf tissue nutrient ratio (a.) (C:N, ± SE) and isotope concentration (b., d.) ($\delta^{13}C$ and $\delta^{15}N$, ± SE) in July 2014, and long-term (2002–2017) average epiphyte cover (c.) (%, ± SE) at long-term monitoring locations: CW = Cawaci, Ovalau; DN = Denarau; ND = Natadola; SV = Nasese, Laucala Bay (Suva). Horizontal shaded band on the C:N ratio represents the area below the accepted seagrass "Redfield" ratio of 20:1 which may indicate N enrichment or reduced light availability (when N is not in surplus) (Abal et al., 1994; Grice et al., 1996). Leaf tissue $\delta^{13}C$ concentration less negative in high light, high productivity environments: more negative $\delta^{13}C$ may indicate that light is limited (Campbell and Fourqurean, 2009; Grice et al., 1996; Hu et al., 2012). Leaf tissue $\delta^{15}N$ concentration indicates the primary N source: nitrogen from sewage = 9 or ~10‰ (Lajtha and Marshall, 1994; Udy and Dennison, 1997b), septic and aquaculture discharge = ~5‰ (Jones et al., 2001), and nitrogen fertilizer = ~0–1‰ (Udy and Dennison, 1997a).

conspecific with *Halophila ovalis* (Waycott et al., 2002). Conversely, Waycott et al. (2004) suggested *Halodule pinifolia* and *Halodule uninervis* are conspecific, recognising that the plasticity of blade size is attributed to local conditions, however recent research using a plastid rbcL marker specific for *Halodule*, confirmed *Halodule pinifolia* and *Halodule uninervis* in the Pacific remain separate species (Wagey and Calumpong, 2013). Reports of *Thalassia hemprichii* occurrence from the Fijian archipelago by Littler and Littler (2003) and Bruckner (2016) are erroneous.

Although 59.19 km^2 of seagrass meadows has been mapped to date with high confidence, this remains an underestimate of the archipelago's total seagrass extent, as many records of seagrass occurrence throughout the archipelago are not coupled with maps of meadow extent, and mapping was ad hoc; focusing on areas considered high conservation value, an important resource for local communities, under threat, or close to academic institutions (McKenzie and Yoshida, 2007). Recent (2018–2020) broad-scale mapping of coral reefs for the *Allen Coral Atlas* project estimated that there is possibly 501.51 km^2 of seagrass in the Fiji Islands (excluding Rotuma) (Allen Coral Atlas, 2020). However, as the *Allen Coral Atlas* is in a beta stage, recognising the maps may have issues (Allen Coral Atlas, 2020), extensive field validation is required using hierarchical approaches (sensu McKenzie et al. (2020)), before the maps can be used with confidence.

In Fiji, seagrasses are distributed throughout the Islands, however the presence of a species at a location depends on availability of viable propagules (e.g. vegetative fragments, fruits or seeds) and suitable local conditions. For example, only *Syringodium isoetifolium* is reported from Rotuma, as the absence of other species may be a consequence of the islands isolation from the main archipelago and limited recruitment. It is also likely that *Syringodium isoetifolium* may be a recent introduction to Rotuma, as viable propagules may have arrived via a rare long-distance dispersal event or anthropogenic introduction (e.g. visiting vessels) (McKenzie et al., 2014).

The local conditions which are critical to whether seagrass will occur along any nearshore area include: physical parameters that regulate the physiological activity of seagrasses (e.g. temperature, salinity, waves, currents, depth, substrate type and day length); natural phenomena that limit the photosynthetic activity of the plants (e.g. light, nutrients, epiphytes and diseases); and anthropogenic inputs that inhibit access to available plant resources (e.g. nutrient and sediment loading). Various combinations of these parameters permit, encourage or eliminate seagrass from a specific location.

The findings from this study show that the seagrass meadows of the Fiji Islands are principally enduring in character, and composed predominately of opportunistic seagrass species with some colonisers; although this can depend on the habitat. Seagrass were found to occur across a diversity of habitats: estuarine; barrier and patch reefs; fringing reefs; bays and lagoons; and deepwater.

An examination of the species at each of the sentinel sites revealed aspects of the meadows based on attributes of seagrass life histories. For example, at the Nadroga Navosa site (NN2) adjacent to Nalovo Creek, in Yanuca Channel, the meadows were composed predominantly of colonising species (low physiological resistance to disturbances, but recovering rapidly) which would suggest a dynamic environment, whereas the majority of meadows with sentinel sites along coastal sand banks (SV, DN) and sandy fringing reefs (CW, ND, TQ) were dominated by opportunistic species (moderate physiological resistance, but ability to rapidly recover from seed or new recruits) (Kilminster et al., 2015).

Over the long-term, Fiji's seagrass ecosystems have generally shown a high capacity to recover after loss. During periods of high disturbance and/or loss, the colonising *Halophila ovalis* quickly establishes in unoccupied areas suitable for growth and rapidly spreads. This colonisation can be concurrently with or followed by the opportunistic species *Halodule* spp. and *Syringodium isoetifolium*, which are the foundational seagrasses in Fiji. The high capacity to recover after disturbance/loss has been previously reported for seagrass meadows of the Fiji Islands, across a variety of habitats. For example, the extensive coastal

Syringodium and *Halodule* meadows at Denarau, first reported in 1991 (Lovell et al., 1991), were lost in 1993 as a result of sedimentation from dredging the north arm of the Nadi River (to create a marina basin and navigational channel leading into Nadi Bay) coupled with the impacts of a cyclone and associated flooding (Tamata et al., 1998). The meadows re-established within four years, assisted by *Halophila ovalis* colonisation, covering about 30% of the remaining habitable area (50% of the former habitable area was lost due to channel dredging and breakwater construction) (Tamata et al., 1998), and after a decade had expanded in extent and abundance (Fig. 4d). Similarly, on reef habitats, analysis of spatial patterns of seagrass meadows on Suva Reef from airborne images showed oscillations in extent and abundance (seagrass meadows extended towards the lagoon in some years and regressed in others) due to major disturbances such as tsunami, cyclones and flood (Vuki, 1994). Regression periods on Suva back reef areas also correlated with periods of high turbidity and siltation from foreshore reclamations (Vuki, 1994).

Over the 15 years of monitoring, seagrass ecosystems of the Fiji Islands demonstrated moderate to high stability, conferring a high level of resilience. This appears primarily a consequence of the predominance of opportunistic species which possess some ability to resist stressors and a high capacity to recovery from large disturbances.

One of the largest climatic disturbances to impact the Fiji Islands in the new millennium was TC Winston in February 2016. Lomaiviti Province in particular was badly hit with 100% of homes damaged or destroyed on Koro Island, and 80–90% of homes were lost on Ovalau (Mangubhai, 2016). A rapid assessment of coral reefs in the Vatu-i-Ra Seascape (Lomaiviti group) from 6 to 15 March 2016 reported significant damage to coral up to 20–30 m below the surface, however seagrass habitats were excluded from the assessment (Mangubhai, 2016). Nevertheless, a post-disaster socioeconomic questionnaire surveyed 154 coastal villages on the perceived damage to fisheries habitats from TC Winston and reported that respondents perceived seagrass habitats had been badly damaged in all provinces. Seagrass areas in Lomaiviti and Bua Province (western Vanua Levu) were believed to be most damaged, with the majority of villages stating damage was between 5 and 50% and 75–100%, respectively (Chaston Radway et al., 2016). However, results from long-term sentinel monitoring sites on Ovalau, within the region of the highly destructive winds, displayed only minor disturbance, indicating a relatively high level of resilience. This was supported by the predominance of opportunistic species providing a moderate level of resistance and a persistent seed bank providing recruits to facilitate recovery. This higher resilience of seagrass meadows of the Fiji Islands, however, does not suggest these important ecosystems are immune to environmental pressures, on the contrary, threats from human activities coupled with climate change are increasing (Waycott et al., 2011).

Threats to Fiji's seagrass ecosystems are driven by broader social and economic drivers (driving forces), including: population growth, urbanisation, tourism, and extractive industries. Driving forces exert pressures which lead to human activities that can adversely impact Fiji's seagrass ecosystems. These threatening activities include: urban/industrial runoff, coastal development, dredging, terrestrial runoff (agricultural, forestry, mining/quarrying), boating (e.g. propeller scars, anchoring), fishing (netting, traps, gleaning), shipping accidents (e.g. oil spills), seagrass harvesting and climate change related impacts (Grech et al., 2012). Climate Change is an overriding threat, particularly with increasing cyclone incidence and alterations to rainfall, temperature and light levels in areas vulnerable to extreme climatic events (Howes et al., 2018; Lough et al., 2011). All these activities can result in multiple and cumulative stressors which can or have the ability to degrade the growth and persistence of Fiji's seagrasses. For example, the higher light required by seagrass to drive photosynthetic rates due to rising sea temperatures, can be compromised by increased turbidity from terrestrial runoff limiting light availability, resulting in reduced growth rates and ultimately plant decline (Collier et al., 2016).

One of the greatest threats to seagrass ecosystems in the Fiji Islands is deteriorating water quality (turbidity and nutrients), from diffuse and direct sources, both chronic and acute in character (Grech et al., 2012; Singh, 2019). Elevated nutrients can affect seagrass by stimulating both epiphytic and macroalgae cover (Cabaço et al., 2013; Nelson, 2017), limiting light availability to seagrass blades for photosynthesis (Frankovich and Fourqurean, 1997; Tomasko et al., 1996) and resulting in seagrass decline (Nelson, 2017). When coupled with global warming, the effects of nutrient enrichment can be amplified (Mvungi and Pillay, 2019). Seagrass leaf tissues at all the sentinel seagrass sites in the present study were found to contain some level of anthropogenic sourced nitrogen, with higher levels at locations adjacent to the highest populations/households, e.g. Laucala Bay, Suva (SV) and Denarau (DN) (Table 1, Fig. 8).

Major anthropogenic sources of nitrogen are from domestic, commercial and industrial wastewater. In the Suva City area, all wastewater is transported to the Kinoya Wastewater Treatment Plant, which discharges secondary treated effluent into the northern part of Laucala Bay via a 1.6 km pipeline (Singh et al., 2009). Although oxidized nitrogen ($NO_x{-}N$) values within the bay, in the vicinity of the discharge, have been reported above ANZECC (2000) guidelines, higher values have been measured closer to shore indicating most elevated nutrients were from land-based sources (Singh et al., 2009). With sewerage infrastructure estimated to cover only 36% of the Suva City area (GoF, 2016, 2018), of concern is the poor water quality reported from small creeks (e.g. Nabukalou, Samabula and Vatuwaqa) which drain some of the most built-up areas and have a history of high contamination levels (nutrients and faecal coliforms); thought to be caused by broken sewage pipes and overflowing septic tanks (GoF and SPREP, 2014). It is therefore not surprising that the source of nitrogen taken up by seagrasses growing on the intertidal banks of Nasese (Laucala Bay), indicates N from primarily septic or treated sewage. The seagrass in Laucala Bay also had the highest $\delta^{15}N$ isotopic signatures of any seagrass assessed across Viti Levu and Ovalau.

Apart from elevated N entering Laucala Bay from creeks, stormwater drains and groundwater, the other significant inputs include informal settlements (*vakavanua* settlers) and watershed discharges. It is estimated that 7% of Fiji's population live in 200 informal squatter settlements around Fiji (Simmons, 2016), with the greatest proportion (71%) in the greater Suva area. Some of the largest and oldest settlements are located on the north-western shores of Laucala Bay at Vatuwaqa, Raiwaqa and Laucala Beach (Koto, 2011). Informal settlements are characterized by poor wastewater management, with raw sewage from pit and shared latrines being dumped directly into creeks and adjacent coastal waters of Laucala Bay. Sanitation facilities, however, are generally lacking for nearly 75% of Fiji's population (Dumaru, 2011), particularly in rural areas, where pit-latrines and inefficient septic tanks discharge into creeks and groundwater, which drain into coastal areas resulting in nutrient enrichment in seagrass ecosystems and macroalgae overgrowth of nearshore reefs, e.g. Coral Coast, Nadi Bay and the Mamanuca islands (Green, 1991; Mosley and Aalbersberg, 2003, 2005; Taloiburi, 2009). With over 90% of Fiji's population and most tourist accommodation located on Fiji's coast, significant volumes of sewage is discharged into the nearby marine areas and reefs. This is often compounded by animal waste (e.g. piggeries and poultries) which is often deposited into nearby waterways. Studies along Fiji's Coral Coast found that piggery waste contributed up to 28% of the nitrogen contained in coastal waters (Mosley and Aalbersberg, 2003). In response, appropriate solutions to pig-waste management have been implemented in some coastal villages to mitigate pollution impacts (Terry and Khatri, 2009).

In Laucala Bay, the other significant contributor of nutrients is the Rewa River. The Rewa River covers the largest drainage basin (2918 km^2) in the tropical South Pacific, approximately a third of the entire land area of Viti Levu, and discharges into north-eastern Laucala Bay (Terry, 2007). Long-term trends suggests water quality in the Rewa

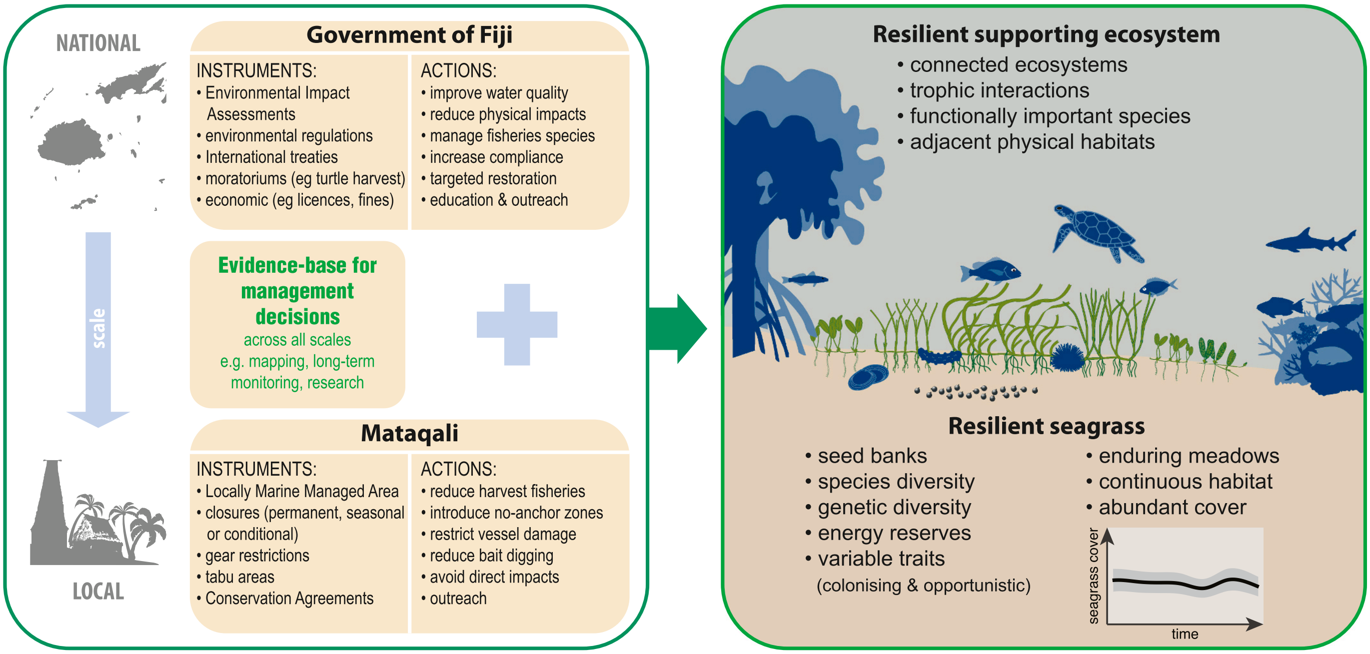

Fig. 9. Managing for resilient seagrass and supporting ecosystem in the Fiji Islands requires integrated management instruments and actions implemented across multiple scales, from national to local, which are underpinned by a solid evidence-base. Seagrass panel (right) modified from Unsworth et al. (2015).

River is deteriorating, indicated by increased algal growth and nutrient loading (phosphate and nitrogen have increased moderately) (GoF and SPREP, 2014). Nutrients discharged from the river originate from sewage pump overflows, industrial discharges, septic tank effluents, fertilizers, stormwater runoff, and other nonpoint sources (Singh et al., 2009). However, the biggest impact from the Rewa River to the seagrass ecosystems of Laucala Bay is its influence on turbidity via its freshwater input (Singh and Aung, 2009). Coupled with the resuspension events from the south-east trade winds, turbidity within the bay is generally high (Singh and Aung, 2009), limiting light available for photosynthesis. As a consequence, seagrass meadows are only found on the intertidal banks or the shallow reefs surrounding Laucala Bay.

Across the Fiji islands, the impact from terrestrial runoff on nearshore ecosystems is of greatest concern on the north and west coasts of Viti Levu and Vanua Levu (Sykes and Morris, 2007). This is likely a consequence of large-scale sugarcane agriculture and deforestation resulting in soil erosion and chemical fertilizers washing into waterways during times of high rainfall (Dadhich and Nadaoka, 2012). In addition, river sand extraction and the small number of mines (gold and copper) create sedimentation and, in some cases, toxic waste run-off into rivers and subsequently into coastal waters (Sykes and Morris, 2007). The only sentinel seagrass site in this study on the west coast of Viti Levu was the coastal meadows at Denarau (DN) in Nadi Bay, where the discharging watersheds are categorised as moderately to highly impacted/degraded (GoF and SPREP, 2014).

Not all activities threatening Fiji's seagrass ecosystems are larger scale and diffuse, as impacts of some activities are localised. Coastal development is a significant local threat in many areas of Fiji, but predominately in Viti Levu and mostly near major urban areas, coastal towns and tourism areas (Dumaru, 2011; Vuki et al., 2000). For example, around Nadi, the Coral Coast and the Mamanuca Islands, excavation of channels and reef-top pools for resort developments have destroyed and disturbed seagrass meadows (Hall, 2001; Hughes et al., 2005; Sykes, 2003). The construction of the resort causeway across Yanuca Channel restricted current flows, resulting in the accumulation of sediments from Nalovo Creek (Terry et al., 2006) and seagrass degradation at the sentinel site (NN2). Around Suva, high turbidity and siltation arising from foreshore reclamation and coral sand dredging have impacted seagrass meadows (Penn, 1981; Vuki, 1994). Other localised disturbances in tourism areas includes the active removal of seagrass by beachfront hotels in the belief that meadows are unsightly or harbour organisms causing injury to bathers (Daby, 2003; Taylor, 2018). Most other localised physical impacts to seagrass in Fiji include incidental damage from trampling while gleaning, or small scale harvesting as a source of agri-fertilizers for local communities. For example, *Syringodium isoetifolium* is harvested by Dakuni villagers in Beqa and added to the base of tomato seedlings, as it is reported to produce bigger, disease and pest-free plants with more fruits (N'Yeurt et al., 2013; N'Yeurt and Iese, 2015).

The threats to seagrass meadows are not only impacting an important resource, in many areas they are also threatening a way of life for those people closely associated either directly or indirectly with the ecosystem (Cullen-Unsworth et al., 2014). All of these issues and associated threats pose a challenge for conserving resilient seagrass meadows in the Fiji Islands.

4.1. Managing for resilience

Seagrass ecosystem management that centres upon resilience requires a hierarchical approach from the most general and large scale (regional and country-wide), cascading down to local and smaller meadow-scale issues (Unsworth et al., 2015) (Fig. 9). There is currently no legislation under which seagrass are specifically protected in Fiji, but they are afforded management considerations through a number of acts, policies and environmental agreements, including: the Environment Management Act 2005; Sea Ports Management Act 2005; National Biodiversity Strategy and Action Plan (GoF, 2017); Convention on Wetlands of International Importance (Ramsar); and Memorandum of Understanding on the Conservation and Management of Marine Turtles and their Habitats of the Indian Ocean and South-East Asia (IOSEA Marine Turtle MoU).

Managing pressures to minimise stressors on seagrass ecosystems depends greatly on the threatening activities, the scale at which they occur and whether they are diffuse or localised. Regional and country-wide management issues are generally approached at a national level. Nationally, the Ministry of Fisheries is the main institution involved in decision-making regarding marine and coastal resources in Fiji. Other government institutions which also have some involvement include:

Department of the Environment; Ministry of Industry Trade & Tourism; and the Land Use Division of the Ministry of Lands and Mineral Resources (Gonzalez et al., 2015). The types of actions that can be taken nationally to increase the resilience of Fiji's seagrass ecosystems may include: improving water quality from catchments and human settlements to reduce algal overgrowth and ensure light availability for photosynthesis; controlling the use and disposal of chemical toxicants which can inhibit plant growth; managing coastal development to ensure seagrass meadows are not directly or indirectly impacted; and managing key fishery species and predators to ensure food webs and herbivory are balanced (Unsworth et al., 2015) (Fig. 9).

Locally, coastal marine resources in Fiji are utilised and managed by local communities/villages (*mataqali*), that traditionally control marine areas as customary fishing grounds (*qoliqoli*), including coral reefs, seagrass meadows and mangroves (Golden et al., 2014; Mangubhai et al., 2020). The fishing rights of each *qoliqoli* are held by the various respective *yavusa* (tribes). There are a number of instruments used locally to manage coastal marine resources, including locally-managed marine areas (LMMAs) (Hastings et al., 2012). A third of the long-term seagrass monitoring locations in the present study were within LMMAs (Table 1). LMMAs integrate traditional ecological knowledge and scientific/expert knowledge, and involve local resource users and government in developing strategies and actions to sustainably manage fisheries resources and biodiversity (Newell et al., 2019; Tyllianakis et al., 2019). Management strategies and actions may include permanent closures (where resource extraction is prohibited permanently), conditional closures (controlled and uncontrolled harvesting), gear restrictions, seasonal/species bans and sacred *tabu* sites (Mills et al., 2011; Tyllianakis et al., 2019). Recognised as one of the more innovative initiatives for conservation of marine resources in Fiji, there are 411 LMMAs covering 30,011.09 km^2 established inside different *qoliqolis* (Sloan and Chand, 2016). The types of actions that can be taken locally to increase the resilience of Fiji's seagrass ecosystems could include: reducing physical impacts from localised development and harvesting activities; minimising damaging activities by improving local people's knowledge of the value, sensitivity and locality of seagrass meadows through outreach programs (e.g. LäjeRotuma Initiative (LäjeRotuma, 2007; Ralifo, 2008)); increase compliance with environmental regulations (e.g. sewage discharge) to improve seagrass health; securing the health of connected habitats such as mangroves and coral reefs; and implementing monitoring to provide early warning of issues of concern by supporting observing networks such as Seagrass-Watch (www.seagrasswatch.org) (Coles et al., 2011; Duffy et al., 2019; Unsworth et al., 2015) (Fig. 9).

An emphasis on promoting ecosystem resilience may result in changes to existing management approaches, such as spatial plans developed for marine protected areas targeting seagrass ecosystems and focusing on protecting key features of resilience and ecosystem services (Unsworth et al., 2018). Targeting research gaps to provide critical information may also be required. Genetics assessments are generally lacking in Fiji and the Pacific Islands, and a key element of resilience is maintenance of genetic diversity and connectivity, where the supply of reproductive material (dispersal distance) if restricted, can render an otherwise healthy meadow recruitment limited (Grech et al., 2016). For example, the *Syringodium* meadow in Maka Bay, Rotuma, is likely to be a single clone highly vulnerable to large scale impacts and if lost would require active intervention strategies such as innovative restoration techniques. Also, in species depauperate meadows, genotypic diversity may provide enhanced physiological resistance and phenotypic variation (the expression of genetic traits) can create diversity in morphometric and resilience traits (Unsworth et al., 2015). The lack of seagrass genetic information for Fiji and the Pacific Islands therefore renders management responses to future losses challenged (Unsworth et al., 2019).

For seagrass meadows to persist and continue to provide their important ecosystems services in the Fiji Islands, in a changing climate, will require an integrated management approach and recognition of importance of cumulative impacts. Any management actions to protect seagrass meadows, however, will depend not only on biological and ecological issues, but also on socio-economic factors (e.g., livelihoods, local scientific capacity, stakeholder involvement, availability of funding) (Unsworth et al., 2015).

5. Conclusions

Over a decade of monitoring seagrass status and condition in Fiji has demonstrated the resilience of the nation's seagrass ecosystems to local and global pressures, including extreme climatic events. This is contrary to reports that seagrass in parts of the Pacific are declining in line with global trends (Short et al., 2014). The resilience of Fiji's seagrass meadows appears primarily a consequence of the foundational seagrass species being opportunistic (moderate physiological resistance, but ability to rapidly recover from seed or new recruits) and the meadows enduring in character.

Seagrass ecosystems are a significant feature in nearshore areas across the Fiji Islands, however, regional and local pressures continue to threaten their persistence and the ecosystem services underpinning local livelihoods. Of concern, is cumulative threats coupled with a globally changing climate. For seagrasses to persist in such an environment, they will need to remain resilient. Minimising or mitigating stressors through effective management is critical and will require informed research and monitoring activities. However, effective management of Fiji's seagrass ecosystems will necessitate consideration of conservation needs within the constraints of a rapidly developing economy.

CRediT authorship contribution statement

Len McKenzie: Conceptualisation, Methodology, Investigation; Formal analysis; Visualization; Roles/Writing - original draft, revised draft. **Rudi Yoshida**: Conceptualisation, Methodology, Investigation; Data curation; Visualization; Roles/Writing - original draft, revised draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.marpolbul.2020.111636. These data include the Google map of seagrass species occurences described in this article.

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