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Seagrass ecosystems of the Pacific Island Countries and Territories: A global bright spot

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ABSTRACT

Seagrass ecosystems exist throughout Pacific Island Countries and Territories (PICTs). Despite this area covering nearly 8% of the global ocean, information on seagrass distribution, biogeography, and status remains largely absent from the scientific literature. We confirm 16 seagrass species occur across 17 of the 22 PICTs with the highest number in Melanesia, followed by Micronesia and Polynesia respectively. The greatest diversity of seagrass occurs in Papua New Guinea (13 species), and attenuates eastward across the Pacific to two species in French Polynesia. We conservatively estimate seagrass extent to be 1446.2 km^2, with the greatest extent (84%) in Melanesia. We find seagrass condition in 65% of PICTs increasing or displaying no discernible trend since records began. Marine conservation across the region overwhelmingly focuses on coral reefs, with seagrass ecosystems marginalised in conservation legislation and policy. Traditional knowledge is playing a greater role in managing local seagrass resources and these approaches are having greater success than contemporary conservation approaches. In a world where the future of seagrass ecosystems is looking progressively dire, the Pacific Islands appears as a global bright spot, where pressures remain relatively low and seagrass more resilient.

1. Introduction

Seagrass ecosystems occur throughout sheltered near-shore marine waters of 163 countries globally (McKenzie et al., 2020), providing structure and biological functions critical for supporting the health and well-being of the environment on which coastal human populations rely. Seagrasses are unique marine flowering plants which engineer shallow coastal environments and form diverse meadows estimated to cover between 160,387 km^2 and 266,562 km^2 globally (McKenzie et al., 2020); nearly half occurring in the Indo-Pacific region.

In the Pacific Island Countries and Territories (PICTs), seagrass ecosystems are recognised for their provision of food and a source of

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livelihoods for Pacific Islanders (Cullen-Unsworth et al., 2014; Unsworth et al., 2018b; Waycott et al., 2011). These seagrass meadows also support high biodiversity that includes charismatic megafauna such as the dugong (*Dugong dugon*) and green sea turtle (*Chelonia mydas*) which are seagrass specialists and culturally important to Pacific Islanders (Craig et al., 2004; Marsh et al., 2011; Woodrom Rudrud, 2010). Seagrasses in the PICTs also provide critical ecosystem contributions such as habitat, coastal protection, nutrient cycling, improving water quality, and mitigating pathogenic bacteria to the benefit of humans, fishes, and marine invertebrates such as coral (Gacia et al., 2003; Lamb et al., 2017; Madsen et al., 2001; McKenzie et al., 2021). In addition, the incorporation of carbon within seagrass tissues can affect local pH, thereby mitigating the effects of ocean acidification affecting coral reefs, and the retention of carbon within seagrass meadow sediments contributes significantly to climate change mitigation as well (Duarte and Krause-Jensen, 2017; Fourqurean et al., 2012; Macreadie et al., 2017; Unsworth et al., 2012). The ecosystem contributions provided by seagrasses across the Pacific Islands therefore make them a high conservation priority (Cullen-Unsworth and Unsworth, 2013; McKenzie et al., 2021; Unsworth and Cullen, 2010; Unsworth et al., 2018a, 2019).

Despite their importance, little is known of the status of seagrass ecosystems across the PICTs, which are likely under increasing threats from anthropogenic activities, further exacerbated by pressures related to global climate change (Coles et al., 2011; Cullen-Unsworth and Unsworth, 2013; Grech et al., 2012; Waycott et al., 2011). As a result of these pressures, the resilience of seagrass ecosystems across the PICTs is becoming compromised. Vulnerability analysis indicates that there is likely to be a moderate loss of seagrass habitats estimated between <5 and 20% by the year 2035 and 10 to 50% by 2100 (Waycott et al., 2011).

To examine seagrass ecosystems across the Pacific Islands, we grouped the countries and territories into Melanesia, Micronesia, Polynesia. Melanesia (5,500,000 km^2) is located in the southwest Pacific, Polynesia (13,200,000 km^2) in the central - eastern Pacific and Micronesia (8,800,000 km^2) in the central - northwest Pacific (Fig. 1). The PICTs have a variety of high islands and low atolls, each with a range of marine environments, some of which are suitable for seagrass colonisation and growth. The regions have rich geological histories, are exposed to frequent extreme events, and include a range of climates and complex oceanographic processes.

To improve our understanding of seagrass distribution, biogeography, and status, we start to fill the gaps in broad regional knowledge by reviewing spatial and temporal data sources and information about seagrass throughout the PICTs. We confirm (validate) the occurrence of seagrass species in each of the countries and territories through extensive literature and herbarium searches, as well as field surveys. We also provide the most up-to-date review of seagrass spatial extent, condition and long-term trends. Finally, we examine the human activities threatening seagrass ecosystems and the management approaches to mitigate these threats, and recommend a number of actions to ensure the long-term resilience of seagrass ecosystems and the continued provision of their natural contributions.

2. Background

2.1. Study area and physical geography

The Pacific Island Countries and Territories (PICTs') refers to 22 large ocean states and territories, including: American Samoa, Cook Islands, Federated States of Micronesia, Fiji, French Polynesia, Guam, Kiribati, Mariana Islands (CNMI), Marshall Islands, Nauru, New Caledonia, Niue, Palau, Papua New Guinea, Pitcairn Islands, Samoa, Solomon Islands, Tokelau, Tonga, Tuvalu, Vanuatu, and Wallis and Futuna (Fig. 1, Table 1). Although the PICTs have a combined Exclusive Economic Zone (EEZ) of >27 million square kilometres, they include some of the smallest countries in the world in terms of land mass, with islands ranging from large continental (e.g. Papua New Guinea and New Caledonia) and oceanic high volcanic (e.g. Solomon Islands, Vanuatu, and Fiji) to medium raised islands (e.g. Niue, Nauru and Tonga), to small low-lying atoll islands (e.g. Kiribati and Tuvalu) (Table 1).

The region has a rich geological history, and although the origins of

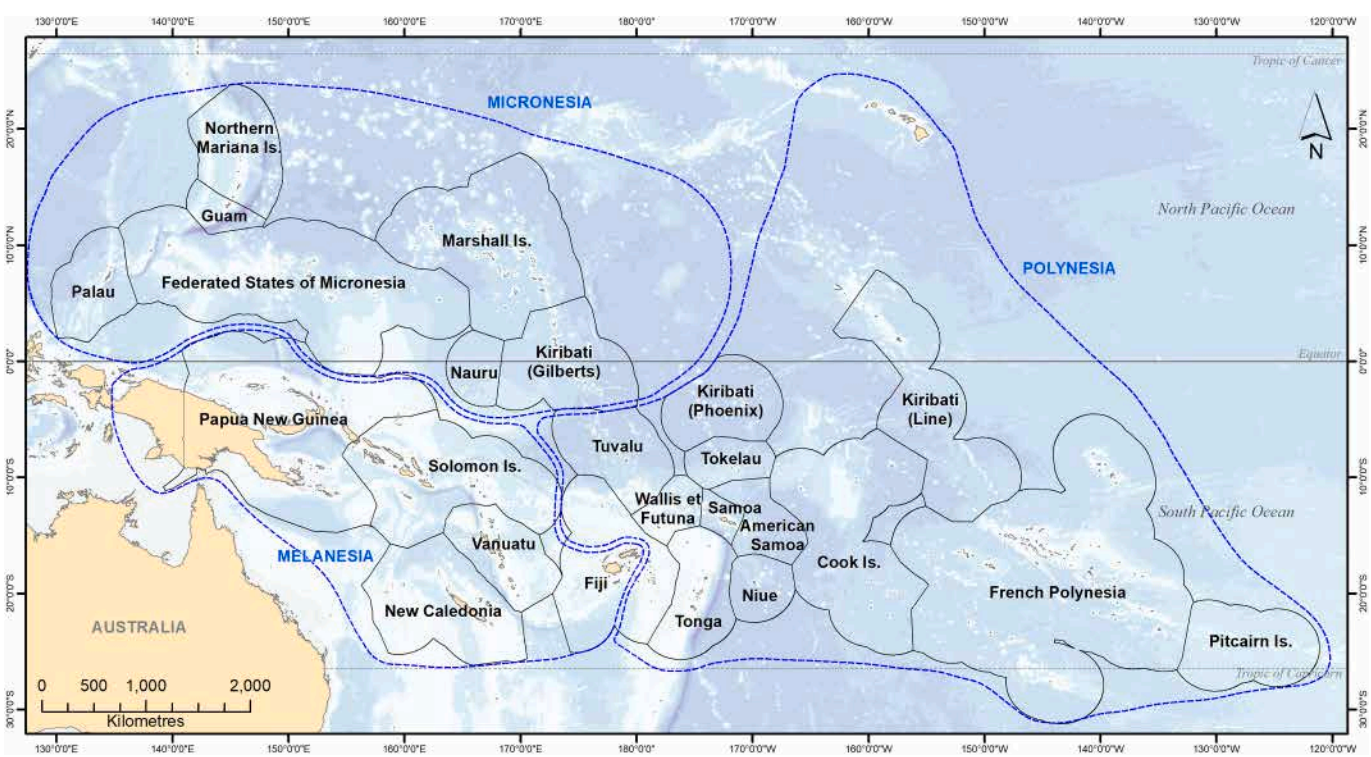

Fig. 1. Pacific Island Countries and Territories (PICTs) and their Exclusive Economic Zones (EEZ). Ethno-geographic delineation based on Taylor and Kumar (2016) and Burley (2013).

Table 1
Description of each PICT, including type and number of islands, land area, length of coastline and population. Land area and coastline length from McKenzie et al. (2020). Population estimates from Andrew et al. (2019).

PICT	Island type/s	Number of islands	Land area (km^2)	Coastline (km)	Population			
					Total	% 1 km	% 5 km	% 10 km
Melanesia			540,260	41,471	7,046,717	18	38	47
Fiji (Republic of)	High islands + many atolls	320 islands	18,333	4638	837,271	27	76	91
New Caledonia	1 high continental + many coral and limestone origin	12 islands	18,576	3624	268,767	57	90	94
Papua New Guinea	High continental and volcanic + few atolls	>600 islands	462,840	20,197	5,190,786	8	21	30
Solomon Islands	Volcanic high islands in double chain running NW to SW	992, with 6 large and many small low-lying islands	28,230	9880	515,870	65	91	98
Vanuatu (Republic of)	Volcanic high islands in Y-shaped archipelago	83 high islands	12,281	3132	234,023	64	94	99
Micronesia			3156	8519	506,541	72	99	100
Federated States of Micronesia	Atolls + volcanic and metamorphic high islands.	607 low-lying atoll islands, with four volcanic ones	701	1295	102,843	89	100	
Guam	Uplifted ophiolite with raised limestone plateau	1 emergent island	541	126	159,358	30	97	100
Kiribati	Volcanic high islands + atolls	29 low-lying coral atolls, 5 islands and 879 reefs	811	1961	109,693	100		
Marshall Islands (Republic of)	Atolls	34 low-lying islets and 607 atolls	181	2106	53,158	100		
Nauru	Elevated coral/phosphate rock island with exposed fringing reef	1 emergent island	21	30	9945	93	100	
Northern Mariana Islands (CNMI)	Chain of high volcanic islands + uplifted coral reefs	14 islands and 8 islets	457	1482	53,883	69	100	
Palau	Volcanic high island + numerous limestone islands and atolls	1 high island and >300 small islands, islets and atolls	444	1519	17,661	93	100	
Polynesia			8126	7807	652,976	73	99	100
American Samoa	Volcanic high islands + atolls	5 high islands and 2 coral atolls	199	116	55,519	61	100	
Cook Islands	High islands + atolls	20 small islands and several are low-lying atolls	237	120	14,974	91	100	
French Polynesia	High islands and reefs + atolls	35 islands and 83 atolls in 5 main groups	3521	5830	268,207	79	100	
Niue	Elevated coral platform with cliffs	1 emergent island	259	64	1460	25	83	100
Pitcairn Islands	High volcanic cliff islands + atolls	2 islands and 2 atolls	47	51	57	100	100	
Samoa	Volcanic high islands + atolls	2 large islands, 2 smaller islands and 5 islets	2934	463	187,820	61	97	100
Tokelau	Atolls	3 low-lying coral atolls	12	101	1411	100		
Tonga	Volcanic high and uplifted limestone islands overlying a volcanic rock base + atolls	169 islands in 3 major groups	749	909	100,691	84	100	
Tuvalu	Small islands + atolls	4 reef islands and 5 low-lying atolls	26	24	10,640	100		
Wallis and Futuna	Volcanic high islands + islets	3 islands and 19 islets, in 2 groups	142	129	12,197	67	100	

the Pacific Ocean extend back 750 Ma, the current ocean floor originated about 167 million years ago, when the Pacific plate spread to the west of Pangea (Neall and Trewick, 2008). As the broad Pacific plate crept NW, a number of major processes resulted in the formation of linear chains of volcanic islands either by mantle plume or propagating fracture origin, atolls, uplifted coralline reefs, fragments of continental crust, abducted portions of adjoining plates and islands resulting from subduction along convergent plate margins, over the past 80–100 million years (Maragos and Williams, 2011). The subduction zones and deep ocean trenches form the eastern borders of the Marianas, New Guinea and Fiji, and stretch from the western end of Samoa through Tonga, Vanuatu, and Solomon Islands. Continental islands lie south westward of the Andesite Line, while the basaltic volcanic islands lie to the east, forming distinct geographic and biogeographic units (Bani and Esrom, 1993). As a consequence, the archipelagos towards the NW are generally older, and younger towards the SE margins of the plate (Neall and Trewick, 2008).

Environmental pressures vary across the PICTs, and include episodic events related to geological activity (e.g. earthquakes and volcanic eruptions) and climate. The eastern PICTs either contain, border or are immediately adjacent to, Pacific plate subduction zones; areas of high prevalence of seismic activity threatening not only people's lives, but the environments on which they rely. The Pacific subduction zones create major earthquake and tsunami events, where subsidence and seismic uplift deepen waters or increase emersion times, and waves heights cause major landslides that deposit sediment onto coastal seagrass meadows. Volcanic ash and rafts of pumice further exacerbate stressors on the marine environment.

2.2. Climate and the marine environment

Climate of the PICTs is tropical, displaying seasonal wet and dry periods driven by the surrounding ocean temperatures. These are influenced by island topography, trade winds, and can vary considerably from year to year due to the El Niño-Southern Oscillation (ENSO). Islands within 10° latitude of the equator experience mean annual air temperatures of 26.5–30 °C (Fig. 2). Climate in the PICT region is significantly influenced by three large-scale wind convergence zones; the Intertropical Convergence Zone (ITCZ), the South Pacific Convergence Zone (SPCZ) and the West Pacific Monsoon (WPM). Large-scale atmospheric circulation patterns influence ocean currents and sea-surface temperature patterns, while the ocean in turn also affects atmospheric winds, temperatures and rainfall. Equatorial trade winds push warm water to the west, giving rise to the Warm Pool, and drive the upwelling of cooler water in the eastern Pacific; while the warmer water near the equator and the Warm Pool in particular, drive strong

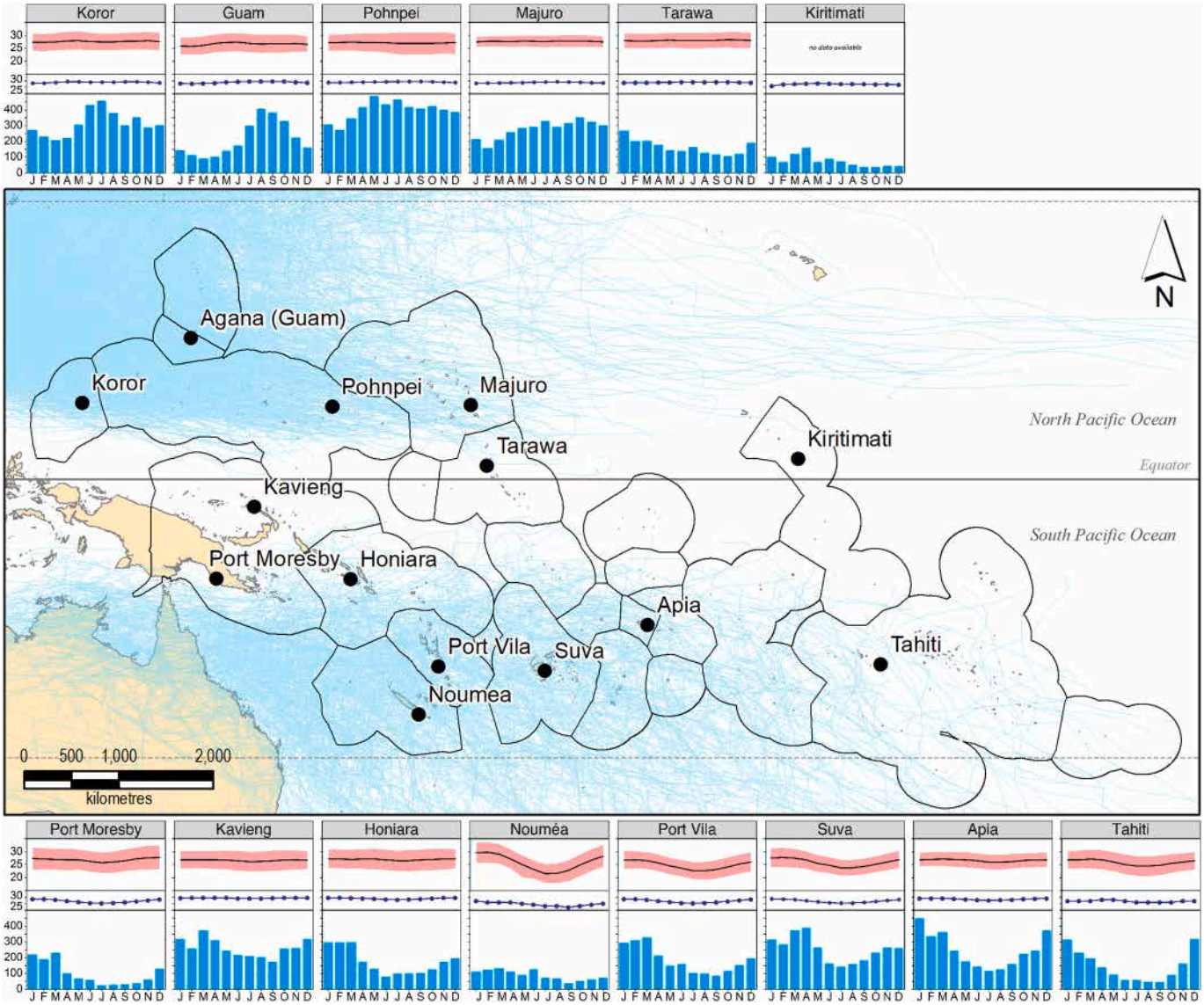

Fig. 2. Long-term seasonal rainfall and air/water temperature plots at key locations in the PICTs, and tracks of tropical cyclones and typhoons (1800–2019). Each plot is divided into three components, each with standardised y-axis; the lowest portion (bar graph) is the monthly rainfall, y-axis = 0-500 mm, tick intervals = 50 mm; the centre portion is the monthly average sea surface temperature, y-axis = 20–35 °C, tick intervals = 5 °C; and the top portion is monthly average temperature (black line) and mean maximum to minimum range (red area), y-axis = 20–35 °C, tick intervals = 5 °C. Climate data from the Pacific Climate Change Data Portal (PCCDP) (www.pacificclimatechangescience.org/). Where required, sea temperatures were accessed from the daily satellite readings provided by the NOAA (www.seatemperature.org/australia-pacific/). Cyclone/typhoon data from the Southern Hemisphere Tropical Cyclone Data Portal (SHTCDP) (www.bom.gov.au/cyclone/tropical-cyclone-knowledge-centre/history/tracks/) and cyclone tracks (light blue lines on map) courtesy International Best Track Archive for Climate Stewardship (IBTrACS), NOAA, https://www.ncdc.noaa.gov/ibtracs/ (Knapp et al., 2010, www.ncdc.noaa.gov/ibtracs/). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

convection in the overlying atmosphere which helps to draw the trade winds across the Pacific Ocean (ABoM and CSIRO, 2011). Most of the PICTs experience extreme events including tropical cyclones/typhoons, storm surges, heat waves, drought and heavy rainfall. Tropical cyclones/typhoons generally occur with 10°–25° latitude in both hemispheres, where the ocean is warm enough to provide the energy for their formation and the strength of the Coriolis effect is sufficient for them to spin up (CSIRO et al., 2015). Tropical cyclones/typhoons produce damaging winds, heavy rainfall and storm surges, which can have devastating impacts on coastal environments.

The ITCZ extends across the Pacific just north of the equator and influences climate in Micronesia, and northern Near and Remote Oceania (Guam, CNMI, Federated States of Micronesia, Kiribati - Gilberts, Marshall Islands, Nauru, Palau, Papua New Guinea and northern Solomon Islands) (Australian Bureau of Meteorology and CSIRO, 2011). The islands within the Warm Pool to the west, experience very high seasonal rainfall variations (between 2000 and 4000 mm annually) associated with the WPM, however in the northern Remote Oceania islands (Nauru, Marshall Islands and Kiribati) the annual rainfall is below 2000 mm (e.g. Kiritimati, Kiribati) (Fig. 2). Rainfall patterns are influenced by the seasonal movement of the ITCZ as it moves north and south of the equator. Islands north of the equator, generally experience a dry season from November to April–May and a wet season from May–June to October, although closer to the equator the seasons are less pronounced (Fig. 2). For example, Kiribati does not have pronounced seasons, although at Tarawa, the driest period is from June to October. Cyclones/typhoons are more frequent to the northwest of the region, attenuating eastward (Fig. 2).

South of the equator, the SPCZ extends from the Solomon Islands to the Cook Islands, and affects most of the Polynesian and Melanesian PICTs by providing warm and humid tropical air, and marked seasonal rainfall variations (to over 3000 mm) (Fig. 2). During the summer wet season (November to April–May) the SPCZ moves south providing precipitation to southern PICTs, although closer to the equator the seasons are less pronounced as rainfall is relatively consistent year-round (e.g. Kavieng, PNG) (Fig. 2) (CSIRO et al., 2015; PNG NWS et al., 2015). Conversely, the climate is dryer and cooler during the winter dry season (May–June to October) when the SPCZ retracts north and subtropical high pressures from the Tasman sea reaches the southern PICTs (Fig. 2). Average annual air temperatures range from 20.8 to 30.7 °C and average annual sea surface temperatures range from 26.2 to 30.5 °C (Fig. 2). South of 10° latitude, the islands are influenced by the SE Trades winds. With increasing latitude towards the Tropic of Capricorn there is a more pronounced dry and cooler season, resulting in mean annual temperatures to 23–24 °C in New Caledonia, Tonga, and parts of French Polynesia (Fig. 2). Tropical cyclones occur in the subequatorial tropics between 10° and 25° latitude, and are more frequent to the west of the region, attenuating eastward (Fig. 2). For example, the Solomon Islands, New Caledonia, Vanuatu, Fiji and Tonga receive 2–3 cyclones per year on average, whereas Samoa, Wallis and Futuna, and Tuvalu receive less than one (Fig. 2).

Yearly variation is linked to ENSO events which result in climate variability on a 3–7 year timescale, particularly affecting winds and precipitation in two extreme phases; El Niño and La Niña (there is also a neutral phase). During El Niño events the SPCZ shift north-east, while the ITCZ shifts closer to the equator, resulting in increased rainfall near the equator and periods of drought occur across the north-west and south-west Pacific, combined with low mean sea levels (MSL) and relatively cool surface waters (CSIRO et al., 2015). In some PICTs, periods of drought can be severe, for example, in the Marshall Islands following severe El Niño events, rainfall can be reduced by as much as 80%, with the dry season starting earlier and ends much later than normal (MI NWSO et al., 2015). Conversely, for the islands to the east, El Niño events tend to bring wetter, warmer conditions than normal (e.g. Tuvalu) (Tuvalu Meteorological Service et al., 2015). During La Niña, however, the ITCZ and SPCZ tend to move away from the equator, reducing rainfall near the equator and increasing it to the north of the equator and south-west Pacific (CSIRO et al., 2015). During La Niña events, increased rainfall and higher than normal sea level can result in significant flooding across the north-west and south-west Pacific, while the eastern Pacific Islands droughts can be very severe (e.g. Kiribati) (CSIRO et al., 2015).

Across the PICTs, ocean currents and sea-surface temperature patterns are influenced by large-scale atmospheric circulation patterns. Both large- and small-scale currents play a major role across the Pacific Island. While water is pushed westward by the winds at the equator, creating the northern and southern equatorial currents, the interaction of the easterly trade winds and the Coriolis force drives surface currents (in the top 10–50 m) poleward away from the equator in both hemispheres via 'Ekman transport' (Ganachaud et al., 2011). These interactions create the eastward flowing counter currents; the North Equatorial Counter Current (NECC) under the ITCZ (near 5°N), and the South Equatorial Counter Current (SECC) under the SPCZ (near 8°S). Current flows can also be modified locally due to the interaction of the trade winds with island topography, creating counter currents and eddies (Australian Bureau of Meteorology and CSIRO, 2011). Currents can also vary inter-annually due to the influence of ENSO. During El Niño events, there is a weakening or even a reversal of the southeast trade winds, particularly in the west, resulting in higher eastward currents speeds along the equator (Ganachaud et al., 2011).

2.3. Human settlement and anthropogenic pressures

Melanesia is the oldest inhabited region, being settled between 13,000 and 47,000 years ago, whereas Polynesia is the youngest being settled more recently, beginning 3000 and 5000 years ago (Kirch, 2017). Non-indigenous (European) settlers moved into the Pacific Islands in the 1700s, beginning with the colonisation of western Micronesia in the early 1700s from the Spanish Philippines (Keppel et al., 2014). Permanent colonisation of remote Oceania by the French and English occurred in the 1800s with the introduction of commercial shipping and trade, and Christian missionaries. With the establishment of plantations and farms in remote Oceania, land ownership disputes and economic instability resulted in European governments intervening and implementing control; first in Polynesia (and also in New Caledonia in Melanesia), and then later in the rest of Melanesia. In Micronesia, the Spanish period was replaced by Germany after 1898 with the exception of the United States in Guam, followed by Japanese occupation between WWI and WWII, after which most of the region went under the control of the United States.

3. Methods

3.1. Seagrass diversity and distribution

To examine seagrass diversity and distribution across the PICTs, observations and field data were collected to create a seagrass baseline checklist. Seagrass species were identified as per Waycott et al. (2004). Additional information on seagrass species reported from the region 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; Nationaal 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); Global Biodiversity Information Facility (GBIF); content analysis of photographs, using the freely accessible photo-sharing website Flickr (Richards and Friess, 2015); and the contributory citizen science and citizen engagement programs iNaturalist and SeagrassSpotter (Jones et al., 2018).

Although the taxonomy of the majority of seagrass species in the PICTs is widely accepted, there remains debate around the identify of *Halophila ovata* and *Halophila minor* specimens reported from Micronesia (Kuo, 2000). As per Tsuda and Sukhrajn (2016), we used the name *Halophila gaudichaudii* J. Kuo in their place until a detailed molecular analyses can be conducted on the Micronesian specimens. We have also retained the use of *Cymodocea serrulata* until a more detailed assessment is completed, as there remains debate about its identity. Phylogenetic and morphological studies by Petersen et al. (2014) showed that *Cymodocea* is polyphyletic, and although Christenhusz et al. (2018) resolved this by transferring *Cymodocea serrulata* to *Oceana serrulata* (R.Br.) Byng & Christenh., Ferrer-Gallego and Boisset (2020) suggested revision to *Caulinia serrulata* R.Br.

The latitude and longitude included with species collections/observations were used to examine the distribution of seagrass species across the PICTs. Where a position was not listed, we estimated the latitude and longitude (WGS1984) using Google Earth (earth.google.com/web/) based on the description of location and included an accuracy estimate (see Table S1). Species occurrence data were used to generate spatial interpolation species richness maps (surface plots and contours) using the geostatistical and spatial analyst extensions in ArcGIS®10.7 (Environmental Systems Research Institute). Seagrass species richness was measured within 2° grids, using occurrence data, and the predictive output spatially interpolated using a simple Kriging algorithm.

To examine temporal trends in species occurrence records, we selected three distinct periods of seagrass science/learning on which to base our assessment: pre-1970, 1970 to 2000, and 2000 to present. This was because prior to 1970, seagrass science globally was predominantly focused on providing an inventory of seagrass species occurrence and morphological taxonomy. Following the publication of the seminal work "The Sea-Grasses of the world" by den Hartog (1970), was three decades where scientists responded to the need for more information on seagrasses by conducting research that resulted in a 100-fold increase in the number of papers published annually (Orth et al., 2006). In 2000, global seagrass monitoring and assessment programs (e.g. Seagrass-Watch Global Seagrass Observing Network) were established, and the following two decades have seen the expansion of the global seagrass observing network (including within the PICTs), the introduction of citizen science initiatives such as SeagrassSpotter, and increased global awareness of seagrass ecosystem contributions to human quality of life (Cullen-Unsworth et al., 2014; Duffy et al., 2019; Jones et al., 2018; McKenzie et al., 2021). In line with the IUCN Red List process (IUCN SPC, 2019), we also recognise a species may be presumed locally extinct within a Pacific Island Country or Territory, where there have been no verified collections for over 50 years.

3.2. Seagrass status and meadow spatial extent

To assess status and trend, an inventory of seagrass meadow extent and a qualitative assessment of seagrass ecosystem trends throughout the region was compiled from published literature and data using online searches (Google Scholar and Google), freely accessible seagrass data portals, and authors' personal data collections. This identified 91 assessments/datasets of long-term trends at locations or sites in the region, which ranged from statistical analysis of measured data to expert opinion. To examine the long-term trends in seagrass ecosystem state, we restricted our analysis to include only sites/locations assessed more than two repeated observation events, over a period >3 years. This resulted in the exclusion of 34 datasets (Table S2). A multi-criteria analysis approach was used to semi-quantitatively score the confidence for each assessment of seagrass ecosystem trends for a location or site. This follows the approach successfully implemented for the Great Barrier Reef Marine Monitoring Program (Waterhouse et al., 2018). Each criterion was scored using a defined set of scoring attributes (Table S3). The determination of confidence for the long-term assessment used five criteria: maturity of methodology (the score was weighted half for this criteria so as not to outweigh the importance of the other criteria), validation, representativeness, directness and measured error (Waterhouse et al., 2018). The strength of this approach is that it is repeatable, transparent and can include contributions from a range of sources.

4. Results and discussion

4.1. Seagrass species

We confirm seagrass to occur in 17 of the 22 PICTs (Table 2), based on 912 verified records (collections from a spatial point) (Table S1). Sixteen species of seagrass have been reported from the PICTs (Table 2), these are: *Cymodocea rotundata* Ehrenberg and Hemprich ex Ascherson; *Cymodocea serrulata* (R. Brown) Ascherson & Magnus; *Enhalus acoroides* (L.f.) Royle; *Halodule pinifolia* (Miki) den Hartog; *Halodule uninervis* (Forsskål) Ascherson; *Halophila capricorni* Larkum; *Halophila decipiens* Ostenfeld; *Halophila gaudichaudii* J. Kuo; *Halophila minor* (Zoll.) den Hartog; *Halophila ovalis* (R. Brown) J.D. Hooker; *Halophila spinulosa* (R. Brown) Ascherson; *Ruppia maritima* Linnaeus var. *pacifica* H. St. John &

Table 2
Seagrass species confirmed within each PICT, including trends in seagrass state, spatial extent of meadows mapped with high confidence, and estimated spatial extent from the Allen Coral Atlas (2020). Most recent period verifying occurrence of species: *P* = 2000 to present (green fill), *p* = 1970 to 2000 (gray fill), and *e* = pre-1970 (presumed locally extinct) (gold fill). Trends in seagrass state are: n = no long-term trend (highly variable or stable), I = increase, D = decrease, – = not determined, parenthesis indicates anecdotal/possible trend. Trend confidence category: # = low; ~ = moderate; ^ = high. For sources, see Supplementary data (Tables S1, S4). Extent sources: a, McKenzie and Yoshida (2020); b, Andréfouët et al. (2010); c, Skewes et al. (2003); d, McKenzie et al. (2020); e, Paulay (2000); f, Purkis et al. (2017); * mapping incomplete.

PICT	# spp	*C. rotundata*	*C. serrulata*	*E. acoroides*	*H. pinifolia*	*H. uninervis*	*H. capricorni*	*H. decipiens*	*H. gaudichaudii*	*H. minor*	*H. ovalis*	*H. spinulosa*	*R. maritima*	*S. isoetifolium*	*T. hemprichii*	*T. ciliatum*	*Z. muelleri*	Trend (including confidence)	Meadow extent (high confidence) (km^2)	Allen Atlas meadow extent (km^2)
Melanesia																				
Fiji	6				P	P		P			P		p	P				n^	59.19[a]*	500.76
New Caledonia	12	P	P	P	P	P	p	P		p	P		P	P	P			n~	936.35[b]	522.2
Papua New Guinea	13	P	P	P	P	P		p		p	P	p		P	P	p	p	n~	117.2[c]*	1,092.5
Solomon Islands	10	P	P	P		P		P		P	P			P	P	P		n~	78.96[d]	506.3
Vanuatu	13	P	P	P	P	P	P	P		p	P		P	P	P			n^		26.97
Micronesia																				
Federated States of Micronesia	8	P	p	P					p		p			p	P	P		n (I)^	48.69[d]	66.71
Guam	3			P		P			P									D~	3.07[d]	5.2
Kiribati	3												p		P	P		I~	2.76[e]*	
Marshall Islands	4	P		P					P						e			–		
Nauru	0																		0	
Northern Mariana Islands	3			P		p			P									D^	6.67[d]	2.48
Palau	10	P	P	P	P	P			P		P			P	P	P		n~	79.98[d]	74.97
Polynesia																				
American Samoa	2										p			P				–		1.18
Cook Islands	0																		0	
French Polynesia	2							P			P							n (I)~	28.7[d]*	1.69
Niue	0																		0	
Pitcairn Islands	0																		0	
Samoa	4					P				P	P			P				I#		14.34
Tokelau	1													P				–		0.11
Tonga	6				e	P					P		e	p				n (I)~	17.65[f]*	22.9
Tuvalu	0																		0	0.01
Wallis et Futuna	4				P	P					P			P				–	24.3[d]	1.45

Fosberg; *Syringodium isoetifolium* (Ascherson) Dandy; *Thalassia hemprichii* (Ehrenberg) Ascherson; *Thalassodendron ciliatum* (Forsskål) den Hartog; *Zostera muelleri* subsp. *capricorni* (Ascherson) S.W.L. Jacobs (Table S1).

Records of confirmed seagrass occurrence (e.g. herbarium specimens) in the Pacific Islands vary greatly over the past two centuries. The earliest seagrass record was *Halophila gaudichaudii* in 1817 from the Northern Mariana Islands, and since then the number of records has increased considerably from an annual rate of 1.5 records in the period leading up to 1970, to 11.2 records annually between 1970 and 2000, and 17.3 records annually thereafter. Prior to the 1970s, Pacific seagrass records were from expeditions of scientific discovery (e.g. Louis de Freycinet voyages 1817–1820 and Challenger expedition of 1872–1876) and botanical collections (e.g. botanists Balansa, Setchell, Stone, Fosberg, and Sachet) (Table S1). From 1970 to 2000, collections increased in association with fundamental research conducted by universities, research institutions and government organisations. In the new millennia, with the mainstreaming of seagrass awareness and conservation advocacy, collections further expanded to include non-government organisations and citizen scientists. The decades with the largest number of records were the 2000s and 1970s (Fig. 3a). Verified records also differ between individual PICTs and regions, with the greatest number from Fiji, while only one record exists from Tokelau (Fig. 3b, Table S1). The occurrence of some species was not confirmed in

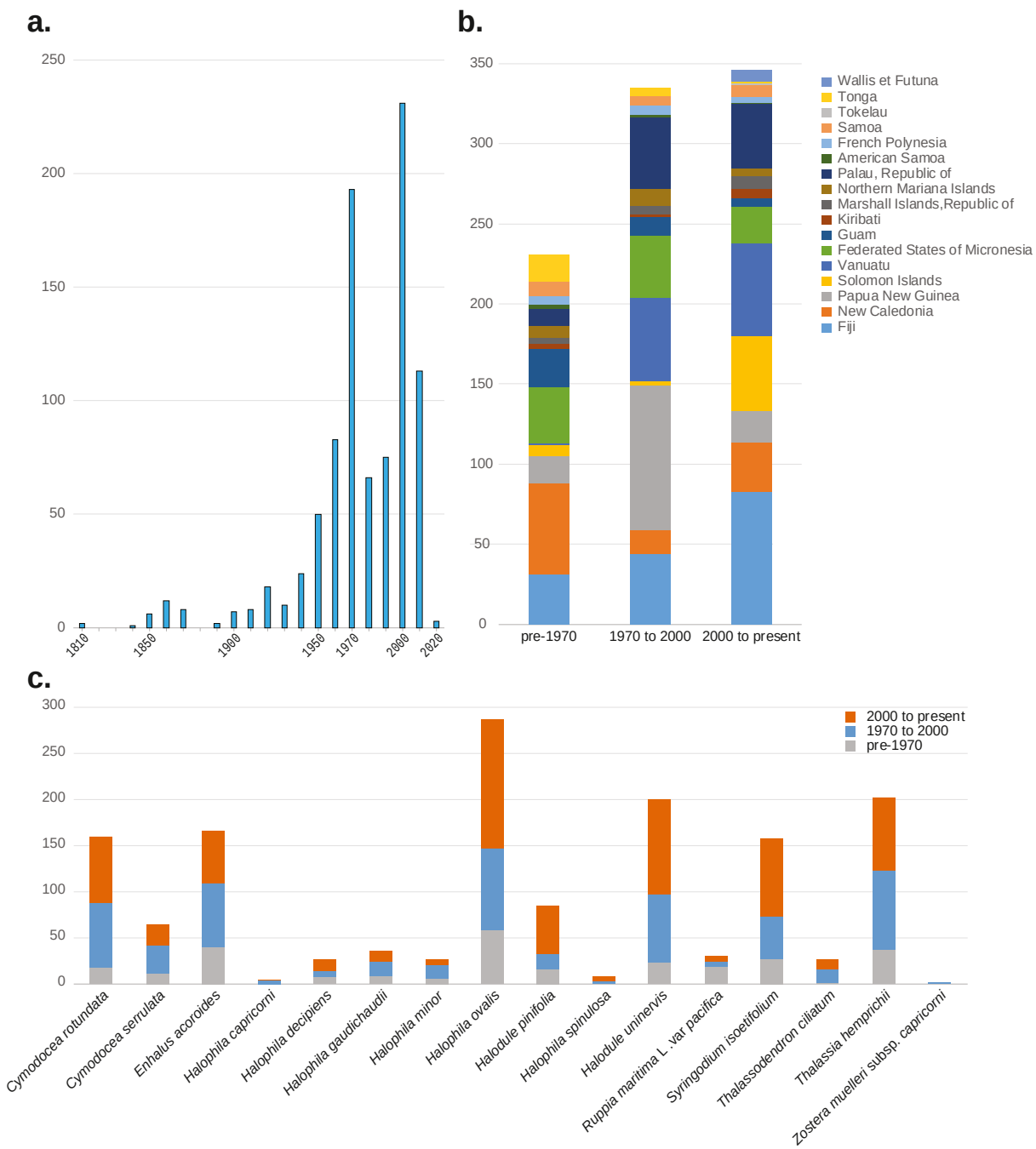

Fig. 3. Occurrence of seagrass records across the PICTs over the last 200 years: a. total number of records within each decade, since seagrass first identified in the PICTs; b. total number of records for each PICT in the three major time periods; c. total number of records of each seagrass species across the PICTs, including within each major time period. Source data from Table S1.

the PICTs until the 1970s (e.g. *Halophila capricorni*, *Halophila spinulosa* and *Zostera muelleri*), and some have not been reported in collection in the new millennia (e.g. *Halophila spinulosa* and *Zostera muelleri*) (Fig. 3c). Seagrass species records in each of the PICTs (Table 2) indicate a level of inconsistency between periods of collection, with the last verified reports of some species over 50 years ago; suggesting local extinction of two species in Tonga and one species in the Marshall Islands (Table 2). Such incidences of presumed local extinction will necessitate targeted investigation to verify possible species loss, as we have no evidence that the locations of occurrence have been revisited. This may require a detailed temporal assessment, as species may be ephemeral colonisers or transitory meadows, e.g. *Ruppia maritima* (Kilminster et al., 2015).

Melanesia was the region with the highest seagrass species richness, followed by Micronesia and Polynesia, respectively (Table 2). The greatest diversity of seagrass within a country or territory is reported from Papua New Guinea (13 species), and attenuates eastward across the Pacific to two species in French Polynesia (Fig. 4). No seagrasses have been reported from the Cook Islands, Nauru, Niue, Pitcairn Islands, and Tuvalu (Table 2). The discontinuity of seagrass in the Cook Islands, however, may be the consequence of limited field surveys as suitable habitats for seagrass colonisation and growth are likely present.

The most widely distributed species was *Halophila ovalis* (Table 2, Fig. S10), which is found in 12 of the 22 countries/territories and extends from the intertidal to a depth of 33 m (Table S1). *Halophila ovalis* forms dense meadows in some locations, but is frequently encountered in small patches. It tolerates a wide variety of substrata from fine muddy sand to coarse sand, mixed sand/rubble or large boulders with sandy patches. The species of the most limited distributions in the PICTs were *Zostera muelleri* and *Halophila capricorni* (Table 2, Figs. S16 and S6). All seagrass species in the PICTs are listed as "least concern" on the IUCN Red List of threatened species, and the global status of only 13% of PICT species are listed as "decreasing", with the majority (69%) "stable" and the remainder "unknown" (Table S1).

Based on the seagrass form-function model (Kilminster et al., 2015), persistent seagrasses of the genera *Enhalus*, *Thalassia*, and *Thalassodendron*, where high standing biomass contributes to their ability to stabilise and/or trap sediment and resist stressors, are only known to occur in Melanesia and Micronesia (Figs. S3, S14, S15). Similarly, opportunistic species of the genus *Cymodocea*, with greater seed production, more robust rhizomes and persisting biomass, also only occur in Melanesia and Micronesia (Figs. S1, S2). The remaining opportunistic genera *Halodule*, *Syringodium*, and *Zostera*, with less robust rhizomes, but greater ability to colonise, produce seeds and invest in clonal growth, occur throughout the PICTs (Figs. S4, S5, S13); except *Zostera* which only occurs in Melanesia (Fig. S16). Similarly, the colonising genera *Halophila* and *Ruppia*, with lower above-ground biomass, shorter ramet turnover times, more rapid sexual maturity and higher investment in dormant seeds production and clonal growth, are scattered throughout the PICTs (Figs. S6 to S11), although *Ruppia* appears absent from Micronesia (Fig. S12).

The patterns of seagrass species diversity for the Pacific Island region are likely the result of their biogeographic and dispersal history, with species richness attenuating eastward. It is generally accepted that seagrass dispersed eastward throughout the Pacific Islands via the Equatorial Counter currents from the Indo-Malayan centre of biodiversity, where seagrasses first appeared in the Tethys Sea at equatorial latitudes (Mukai, 1993). Waterborne dispersal success depends on the buoyancy potential of viable propagules (i.e. vegetative fragments, fruits and plant fragments with attached fruits and seeds) (Grech et al., 2016; McMahon et al., 2014). However, most tropical seagrass fruits are short-lived, and have negatively buoyant seeds with primary movement generally <100 km, except during extreme weather events when dispersal has been recorded over distances of up to 400 km (Lacap et al., 2002). Nevertheless, it is possible for vegetative fragments (including attached fruits and seeds) to be transported over much larger distances in rare instances, as reported from dispersal simulations along the tropical Great Barrier Reef where the maximum dispersal distance possible was 950 km (Grech et al., 2016). Similarly, seagrass seeds can also be transported over large distances by biotic vectors, including fish, birds, sea turtles, dugongs and humans (Kleyheeg and van Leeuwen,

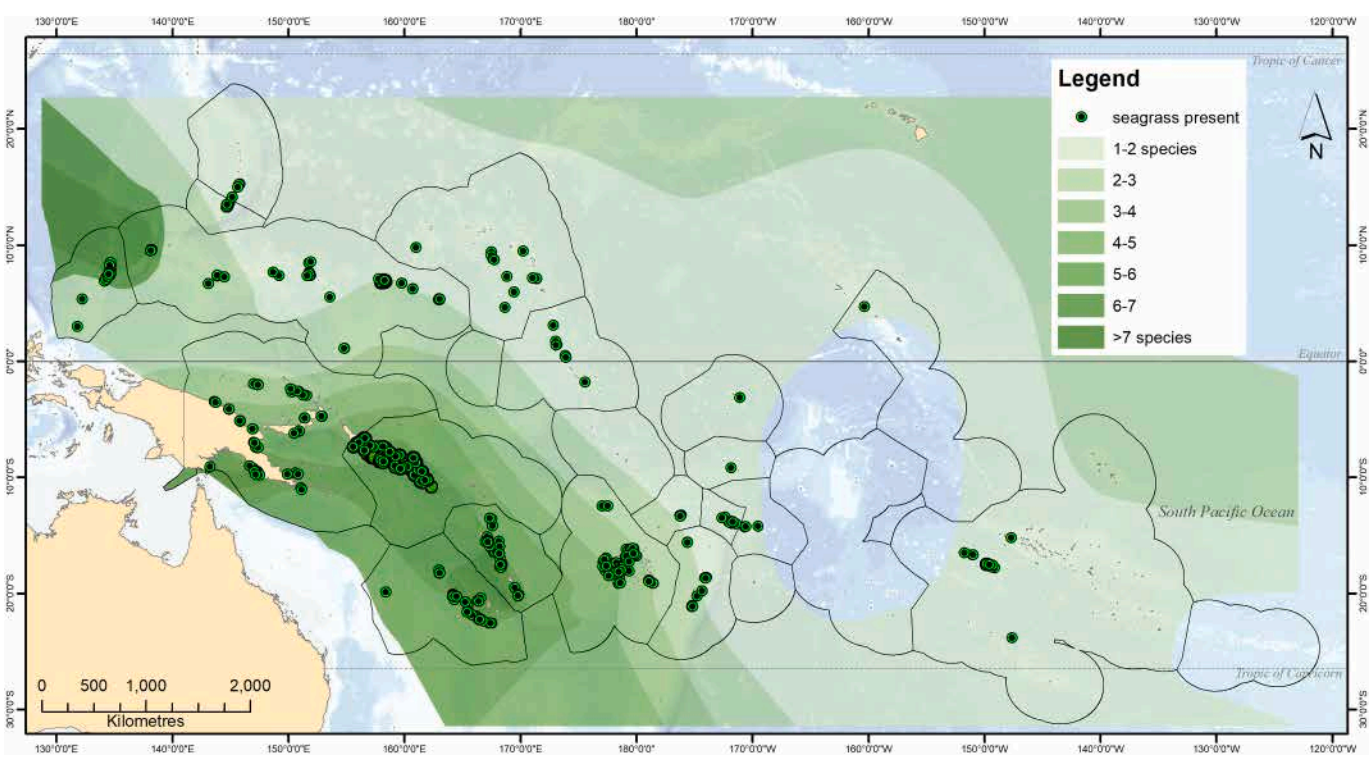

Fig. 4. Seagrass occurrence and species richness across the PICTs. Seagrass species richness (source Table S1) measured within 2° grids and predictive output spatially interpolated using a simple Kriging algorithm.

2015; McMahon, 2005; Tol et al., 2017). For example, *Ruppia maritima* is known to be transported on the feathers and in the gut and faeces of water fowl, and the close phylogenetic connection of Vanuatu populations to those in China and India (Martínez-Garrido et al., 2017), supports dispersal via the West Pacific Flyway. Therefore, it is likely that seagrass dispersal across the PICTs is a complex function of the type of viable propagule, dispersal time, wind and water movement, coastal topography, and biotic vectors.

4.2. Seagrass ecosystems and meadow spatial extent

Across the PICTs there is a great diversity of island types and marine environments. Most seagrass across the PICTs is found in waters shallower than 10 m and appear to be primarily influenced by the degree of wave action (exposure), water clarity and possibly nutrient availability (McKenzie et al., 2006; McKenzie and Rasheed, 2006; McKenzie and Yoshida, 2020; Waycott et al., 2011). Overall, sheltered, intertidal shores provide the most favourable habitat for seagrasses. Such habitats have both the greatest diversity and abundance of seagrasses. Seagrass diversity and abundance are generally lowest in the deeper subtidal habitats. Seagrass habitats across the PICTs can be generally categorised into five major habitat types: estuaries/inlets; bays and lagoons (behind reef or within atoll); fringing reef (sheltered and exposed); patch and barrier reef (including reef crest, reef flat or reef passage); and deep-water (McKenzie and Rasheed, 2006; Waycott et al., 2011).

Estuary/Inlet habitats are generally associated with high-islands, with larger rivers discharging into coastal bays, and dominated by persistent high standing biomass species such as *Enhalus* (Fig. 5a). Bays and lagoons (behind reef or within atoll) are sheltered habitats dominated by abundant persistent and opportunistic genera such as *Enhalus*, *Thalassia*, *Cymodocea*, *Halodule*, and *Syringodium* (Fig. 5b, c, d, e, f). Fringing reef (sheltered and exposed) habitats can have varied seagrass ecosystems often found in succession from the beach seawards (Fig. 5g). Barrier and Patch reef habitats (including reef crest, reef flat or reef passage), can be both subtidal and intertidal. Barrier reef habitats are generally dominated by *Thalassia hemprichii* (Fig. 5h) although

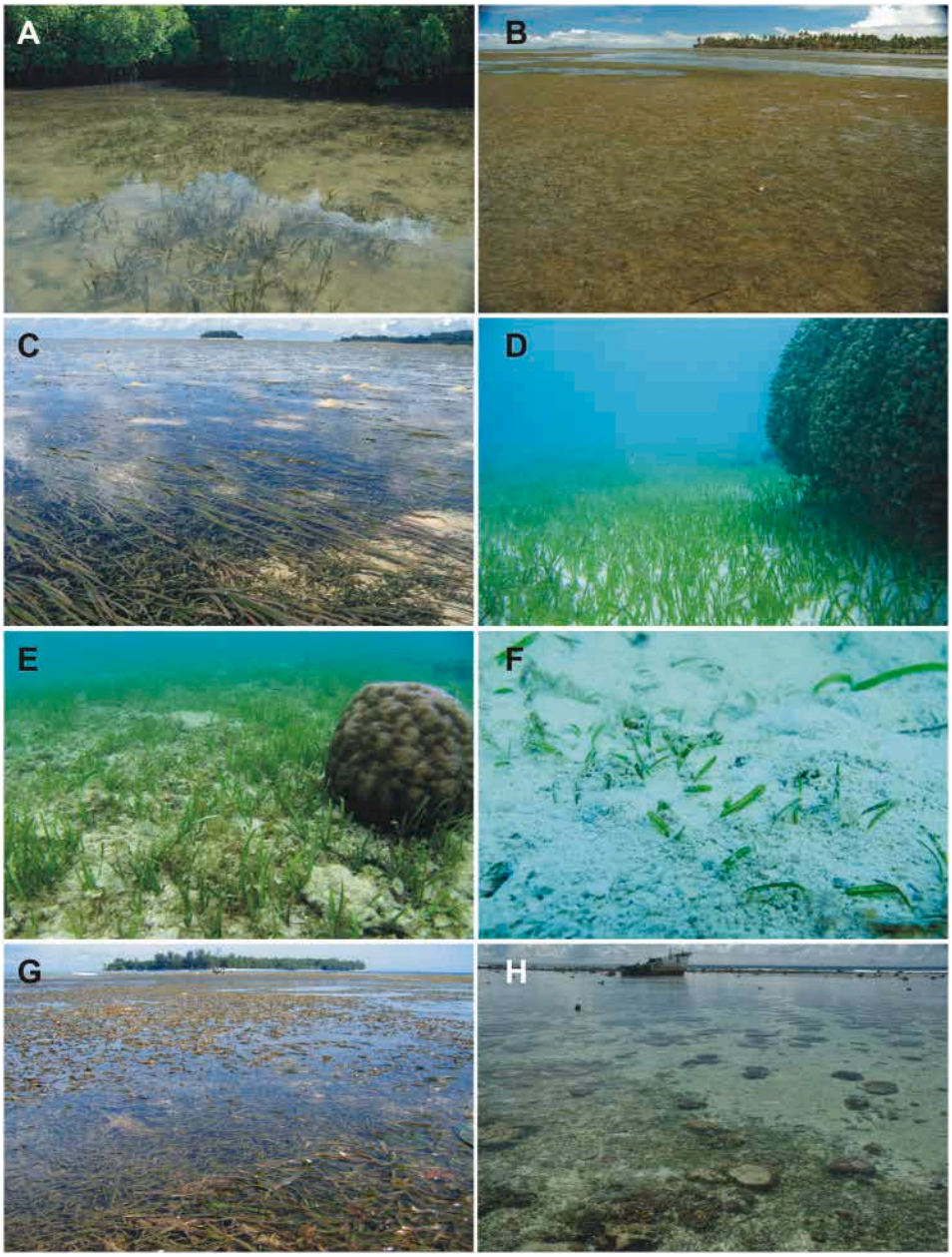

Fig. 5. Seagrass meadows in the PICTs occur in a variety of habitats: A *Enhalus acoroides*, Dausokele estuary, Pohnpei, FSM; B *Halodule/Halophila* meadow on the shores of Nasese, Lacuala Bay, Fiji; C *Enhalus/Thalassia*, Chirovanga lagoon, Choiseul Is., Solomon Islands; D *Cymodocea rotundata*, And (Ant) Atoll, FSM; E *Cymodocea/Halodule/Halophila*, Espiritu Santo, Vanuatu; F Elongate leaf form of *Halophila ovalis*, Erakor lagoon, Efate, Vanuatu; G *Enhalus/Cymodocea/Halodule*, Sivasat fringing reef, Kavieng, Papua New Guinea; H *Thalassia hemprichii*, Namwmour barrier reef, Pohnpei, FSM.

Thalassodendron ciliatum can often occur on the seaward margin of islands where this species exists. Deepwater (>10 m) is the least surveyed seagrass habitat in the PICTs, where only the colonising *Halophila* species occur.

Mapping of seagrass spatial extent across the PICTs is geographically unbalanced and variable in focus, approach and scale. Some PICTs have only mapped localised meadows (e.g. south Tarawa Atoll, Kiribati (Paulay, 2000)), while others have conducted more broadscale mapping (e.g. Solomon Islands (McKenzie et al., 2006)). Some mapping is approached with a high level of field observations coupled with aerial photography or very high spatial resolution satellite images (e.g. Andréfouët et al., 2010; McKenzie and Rasheed, 2006), while other approaches use earth observing as part of habitat characterisation exercises with limited field observations (e.g. NOAA NCCOS, 2004); in the latter, however, classification often fails to distinguish seagrass cover <10 percent. Nevertheless, we conservatively estimate the seagrass spatial extent in the PICTs to be 1446.2 km^2, with the greatest extent in Melanesia (1218.7 km^2) followed by Micronesia (141.2 km^2) and Polynesia (86.3 km^2) (Table 2). For PICTs where mapping with field/*in situ* observations has not been conducted (Vanuatu, American Samoa, Samoa and Tokelau), we used estimated values from the Allen Coral Atlas (2020) (Table 2). Regardless, our seagrass spatial extent remains an underestimate of the PICTs total seagrass extent, as many records of seagrass occurrence throughout the PICTs are not coupled with maps of meadows, and large areas of some countries (e.g. Papua New Guinea) remain unmapped. Recent (2017–2020) broad-scale mapping of coral reefs for the *Allen Coral Atlas* project included seagrass benthic maps in the PICTs (excluding Kiribati and Marshall Islands) (Table 2). However, mapping across several countries/territories is similarly incomplete, and the *Allen Coral Atlas* is also in a beta stage (Allen Coral Atlas, 2020); requiring extensive field validation using hierarchical approaches across spatial scales and water depths (including waters >15 m) (sensu McKenzie et al., 2020), before the maps can be used with higher confidence.

Information on the seagrass species present (including attributes of their life history), habitat, meadow form and the locations where they occur within each PICT is fundamental for evidence-based planning and decision making. Examination of seagrass ecosystems within each country/territory, demonstrates regional similarities and differences across the Pacific Islands.

4.2.1. Seagrass ecosystems of Melanesia

4.2.1.1. Fiji (Republic of). Six seagrass species are confirmed from the Fiji Islands (Table 2). Seagrasses are found in a range of habitats including: estuarine; barrier and patch reefs; island fringing reefs; bays and lagoons; and deepwater (>10 m) (McKenzie and Yoshida, 2020). *Halodule pinifolia* occurs in the high intertidal to upper subtidal areas of sheltered bays and reef platforms. *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 (Fig. 5b). *Halophila ovalis* is the most widespread of all seagrasses in Fiji and extends from the intertidal to 10–12 m deep, occurring across all habitats, as it tolerates a wide variety of substrata and environments. *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 brackish water estuarine habitats in Viti Levu (Table S1). *Halophila decipiens* is a recent addition to the seagrass inventory in Fiji, occurring in waters >6 m depth, along the reef channels of Cakaulevu Reef (Great Sea Reef), northern Vanua Levu (Table S1). This likely reflects its adaptation to deeper low light environments.

4.2.1.2. New Caledonia (French overseas territory). Seagrasses are found principally across the nearshore areas of New Caledonia within estuaries, on sandy intertidal fringes, deep lagoon sandy bottoms and internal sheltered reef flats (Baron et al., 1993; Payri, 2005). Twelve seagrass species are confirmed from New Caledonia (Payri, 2007, Table 2). Most seagrasses are found in waters shallower than 10 m depth, however, *Halophila decipiens* and *Halophila capricorni* are commonly observed in clear deepwater channels (down to 60 m) of the lagoon surrounding Grande Terre (Payri, 2005). All 12 species are found around Grande Terre, although only five species are reported from the Loyalty Islands, six species from the Isle of Pines and two species of *Halophila* from Chesterfield-Bellona and Entrecasteaux reefs. Examination of the *Zostera capricorni* specimen reported from the Isle of Pines (BM000984102) confirmed misidentification, and possibly incorrect location details (see Table S1 notes). Across Grande Terre, the most extensive meadows are in the Northern Province near Balabio Island and at the Plateau des Massacres (Andréfouët et al., 2010; Hily et al., 2010). The South Province's most extensive areas are between Bourail and Poya. The seagrasses found deepest (*Halophila decipiens* and *Halophila capricorni*) form sparse meadows covering an estimated 16% of the soft bottoms of Grande Terre's south lagoon. Remote sensing based mapping coupled with several field observation campaigns that occurred between 2004 and 2012 suggest that up to 936 km^2 of seagrass are present, although 356 km^2 only are medium – to dense meadows (Andréfouët et al., 2010; Hily et al., 2010). About 80 different types of meadows could be defined based on specific composition and density (Andréfouët, unpublished data).

4.2.1.3. Papua New Guinea (Independent State of) (PNG). We confirm the PNG seagrass flora consists of 13 species (Table 2). The earliest seagrass record in PNG comes from New Hanover in 1875 (Table S1). Seagrass species diversity is highest in the southern part of the country (adjacent to Torres Strait) and declines eastward (Fig. 4). The highest number of species reported at a single location is 13, from Daru in the northern Torres Strait (Johnstone, 1979). Eight species are widely distributed while five species are restricted to a few localities (Table S1); the rarest are *Thalassodendron ciliatum* at Manus Island and *Zostera muelleri* at Daru (Table S1). *Zostera muelleri* just reaches PNG as a northern extension of its Australasian range, and although suggested to occur along the New Guinea coastline west of Daru, recent mapping reported *Zostera muelleri* absent (Carter and Rasheed, 2016).

Seagrass communities occur on fringing reefs, in sheltered bays, on the sheltered side of barrier reefs and the lee of islands. Major seagrass meadows occur along the north coast of Manus Island in Seeadler Harbour, in the coastal bays surrounding Wewack and Port Moresby, on the island reef complexes of Milne Bay province and on the reef platforms surrounding the Tigak Islands and Kavieng (Fig. 5g). Seagrass meadows are also a significant feature at several other localities (e.g. Rabaul, Kimbe) and scattered areas of seagrass line much of the mainland coast (e.g., Madang, Morobe and Western provinces) and the offshore islands (including Lihir and Mussau). The majority of seagrasses occur from nearshore intertidal to shallow subtidal (10 m depth), although *Halophila decipiens* has been reported down to 40 m near Laing Island, Hansa Bay on the north coast in Madang Province (Bay and Demoulin, 1989). Extensive mixed species meadows are the dominant community type in the bays, harbours and sheltered capes along the coasts of the PNG mainland and the islands of New Britain and New Ireland (Brouns and Heijs, 1985, 1986; den Hartog, 1970; Johnstone, 1982). These extensive seagrass meadows are dominated by *Thalassia hemprichii* and/or *Enhalus acoroides*. In the more protected bays and the shallow lagoons surrounding Kavieng, *Enhalus acoroides* borders the gentle sloping mangrove fringes. Smaller islands are generally characterised by relatively small fringing reef platforms, where seagrass are restricted to shallow fringing reef-flats with lagoons (0–2 m depth). In regions without large islands (e.g. Louisiades), low cover seagrass mainly occurs on the tops of the reefs and shoals with reef flats (Skewes

et al., 2003).

4.2.1.4. Solomon Islands. Ten species of seagrass are confirmed from the Solomon Islands (Table 2). Most seagrasses occur in waters shallower than 10 m and meadows can be monospecific or consist of multispecies communities, with up to 6 species present at a single location (McKenzie et al., 2006). The dominant species throughout the Solomon Islands are *Enhalus acoroides* and *Thalassia hemprichii* (Fig. 5c). Seagrass occurrence appears to be primarily influenced by the degree of wave action (exposure) and nutrient availability. It is estimated that just over half of all seagrass meadows (per hectare basis) occur in Malaita Province, with other provinces each including <12% of the country's extent. Solomon Islands' seagrass habitats can be generally categorised into four broad habitats: estuaries (incl. large shallow lagoons), coastal (incl. fringing reef), deep-water and reef (e.g., barrier or isolated). In calm localities with a relatively wide lagoon (30–100 m), such as Tetel Island (Florida Islands) and Komimbo (north-west Guadalcanal), the sand-mud flats are generally dominated by *Thalassia hemprichii* shoreward and *Enhalus acoroides* seaward and often bordered by mangroves (*Avicennia*, *Rhizophora* and *Bruguiera*) when near rivers or streams.

4.2.1.5. Vanuatu (Republic of). To date, 12 seagrass species have been confirmed from the waters of Vanuatu (Tables 2 and S1). The earliest records of seagrass are of *Cymodocea rotundata* on the reef at Lamap (Port Sandwich, Malekula) in 1935–36 (Guillaumin, 1937). Since then, expeditions in the 1970s, 1980s and 2000s have improved the species occurrence list. The most widespread species are *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*, *Halophila ovalis* and *Thalassia hemprichii* (Table S1). Seagrass distribution is most likely influenced by shelter, sediment characteristics, water clarity and tidal exposure. Much of Vanuatu's seagrass meadows appear restricted to narrow fringing and inner reef areas or sheltered lagoons (e.g. Erakor, Éfaté) (Fig. 5f), bays (e.g. Palikoulo Bay, Espiritu Santo) (Fig. 5e), inlets (e.g. Mosso Islet, Éfaté), where they are generally reported to occur in scattered patches or form small meadows (e.g., <100 m wide zones) (Chambers et al., 1990; Payri, 2011). Extensive meadows, however, can occur on the comparatively wide intertidal areas around the Maskelyne Islands and along the east and southeast coast of Malakula (e.g. Crab Bay and Lamap) (Hickey, 2007). Denser meadows of predominantly *Cymodocea rotundata*, *Enhalus acoroides*, *Halodule uninervis*, and *Thalassia hemprichii* occur in shallow lagoons, bays and intertidal areas, particularly where the major or only substrate is sand. Seagrass diversity and abundance is generally lower at reef habitats where sediments are coarser, the sediment depth is less and the physical disturbance from waves is greater (Chambers et al., 1990). Little is known of deepwater (>10 m) seagrasses, however, *Halophila decipiens* and *Halophila capricorni* have been reported from the channels and deep outer reef slopes of southern Espiritu Santo (N'Yeurt and Payri, 2007; Payri, 2011). The rarest species is *Ruppia maritima*, which occurs in the brackish waters of river mouths (e.g. Adisone River, Espiritu Santo) or coastal ponds (e.g. Port Resolution, Tanna). The records of *Thalassodendron ciliatum* reported by Chambers et al. (1990) could not be verified, as no herbarium specimens could be located. It is likely these records were incorrect identifications of long stemmed *Cymodocea serrulata*. This is because a separate collection from one of the same places (Anelgahoat, Aneityum (Taféa) by Raynal in 1971), was similarly incorrectly identified (Table S1). The inclusion of *Zostera capricorni* in the Vanuatu seagrass list by Green and Short (2003) and Ellison (2009) is most likely an error, as it is not supported by herbarium specimens and not within the species' likely geographic range and environmental window.

4.2.2. Seagrass ecosystems of Micronesia

4.2.2.1. Federated States of Micronesia (FSM). Eight species of seagrasses are confirmed from the FSM (Table 2) with diversity attenuating eastward (Fig. 4) (Colin, 2018; Kock and Tsuda, 1978; McDermid and Edward, 1999; Tsuda et al., 1977). Seven species, except *Thalassodendron ciliatum*, are present in Yap State and six species except *Cymodocea serrulata* and *Halophila gaudichaudii* are present in Chuuk State. *Thalassodendron ciliatum* has been reported from Gray Feather Bank (Namonuito), a submerged atoll in Chuuk State (Colin, 2009). Only three species (*Thalassia hemprichii*, *Enhalus acoroides* and *Cymodocea rotundata*) are present in Pohnpei and Kosrae States (McKenzie and Rasheed, 2006; Hodgson and McDermid, 2000; Tsuda et al., 1977; Lobban and Tsuda, 2003; McDermid and Edward, 1999). Most seagrass occurs in water <3 m deep, and meadows can be monospecific or consisting of multispecies communities, with up to 3 species present at a single location (Table S1).

4.2.2.2. Guam (Territory of the United States). Seagrass meadows occur on Guam's fringing reef flats, sheltered bays and lagoons. The first atlas of Guam's seagrass was prepared by Randall and Eldredge (1976) with line drawn maps of the reefs and beaches of Guam depicting along the coast and in Cocos Lagoon. Although more detailed mapping using earth observing, coupled with field observations, occurred at the beginning of the new millennia, only seagrass >10% cover was included and species were not differentiated (Burdick, 2005). We confirm three seagrass species from Guam (Table 2). The persistent species *Enhalus acoroides* forms raised circular anaerobic mounds and inhabits the intertidal and shallow subtidal waters (<0.5 m) adjacent to the silty mouths of the streams and narrow rivers along the southern half of the island. Large meadows of *Enhalus acoroides* are present on the shallow wide reef flat of Achang Bay (east of Merizo village) (LaRoche et al., 2019), and also located on the shallow fringing reef flats at Agat (L. McKenzie, Pers. Comm.) and Ipan (Talofofo) (Tsuda, 2007); on the western and eastern shores of Guam respectively. The opportunistic species *Halodule uninervis* inhabits the shallow subtidal waters of the inner reef flat and is most abundant along the sandy lagoon waters off Cocos Islet (<2.5 m). *Halodule uninervis* occurs in the calcareous sands adjacent to the natural swimming pool at Inarajan (eastern shores of Guam) (L. McKenzie, Pers. Comm.) and is abundant in Cocos Lagoon; a few patches can also be found on the shallow sandy reef flats near shore in the southern bays (Tsuda, 2007). The colonising species *Halophila gaudichaudii* can be found in the shallow subtidal waters (<0.5 m) of the sandy inner reef flats, especially adjacent to *Enhalus* mounds in the deeper sections of Cocos Lagoon in the south and Apra Harbor in the north east (Tsuda, 2007). The occurence of a forth species in Guam is highly likely, as indicated by recent reports of *Syringodium isoetifolium* from Achang Bay and Piti (V. Vuki, Pers. Comm.), however, confirmation will require collection of herbarium specimens.The occurrence of *Ruppia* and *Thalassia* in the literature are is unverified and likely erroneous (Merrill, 1914; Safford, 1905; Stone, 1970; Walker and Rodin, 1949).

4.2.2.3. Kiribati (Republic of). Three species of seagrass are confirmed from Kiribati (Table 2). With the exception of *Ruppia maritima*, seagrass meadows reportedly only occur in the Gilbert Islands. Extensive meadows have been reported fringing the lagoons of several Gilbert Island atolls (Wilson, 1994), particularly those in the north, including Tarawa (ADB, 2018; Brodie and N'Yeurt, 2018; Delisle et al., 2016; Paulay, 2000), Butaritari (Delisle et al., 2016) and Abaiang (Awira et al., 2008; Fay-Sauni and Sauni, 2005). At Tarawa, seagrass meadows are reported from the southern, eastern and northern margins of the lagoon, adjacent to the longest islets. The largest extent is a near unbroken narrow meadow along the southern Tarawa sand bank from Banraeaba to Bikenibeu (ADB, 2018; Paulay, 2000; Tebano, 1990). Widespread meadows are also reported in the far northern Tarawa, around Buariki (Paulay, 2000). Patchy meadows have been reported along the eastern margins between Bikenibeu and Buota, off Abatao Islet and lagoonward of the passage between Tabangaroi and Tabonimata islets (Paulay, 2000).

In the central Gilberts, isolated patches of *Thalassia hemprichii* and *Thalassodendron ciliatum* were reported from the sheltered northern portion of Abemama lagoon, near Tabiang (Awira et al., 2008, Table S1); however seagrass was absent from the sandy pseudo lagoon at Kuria (Awira et al., 2008). In the southern Gilberts, *Thalassia hemprichii* has only been reported from the north islet in Ouotoa Atoll (Table S1).

Apart from *Ruppia maritima* in Washington lake on Teraina (northern Line Islands) (Table S1), the absence of seagrass has been confirmed from both the Phoenix and Line Islands, including: Kiritimati (Awira et al., 2008; K Tietjen, UVic, Pers. Comm.) and Palmyra Atoll (J. Seymour, JCU, Pers. Comm.), the northernmost Line Island and territory of the United States.

4.2.2.4. Marshall Islands (Republic of). Four seagrass species are confirmed from the Marshall Islands (Table 2). The Marshall Islands is the eastern limit for *Enhalus acoroides*, *Cymodocea rotundata* and *Halophila gaudichaudii* in the Pacific Ocean (Table S1, Figs. S1, S8). Seagrass meadows are reported fringing the inner lagoons of atolls, in the lee of vegetated islets, e.g. Kwajalein and Roi-Namur Islands, Kwajalein Atoll. Within Majuro lagoon, there are several *Cymodocea rotundata* meadows located on the west adjacent to Laura islet and on the east in the Aeanen group (Vander Velde, 2003). *Thalassia hemprichii* has been reported forming dense intertidal meadows at Ujelang Islet (Ujelang Atoll) and near mangroves at Airik Islet (Ailinglapalap Atoll), while occurring at the bottom of the lagoon adjacent to Pinglap Islet (Jaluit Atoll) (Fosberg, 1976). *Halophila gaudichaudii* is present in a few areas on Kwajalein Island, although it is more abundant at Roi-Namur where large meadows occur between the two piers (U.S. Army, 1989). Seagrass is reported to not occur at Bikini, Rongelap, Rongerik (Emery, 1954), Lae, Ujae, Wotho, Likiep, Aihik, Bikar, Pokak (Fosberg, 1955) and Enewetak Atolls (Colin, 1987; Tsuda, 1987).

4.2.2.5. Nauru (Republic of). We find no evidence of seagrass occurring in Nauru (Fenner, 2019b; Thaman et al., 1994). This appears a consequence of geographic isolation coupled with paucity of suitable habitat (high-energy reef-flat environment) (Tim Adams, NFMRA, Pers. Comm.). The fringing reef surrounding the island was extensively surveyed in 2005 and 2015, and no seagrass or suitable environment for seagrass to establish was identified (Harris et al., 2016; PROCFish/C and CoFish Team, 2007; Skelton, 2015).

4.2.2.6. Commonwealth of the Northern Mariana Islands (CNMI) (Territory of the United States). Three species of seagrasses are confirmed in CNMI, occurring on only three of the 14 islands (Tables 2, S1). *Enhalus acoroides* is the most widely distributed, occurring at Saipan, Tinian and Rota. On both Tinian and Rota, *Enhalus acoroides* occurs in single locations; Unai Chiget at Tinian and as a narrow band in the West Dock area at Rota (Eldredge and Randall, 1980). The dominant seagrass in the shallow sandy near-shore waters of the Saipan lagoon is *Halodule uninervis*, while *Enhalus acoroides* is conspicuous at the mouths of streams emptying into the lagoon. Houk and van Woesik (2008) provide a colour map of the habitats of Saipan Lagoon which includes separate *Enhalus* and *Halodule* meadows. The study also showed that the spatial extent of *Enhalus* was positively related with the adjacent watershed and lagoon width, although *Halodule* showed no relationship with watershed size. The colonising *Halophila gaudichaudii* occurred along the shallow lagoon waters near the coastline. The lack of seagrasses on the other islands in the Marianas, appears due to a lack of habitat conducive for seagrass establishment and growth.

4.2.2.7. Palau (Republic of). We confirm a total of 10 seagrass species to occur in Palau (Table 2). The most common seagrass species are *Enhalus acoroides*, *Thalassia hemprichii*, *Halophila ovalis*, *Halodule uninervis*, *Syringodium isoetifolium*, and *Cymodocea rotundata*. *Halodule pinifolia* occurs on intertidal sand flats along the east coast of Babeldaob and throughout the rock island sandy shallows. *Halophila gaudichaudii* is uncommon, and has only been reported from Ngermeduu Bay. Intertidal meadows in Palau occur from both protected lagoon and inshore waters, to exposed fringing reef flats. Shallow subtidal meadows occur in many locations, some from sheltered areas which are known to have persisted for decades, while others appear to have been of relatively recent (decade level) origin. The most extensive seagrass meadow in Palau is dominated by *Enhalus acoroides* and *Thalassia hemprichii*, and found within the lagoon north of Peleliu Island covering roughly 7 km^2. There are also large areas of shallow subtidal flats in the Rock Islands and on the periphery of Babeldaob with mixed seagrass and coral/algal communities. Seagrasses are rare on outer reef slopes; the main exception to this generality are the few areas with only a sediment slope ("sand falls") where species of *Halophila* occur to 30–35 m depth. The deepest lagoon bottoms (35–60 m depth), found in the northern lagoon (within the main reef complex) and at Velasco Reef, often have dense beds of macroalgae, but appear to lack seagrasses. *Thalassodendron ciliatum* occurs as isolated patches on the eastern fringing reef of Babeldaob, at a few locations on the inside edge of the barrier reef at Kayangel Atoll and most abundantly as deep (15–25 m) eroding meadows on the sunken atoll rim of Velasco Reef, particularly at its the northern end (Colin, 2018). These deep meadows are largely unknown globally; only other similar records in PICTs come from reports from Gray Feather Bank (Chuuk, FSM).

4.2.3. Seagrass ecosystems of Polynesia

4.2.3.1. American Samoa (Territory of the United States). Only two seagrass species are confirmed from American Samoa (Tables 2, S1). *Halophila ovalis* has been reported on the shallow water fringing reef platforms around Tutuila (Birkeland et al., 1987). The meadows are reported to be very sparse from near the shoreline to at least 30 m deep (at Fatagele Bay, Tutuila) (Fenner, 2019a). The bullate variety of *Halophila ovalis* was first described by Setchell (1924) from collections from Tutuila Island. *Syringodium isoetifolium* has been reported from Ta'ū (Table S1), the easternmost volcanic island of the Samoan Islands.

4.2.3.2. Cook Islands. We can find no evidence of seagrass in the Cook Islands (Mukai, 1993; G McCormack, Pers. Comm. CINHT; Kelvin Passfield, Pers. Comm., IUCN), however, we are not aware of any detailed benthic surveys conducted across the archipelago.

4.2.3.3. French Polynesia. Two seagrass species are confirmed from French Polynesia (Emmett, 1996; Vowles et al., 2001, Table 2). Scattered meadows of *Halophila ovalis* and *Halophila decipiens* are reported in low to average density in deeper parts of lagoons and passes throughout the islands (Hily et al., 2010; Andréfouët and Adjeroud, 2019; Butaud, 2009; Payri et al., 2000). Around Moorea, homogenous meadows of *Halophila decipiens* occur in the estuarine and lagoon habitats of Cook's and Opunohu Bays; from low water down to at least 20 m depths (Vowles et al., 2001). On the gently sloping "sandy plains" on the outer slope of Moorea, *Halophila decipiens* usually forms isolated patches down to 45–47 m deep (Mazeas, 1993). *Halophila ovalis*, although not found around Moorea, can be found around the Tuamotu Archipelago (Delesalle et al., 1985). Larkum (1995) reported *Halophila decipiens* from 3 to 5 m in the Society Islands and it is also present in Leeward and Windward Islands and western Tuamotu (Andréfouët and Adjeroud, 2019). Seagrass are not reported from the Marquesas.

4.2.3.4. Niue. We can find no evidence of seagrass on the fringing reefs surrounding Niue. Niue is a raised coral platform (one of world's largest coral islands), with steep limestone cliffs along its coast. A fringing reef surrounds the island, with the only major break in the reef being in the central western coast. There appears a lack of suitable habitat for seagrass establishment and growth.

4.2.3.5. Pitcairn Islands (British Overseas Territory). We can find no evidence of seagrass in the volcanic Pitcairn Islands (Irving et al., 2019). There appear no suitable habitats for seagrass to establish on Pitcairn, as it has a rough, rocky, cliff-dominated coastline with no coral reef. Henderson also has a high cliff along much of its coastline, but it is surrounded by a fringing coral reef with two narrow passages that lead to a sandy beach. Oeno and Ducie are atolls with shallow central lagoons and fringing reefs of low biodiversity (Friedlander et al., 2014). Ducie atoll, the most easterly island of the group, is the most southerly coral atoll in the world (Irving et al., 2019).

4.2.3.6. Samoa (Independent State of). Two species of seagrass are confirmed from Samoa (Fosberg, 1976; Skelton and South, 2006) (Tables 2, S1). *Halophila ovalis* (including bullate form) is widespread and has been reported to 25 m depth in the Palolo Deep Marine Reserve "blue-hole" (Lovell and Toloa, 1994). *Syringodium isoetifolium* is usually found in the shallow subtidal areas (1–15 m depth), grows to at least 30 cm tall, forming dense meadows, with some occasionally exposed during extreme low tide on the reef flats (Fenner, 2019a; Skelton and South, 2006). Between March 1990 and December 1991, seagrass were assessed as part of a rapid inshore fisheries resource inventory for Upolu and Manono (Zann, 1991). Extensive seagrass meadows were reported around Manono, the westernmost end of Upolu along the coast of Falelatai and the northern coasts of Upolu, particularly on the wider sections of the fringing reef platform (e.g. around Apia), where meadows dominated the benthos in the nearshore inner lagoon areas (mainly *Syringodium* with diffuse *Halophila*) (Zann, 1991). Off the coast of Aleipata, on the south-eastern coast of Upolu, large dense continuous meadows of *Syringodium* were reported in 1989 to occur along the lagoon north of the jetty, while south of the jetty meadows were smaller and less-continuous (Andrews and Holthus, 1989). Within the lagoon at Aleipata, *Halophila* dominated the broad sand flats, with denser meadows occupying areas of compact, medium-grained sand between the shore and the much denser *Syringodium* meadows (Andrews and Holthus, 1989). Meadows were also reported to occur in the shallows of Safata lagoon, an estuarine habitat on Upolu south coast, and supporting a major intensive fishery (Zann, 1991). On Savai'i, small meadows are scattered on the northern coast, with the majority located on the reef complex north of Salelologa on the easternmost end (Government of Samoa, 2013).

4.2.3.7. Tokelau Islands (Territory of New Zealand). Only *Syringodium isoetifolium* is reported from Nukunonu, but no details of its habitat are available (Whistler, 2011) (Tables 2, S1). Although the Allen Coral Atlas (2020) predicted seagrass to occur within Fakaofo lagoon, we can find no in situ/field observations to confirm its existence.

4.2.3.8. Tonga (Kingdom of). Six seagrass species are confirmed from Tonga (Tables 2, S1). Seagrass meadows occur in the shallow sheltered bays and lagoons of many of Tonga's islands. The earliest record of seagrass was in July 1874 when the Challenger expedition dredged flowering *Halophila ovalis* in abundance off Tongatapu in 33 m (Moseley, 1892). The most extensive meadows occur in the Tongatapu Island group, with its extensive coral reefs to the north which includes large shallow bays and sheltered lagoons. On the western side of Tongatapu lagoon, seagrass meadows dominate the coastal reef flat around Ha'atafu (Friedman et al., 2009). Intertidal and shallow subtidal meadows cover much of the nearshore reefs fringing Nuku'alofa harbour, and extensive meadows occur between the islands of Makaha'a, Manima and 'Oneata (Lovell and Palaki, 2002). Along the south western shores of Pangaimotu Island, Nuku'alofa harbour, the meadows extend to 20 m depth on coarse sandy substrate (Bell et al., 1994; Bobko, 1993). Nearby, *Halodule uninervis* and *Halophila ovalis* meadows cover large areas of the shallow enclosed Fanga'uta Lagoon, bordering Nuku'alofa (Prescott et al., 2004). On the north east of the main island, shallow-reef habitat meadows occur off Manuka. Located on the eastern side of the lagoon, opposite Manuka, are extensive and dense meadows to the north west of Onevai island (Friedman et al., 2009). Seagrass meadows are also scattered across the large number of bays and coves located in Ha'apai and Vava'u Island groups (Purkis et al., 2017). Extensive meadows have been reported across the western reef flat of Lifuka, the main island of the Ha'apai Island group (Baleilevuka et al., 2014; Friedman et al., 2009).

4.2.3.9. Tuvalu. We cannot confirm the presence of seagrass in Tuvalu (Table 2). Hisabayashi et al. (2018) using remote sensing, classified the photosynthetic vegetation on the reef flat surrounding Fualefeke as "seagrass", however, there was no field validation and it is likely a misclassification of macroalgae. Although Sauni (2002) mentions "the "turtle-grass", *Syringodium isoetifolium* is also found in Funafuti lagoon", no seagrass has been reported from surveys of the region to occur in Funafuti lagoon (Buckley, 1985). It is suspected that very patchy sparse meadows possibly exists in locations such as Vaitupu atoll where stable finer sediments and mangroves occur (M. Batty, SPC, Pers. Comm.).

4.2.3.10. Wallis and Futuna Islands (Territory of the). Four seagrass species have been confirmed from Wallis (Andréfouët and Dirberg, 2006; N'Yeurt and Payri, 2004) (Tables 2, S1). Seagrass meadows occur within the sheltered, shallow and soft-bottomed areas of Wallis lagoon and are particularly extensive in the inner reef areas, especially on the fringing reefs where three types are found in succession from the beach seawards: nearest the beach are dominated by *Halodule pinifolia* on sand/mud sediments, followed by *Halophila ovalis* on coarser sand and frequently associated with *Halimeda*, and finally in the sandy subtidal is *Halodule uninervis* and *Syringodium isoetifolium*, usually accompanied by *Turbinaria* (N'Yeurt and Payri, 2004; Vanai, 2002). *Halophila ovalis* is the most widely distributed species, occurring to 10 m depth and also in the barrier zones (Andréfouët and Dirberg, 2006; N'Yeurt and Payri, 2004). No seagrass were found at Futuna or Alofi during a 2005 habitat mapping survey (Andréfouët and Dirberg, 2006).

4.3. Seagrass status and trend

The current state and/or temporal change in seagrass ecosystems has received limited consideration across the PICTs. Where change has been assessed, this has revealed proposed losses (Short et al., 2014), but data was of insufficient scale to be indicative of region-wide trends. Changes in seagrass spatial extent have been reported from only a limited number of locations, predominantly places where anthropogenic pressures are higher, e.g. port and coastal development, or due to localised extreme events. For example, in Saipan lagoon (CNMI), approximately a third of the *Halodule uninervis* dominated meadows were lost between 1949 and 2004 due to nutrient pollution from human development and associated watershed runoff (Houk and van Woesik, 2010). Conversely, the relatively pristine seagrass meadows in Roviana (Solomon Islands), impacted by a magnitude 8.1 earthquake and subsequent relative sea-level rise of 30–70 cm in 2007, increased by 48% in spatial extent due to the increased habitat suitable for seagrass colonisation (Albert et al., 2017).

A qualitative assessment of trends in seagrass ecosystem state (e.g. extent, percentage cover, or biomass) from 66 locations across the Pacific Islands, indicated that 53% of the countries/territories showed no trend (Fig. 6, Table S2). Seagrass state (extent and/or abundance) increased in Kiribati and Samoa, decreased in the Marianas (Guam and Northern Mariana Islands), and was unable to be determined for 24% of countries (Fig. 7). Although seagrass state may have varied within and between years and/or locations, Melanesia appears relatively stable with 64% of locations showing no discernible trend, followed by Micronesia (45% of locations) (Fig. 7). The regions with the largest proportion of locations increasing and decreasing were Polynesia (31%)

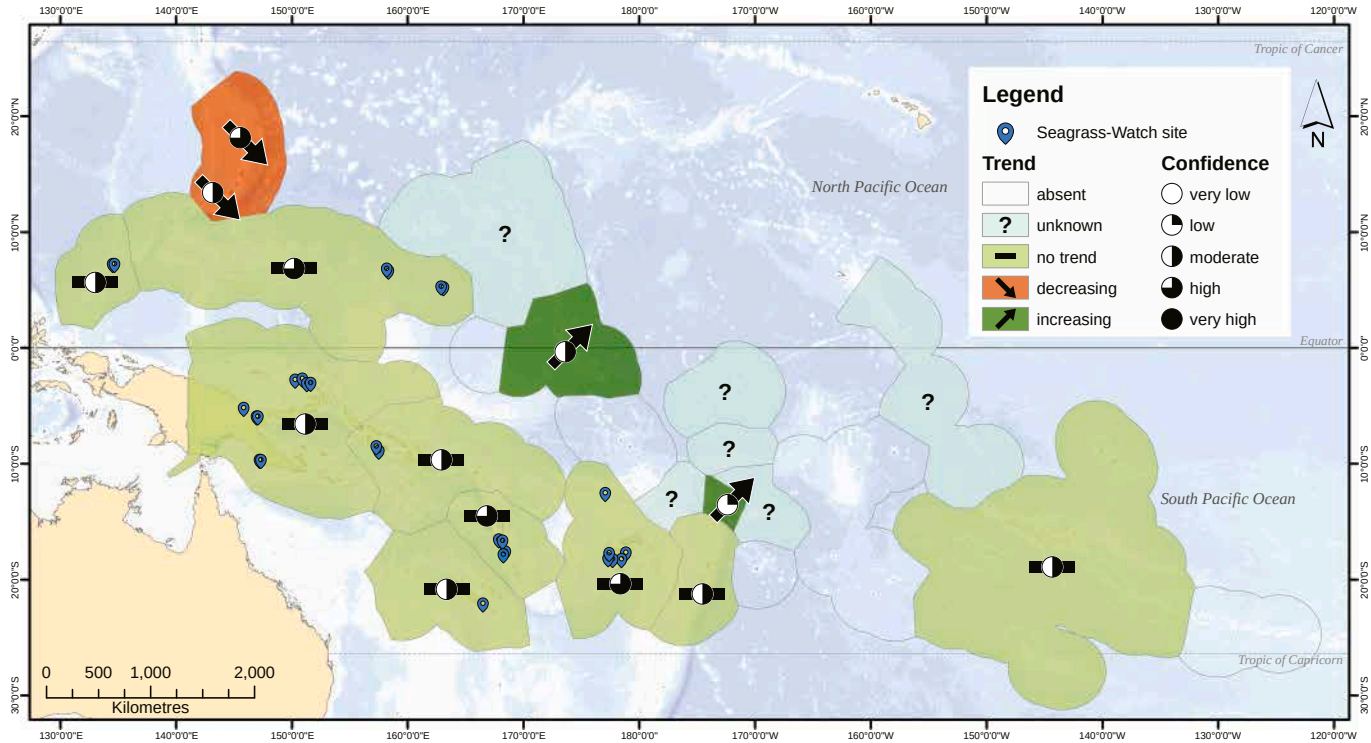

Fig. 6. Trends in seagrass ecosystem state and location of Seagrass–Watch Global Seagrass Observing Network sites across the PICTs. Source data Table S2. Confidence categories and scoring used for each trend: very low, ≤5; low, >5 ≤ 7.5; moderate, >7.5 ≤ 10; high, >10 ≤ 12; very high, >12 (see Table S3, modified from Waterhouse et al., 2018).

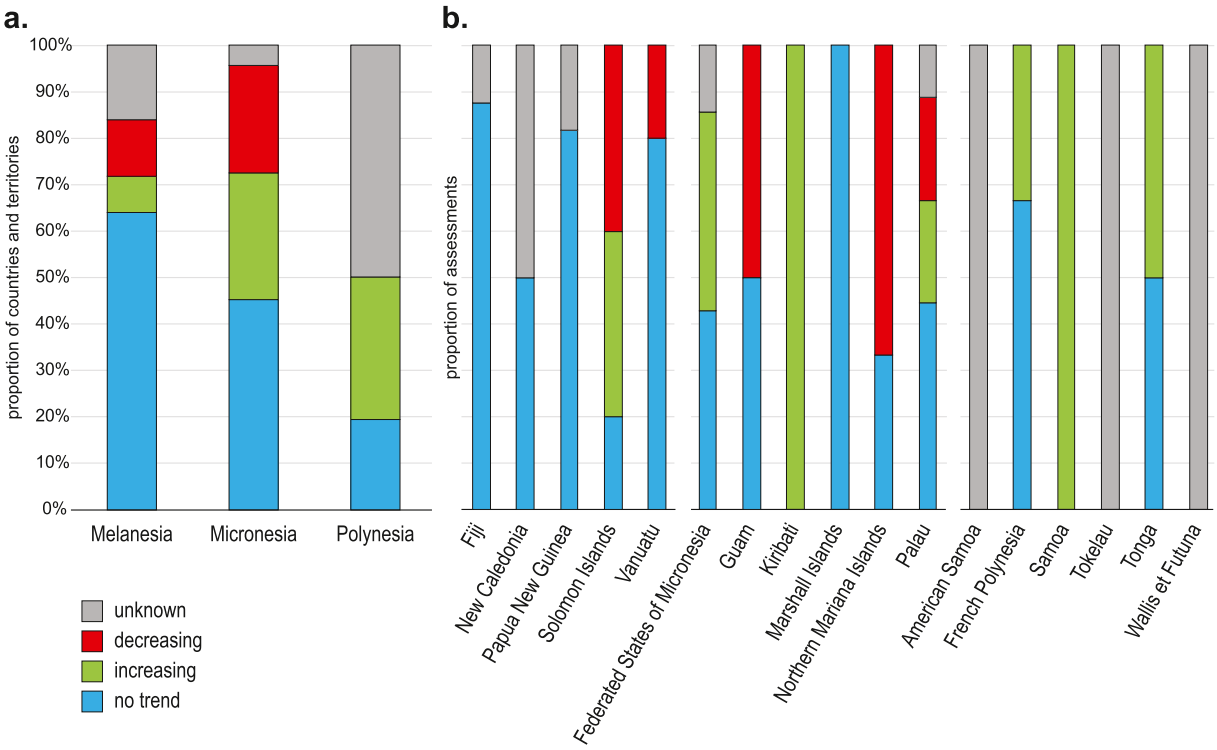

Fig. 7. Qualitative assessment of trends in seagrass status (abundance and/or extent) in each Pacific Islands region (a.) and country/territory (b). Assessment is proportion of reported trends for an individual country or territory (locations pooled, excluding sites with only one observation). No trend and increasing includes trend unknown when anecdotal indication of possible no change and increase, respectively. Source data Table S3.

and Micronesia (28%), respectively (Fig. 7). Confidence in the long-term trends varied depending on the sites/locations, the method of measurement and across the PICTs (Fig. 6, Table S2). The region with the least confidence in seagrass ecosystem state was Polynesia, as trends could not be determined for half of the Polynesian locations (Fig. 7, Table S2). Unfortunately, dedicated long-term monitoring of seagrass ecosystems was limited across the PICTs, and the most widespread was the Seagrass-Watch Global Seagrass Observing Network (Fig. 6).

Melanesian and Micronesian seagrass meadows were principally enduring in character, occurring for durations greater than five years (sensu Kilminster et al., 2015), and composed predominantly of opportunistic and persistent seagrass species, with some colonisers; although this was habitat dependent. These attributes and composition provide the seagrass ecosystems with a high level of resilience, with persistent species possessing a higher ability to resist stressors and opportunistic species with a higher capacity to recovery from large disturbances. Conversely, Polynesian seagrass meadows were more variable and composed predominantly of colonising seagrass species with some opportunistic species. Although this provides the seagrass ecosystem with a higher capacity to recover, a consequence of the higher sexual reproductive output of the colonising species, the ability to resist stressors is only moderate. Higher resilience was demonstrated at locations where localised losses/declines were followed by successive recovery. For example, the seagrass dredged from around Kayangel dock (Palau) in 2002, recovered within a decade (Fig. S19). Also, recovery after large scale disturbances (typhoons and cyclones) has been reported from Melanesia (e.g. McKenzie and Yoshida, 2020) and Micronesia (e.g. Colin, 2009).

With the exception of a few locations, declines and increases in seagrass ecosystem state appear generally a consequence of anthropogenic pressures. The exceptions include climatic or geological phenomenon. For example, seagrass abundance and species declined at Tetepare and Rendova Islands (Solomon Islands), following an earthquake in January 2010, which caused in a 7 m tsunami and increased exposure to waves due to the resulting subsidence (Moseby et al., 2020). The exceptions may also not be immediately apparent. For example, Short et al. (2014) attribute the seagrass losses at two cross-reef transects in Palau (Koror and Babeldaob) to wastewater discharge and sediment runoff (from road construction), however a more likely hypothesis is that the changes observed were a consequence of climatic events; from the start of the study (mid-2001), mean sea levels in Palau dropped 500 mm by early 2003 (a phenomenon which occurs due to El Niño Southern Oscillation shifts at intervals of several years), which would have resulted in greater daytime aerial exposure times of intertidal seagrasses, increasing desiccation stress and carbon limitation, and potential mortality.

4.4. Anthropogenic pressures (including climate change)

With 95% of the PICT population (excluding PNG) living within 10 km of the coast (Table 1), pressures from human activities are likely to place significant stress on seagrass ecosystems. Melanesia is the most populated region, with 86% of the PICTs population (Table 1). PNG, Fiji and the Solomon Islands are the most populated with 63%, 11% and 7% of the PICTs inhabitants respectively, while the Pitcairn Islands, with a population of 57, is the least populated political entity in the world (Table 1). Halpern et al. (2008), however, estimated the cumulated human impact status in the PICT coastal seas as low, with Northern Mariana Islands, Guam, Samoa, American Samoa and Fiji scoring the greatest because of shipping impacts.

The PICTs are quite diverse; politically, economically, geographically, and ethnically. However, many of the human activities that exert pressures on seagrass ecosystems are similar across the regions. Threatening activities (pressures) are driven by broader socio-economic and socio-cultural driving forces, including: population growth, urbanisation, economic growth, agricultural production, development and harvest industries. These driving forces lead to human activities which can adversely impact seagrass ecosystems, including: urban/industrial runoff, coastal development, dredging, terrestrial runoff (agricultural, forestry, mining/quarrying), boating (e.g. propeller scars, anchoring), fishing (e.g. netting, traps, gleaning), shipping accidents (e.g. oil spills), and climate change related impacts (Grech et al., 2012) (Fig. 8). How a threatening activity affects a seagrass ecosystem (directly or indirectly), depends on the spatial scale and frequency of the pressure, the ability of the ecosystem to resist the pressure, and the recovery time needed for the affected aspects of the community to return to their 'natural' or previous state following removal of the pressure (Halpern et al., 2007). The spatial scale at which a threat exerts a pressure can be small (<1 km^2 or 1–10 km^2), medium (10–100 km^2) or large scale (>100 km^2), and the frequency (rare, occasional, regular or persistent/chronic). The most threatening activities are those that frequently exert pressure over a large scale, impacting seagrass ecosystems which have poor resistance and poor capacity to recover.

Direct proximal impacts to seagrass ecosystems are generally highly localised and small-scaled (<1 km^2). For example, jet skis and motorised personal watercraft are reported to disturb nearshore seagrasses in East Agana Bay (Guam) and Saipan lagoon (CNMI) (Burdick et al., 2008; Houk and van Woesik, 2008). In some tourism areas, seagrass plants and wrack are actively removed from designated swim zones by hotel operators in the belief that meadows are unsightly or harbour organisms causing injury to bathers (McKenzie and Yoshida, 2020; Starmer et al., 2008). In Tumon Bay and East Agana Bay (Guam), the beaches are mechanically cleaned of seagrass wrack four or five times a week (Burdick et al., 2008). Other small-scaled direct impacts include seagrass harvesting as a source of agri-fertilizers for local communities (N'Yeurt and Iese, 2015; WorldFish, 2017), physical disturbance from litter (Fig. 8g), boat anchoring and moorings (Fig. 8h), and scouring from derelict vessels (Lord et al., 2003; Starmer et al., 2008). It is also likely that the trampling, foraging and digging by feral pigs in nearshore seagrass meadows in PNG, Tonga and Vanuatu has resulted in significant alterations to the local nature and character of sediments, plant biomass and diversity, nutrient cycling and erosion – similar to tropical freshwater ecosystems (Mitchell, 2010) (Fig. 8f).

Some fishing practices can also result in direct, localised, and small-scaled impacts; although most appear relatively minor compared to regions such as southern and south-east Asia where impacts are severe and far-reaching (Exton et al., 2019). Traditional fish fences (made of mangrove sticks) and stone fish traps (rock weirs) not only non-selectively and passively fish, but physically impact the inshore seagrass meadows in which they are positioned. Traditional fish fences and weirs are used to various degrees across the PICTs, including Fiji (MACBIO, 2017; Siwatibau, 1984; Veitayaki, 1995; Veitayaki et al., 2014), Samoa (Fa'asili and Kelekolo, 1999; Johannes, 2002; King et al., 1995), Micronesia (Takeda, 2001), French Polynesia (Clua et al., 2005), Tonga (King et al., 1995) and Vanuatu. In Fiji, some of the largest fish fences (*Ba ni ika*) can be found at Waiqanake (Navakavu, near Suva) (Waqairawai et al., 2018). Gleaning for invertebrates is popular across the PICTs, and although damage is predominately incidental, some communities reportedly use knives to cut the seagrass leaves to find fish, or dig for worms, crabs, shellfish and octopus (e.g., Vanuatu). Gleaning also has the capacity to create localised disturbance through trampling (Furkon et al., 2020). Finally, the indirect impacts from overfishing on seagrass ecosystems are a concern across the PICTs. For example, it has been suggested that overfishing of sea cucumbers could have a negative impact on the productivity of seagrass ecosystems, as seagrass may benefit from the sedimentary oxygenation and the recycling and remineralization of organic matter afforded by sea cucumber feeding, excretion, and bioturbation processes (Lee et al., 2018; Wolkenhauer et al., 2010).

The most significant localised threat to nearshore seagrass ecosystems in many areas of the PICTs is coastal development, particularly around major urban, tourism, and industrial areas. In the PICTs,

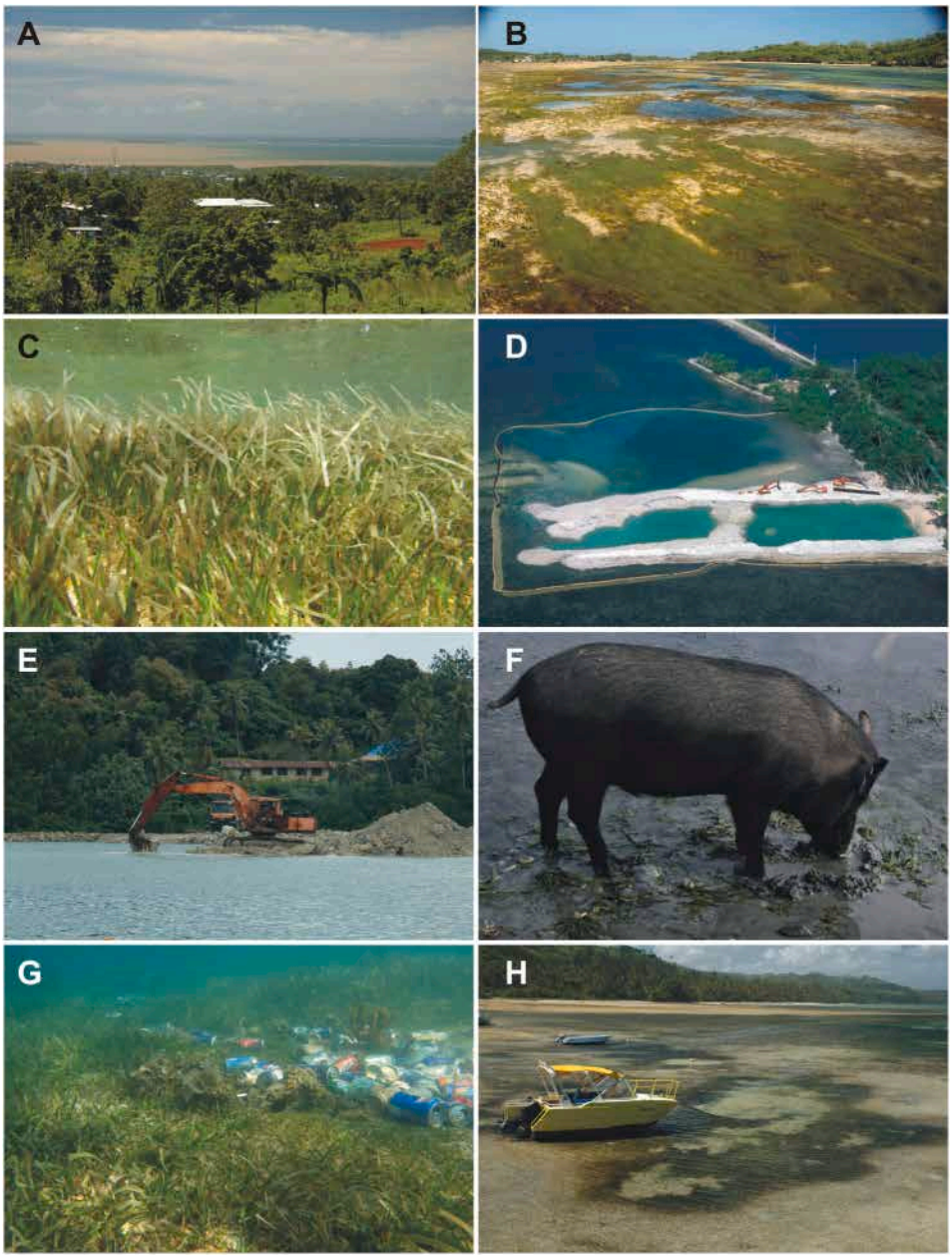

Fig. 8. Seagrass meadows in the PICTs are threatened by cumulative anthropogenic activities, including: A. Terrestrial runoff, Rewa River into Lacuala Bay, Fiji; B. Macroalgae blooms from elevated nutrients, Natadola, Fiji; C. Bleached seagrass leaves after burning due to elevated seawater temperatures, Natadola, Fiji; D. Dredging for coral sand road fill material, Ngiwal, Babeldaob, Palau; E. Dredging and reclamation for coastal development, Pohnpei, FSM; F. Pig digging in intertidal meadows, Huon Peninsula, Papua New Guinea (S. Winderlich); G. Litter, Anse Vata, New Caledonia; H Boat mooring scars, Maui Bay, Fiji.

building at the water's edge is common, and in some locations unavoidable. Coastal development can be small (1–10 km^2) or medium scale, depending on type of construction. Reclamation, construction of hotels, ports, marinas and groynes, shoreline hardening and channel deepening can all lead to alteration, fragmentation or loss of habitats available for nearshore seagrasses. For example, construction of the resort causeway across Yanuca Channel (Fiji) restricted current flows, resulting in the accumulation of sediments and seagrass degradation (McKenzie and Yoshida, 2020; Terry et al., 2006). Whereas, the simple permeable causeway constructed at Nan Madol (Pohnpei, FSM) only altered seagrass ecosystems immediately shoreward and seaward (Coles et al., 2005).

Dredging, sand extraction and reclamation occurs across the PICTs, is particularly common within the larger ports serving deep sea shipping, e.g. New Caledonia, Fiji, Guam, CNMI, French Polynesia and Vanuatu. Reclamation directly results in seagrass loss by permanently removing habitat for seagrasses, and altering nearshore hydrodynamics thereby affecting seagrass in the near vicinity. Dredging similarly removes seagrass habitat, and the movement of sediments can impact both the seagrass adjacent to the operations and at the site of disposal. For example, around Suva, high turbidity and siltation arising from foreshore reclamation and coral sand dredging have impacted seagrass meadows (Penn, 1981; Vuki, 1994). In Wallis and Futuna, the extraction of coral sand and "coral soup" (material used for road works), resulted in the localised loss of nearby seagrass meadows through sedimentation and turbid plumes (GoFR, 2006). Coastal development also increases the incidence of other cumulative impacts, in particular reduced water quality from sewage discharge, industrial/urban runoff.

Reduced water quality from elevated nutrients, sediments and toxicants can affect seagrasses locally, but impacts generally occur at a medium scale (10–100 km^2) (Lincoln et al., 2021). Across the PICTs, it is not uncommon for wastewater (domestic and industrial) to be released into adjacent coastal waters and seagrasses meadows (Devlin et al., 2020; Graves et al., 2021; Graham et al., 2020). An examination of *Enhalus acoroides* around Guam, reported sewage-derived N in leaf tissue over 10 km from the source, and increasing with population density

(Pinkerton et al., 2015). Elevated nutrients generally increase seagrass abundance (extent and density) (e.g. Kiribati (Paulay, 2000)), until a threshold is reached and seagrasses begin to decline. Of particular concern are bays and lagoons where water residence times are high, which can result in reduced water clarity and eutrophication (Thomas et al., 2010). For example, in the Bourail area, north of Noumea lagoon, several eutrophication events linked to fertilizer spills and sewage discharges, have triggered blooms of the green alga *Ulva*, which displaces seagrass and alters the habitat (unpublished data).

Some of the most threatening activities to seagrass ecosystems across the PICTs are indirect, and generally occur at much larger scales (>100 km^2). Indirect impacts are activities that may affect seagrass ecosystems far removed from the sources of the disturbance. The most significant indirect impacts are the result of reduced water quality, due to anthropogenically enhanced terrestrial runoff from modified catchments/watersheds (Fig. 8a). In the high islands, particularly those in Melanesia and Micronesia, where rainfall is seasonally high, the impacts from terrestrial runoff can be considerable. For example, unregulated land clearing for planting sakau, *Piper methysticum*, on the steep slopes of Pohnpei (FSM) increases soil erosion and sedimentation in nearshore areas especially after heavy rain events (Victor et al., 2006). This has led to a reduced diversity and condition of seagrass meadows (McKenzie and Rasheed, 2006). Often, the relationship between the extent and integrity of seagrass meadows and watershed size and development can be complex. For example, the *Enhalus acoroides* meadows in Saipan Lagoon (CNMI), expanded with increasing watershed development, while the *Halodule uninervis* meadows decreased in abundance due to pollution related increased macroalgae growth (Camacho and Houk, 2020; Houk and van Woesik, 2008). In Melanesia, soil erosion related to land clearing for logging (e.g. Marovo lagoon, Solomon Islands (McKenzie et al., 2006)), and the discharge of mining operations (e.g. nickel mining, New Caledonia lagoon (Ouillon et al., 2010; Grenz et al., 2013)) are also threatening nearshore seagrasses.

By far, the largest threat to seagrass ecosystems across the PICTs is anthropogenic climate change; altering rainfall, temperature and sea levels in areas vulnerable to extreme climatic events (Howes et al., 2018; Lough et al., 2011). All of the PICTs have reported increasing temperatures since the 1940s–1950s, with annual mean temperatures increasing from 0.12 °C to 0.30 °C per decade in the Solomon Islands and Kwajalein (Marshall Islands), respectively (SIMS et al., 2015; MINWSO et al., 2015). Elevated sea water temperatures (e.g. 38 to 42 °C) physiologically stress tropical seagrasses, with extreme temperatures (>42 °C) causing inactivation of photosystem II, resulting in leaf "burning" and plant death (Fig. 8c) (Campbell et al., 2006; Collier and Waycott, 2014). No clear trends in rainfall are apparent across the PICTs, as rainfall varies from year to year, however at Kiritimati (Kiribati) in the east, wet season rainfall has shown a clear increasing trend since 1946 (KMS et al., 2015). Although the number of tropical cyclones/typhoons have decreased in the tropical western Pacific (Murakami et al., 2020), projections suggest by the end of this century a possible shift towards more intense categories and a possible poleward shift in occurrence (Lough et al., 2011). As a consequence, the frequency of associated flood events is expected to increase. These severe weather and climate extremes can have some of the most pronounced impacts on nearshore seagrass ecosystems.

All these activities can result in multiple and cumulative stressors (e.g. increasing temperature, poor water clarity, increased physical disturbance), which can amplify the impact to degrade seagrass growth and persistence. How seagrass ecosystems respond is dependent of the frequency and intensity of the pressure, and the seagrass species present. There was a strong consensus in 2011, that seagrass ecosystems of the PICTs had moderate vulnerability to climate change impacts, with projected percentage losses ranging from 5 to 20% by 2035; but by 2100, the losses could be as great as 5–30% and 10–35% for low and high emission scenarios, respectively (Waycott et al., 2011).

4.5. Management response

Across the PICTs, seagrass ecosystems are acknowledged as important marine habitats, although marginalised throughout the policy and management landscape. We can find no legislation specifically protecting seagrass ecosystems in the PICTs, although they are afforded management considerations through a number of acts, policies and environmental agreements. In Vanuatu, for example, the National Biodiversity Strategy and Action Plan 2018–2030 specifically lists seagrass meadows as an important ecosystem for communities, but doesn't specify any conservation actions/activities. Most countries and territories also have Biodiversity Strategies and Action Plans to protect biodiversity and ecosystems, and many also include their significant role in culture, society and environment. Similarly, most PICTs are signatories to a number of international conventions (e.g. Convention on Wetlands of International Importance (Ramsar), Convention on Biological Diversity) or Memoranda of Understanding for the management of threats to the existence of protected and endangered species or their critical habitat (e.g. IOSEA Marine Turtle MoU). However, the legislation to protect against threats and mitigating actions can sometimes be vague and lacking substance. In Vanuatu, for example, the Fisheries Act No. 10 of 2014 protects dugongs, as the whole of the EEZ is a marine mammal sanctuary, but it doesn't specifically protect habitat, i.e. it fails to mention seagrass.

Managing threatening anthropogenic activities (pressures) to minimise impacts on seagrass ecosystems essentially depends on the type of activity (e.g. direct, indirect), and the scale at which they occur. Regional and country-wide management issues are generally approached at a national level. These generally include environmental codes, often related to commercial fishing, destruction of habitat and water quality issues, particularly around urban areas and port facilities (e.g. Fiji's Environment Management Act 2005; Sea Ports Management Act 2005). Across many PICTs, the existing legal framework is adequate to address medium to large-scale anthropogenic threats to the broader coastal ecosystems, although enforcement is often deficient or non-existent.

The management of coastal areas can be complex, falling under the jurisdiction of individual provinces (e.g. New Caledonia) or government departments (e.g. Guam's "special aquatic sites"), where sharing of powers and responsibilities can sometimes be unclear, particularly when dealing with indirect activities/pressures. This may be further complicated by the strong customary tenure and management practices primarily vested with the traditional custodians. Customary owners are provided the right to manage their nearshore areas as they have traditionally done for millennia through a combination of traditional beliefs and practices, including privileged user's rights, species-specific prohibitions, seasonal closures, food avoidance and tabu areas (e.g. the Amal/Crab Bay Tabu Eria, Malekula (Vanuatu) which is dominated by seagrass meadows (Hickey, 2007)). The success of implementing such agreements is evident by healthy seagrass meadows across PICTs compared to declining trends in other parts of the world. Local ownership also provides climate change adaptation (Basel et al., 2020), by mitigating local pressures and ensuring the long-term resilience of seagrass ecosystems and the continued provision of their natural services. PICTs that have employed such arrangements (e.g. Fiji) can demonstrate the resilience and sustainability of their seagrass ecosystems (McKenzie and Yoshida, 2020).

An effective approach used across the PICTs for managing marine resources and mitigating threatening activities is marine protected areas (MPAs). When MPAs are well placed, well resourced, and well managed they can address threats such as local pollution (including water quality), poorly planned coastal development, and destructive fishing practices; which all act to decrease the health and productivity of the ecosystem, thereby reducing ecosystem resilience. Approximately 64,443 km^2 of nearshore areas within the PICTs are designated as MPAs (including conservation areas, reserves, sanctuaries, parks, and

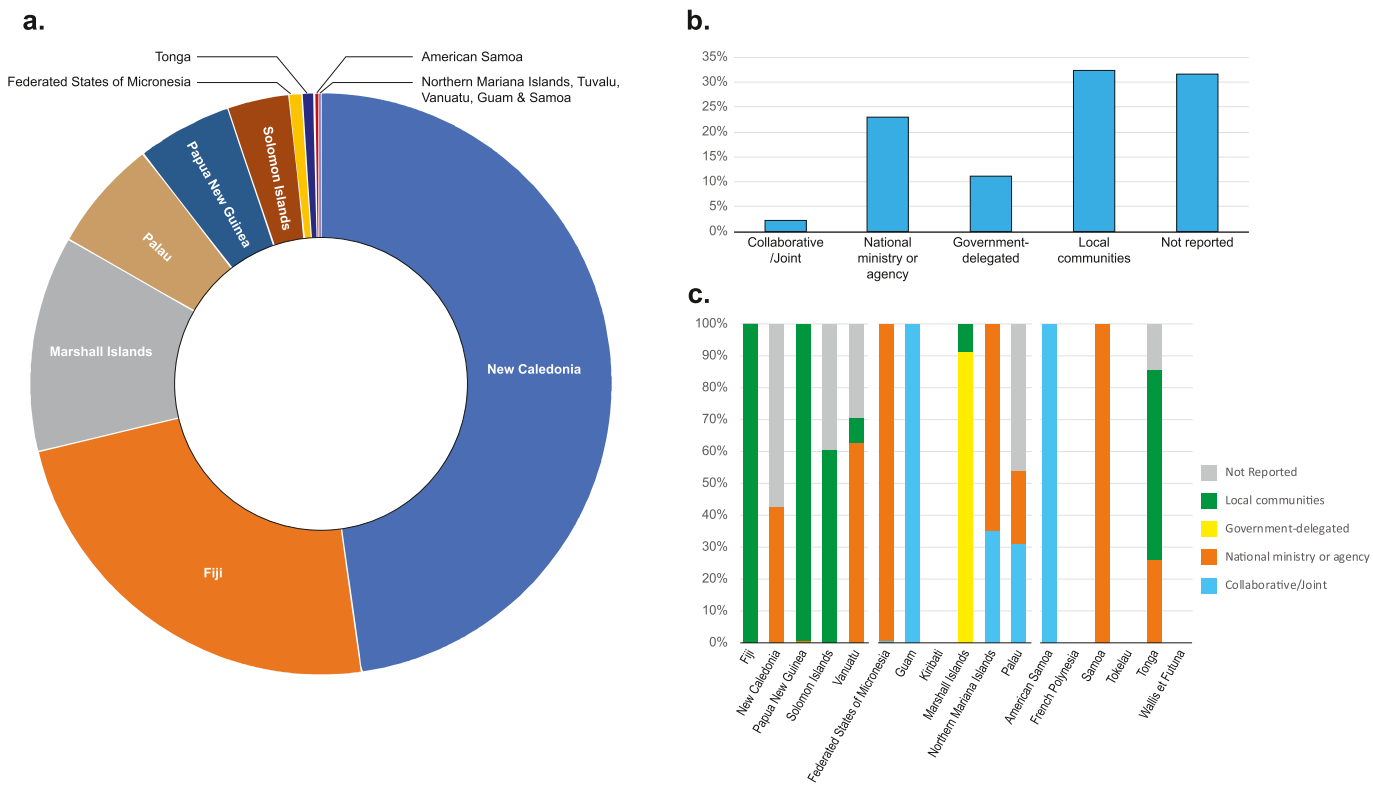

Fig. 9. Marine Protected areas of the PICTs: a. Proportion of total protected areas in each of the PICTs; b. Proportion of governance types managing MPAs across PICTs; c. Proportion of governance managing MPAs in each of the PICTs. Data source UNEP-WCMC and IUCN (2020).

management areas) (UNEP-WCMC and IUCN, 2020). Although the median MPA size across the PICTs is only 3.9km^2, the largest combined area of MPAs is located within New Caledonia's EEZ, followed by Fiji, Marshall Islands, Palau and PNG respectively; which combined make up 95% (Fig. 9). The governance of nearly half of the 345 individual MPAs (a third of the total nearshore protected areas), is vested within local communities (including Indigenous), with an additional 3% joint/collaboratively managed between communities and governments, and the remainder are either Federal or National ministry or agency managed, Government-delegated management, or Not Reported (Fig. 9). The greatest number of MPAs within an individual country or territory is 104 in Fiji (UNEP-WCMC and IUCN, 2020). Countries, such as Fiji, currently implement a network of locally managed marine areas (LMMAs) nested within a broader management framework for sustainable fisheries, climate change, and biodiversity protection (McKenzie and Yoshida, 2020). However, only around 16% of Fiji's seagrass meadows are estimated to occur within the MPA boundaries (Allen Coral Atlas, 2020; UNEP-WCMC and IUCN, 2020).

The majority of MPAs in the PICTs are focussed on protecting coral reefs and general sustaining or enhancing reef fisheries. Protection of seagrass habitats to meet the criteria for representation and connectivity could be improved by setting greater spatial targets for inclusion in MPAs. Globally the Aichi Biodiversity Target 11 calls for the conservation of "at least … 10% of coastal and marine areas" by 2020 (CBD, 2010). However, there is no scientific consensus that protecting 10% would be sufficient to meet resilient design criteria, and a higher representative proportion (e.g. 30% - Torres-Pulliza et al. (2013)) is recommended. Moreover, Aichi compliance assessments around the world need to take into account variability and bias in habitat description, including seagrass meadows (Gairin and Andréfouët, 2020). Implementation of conservation targets can only be successfully achieved with the participation and leadership of local peoples/communities who have the cultural understanding to ensure the most appropriate tools are implemented. There is a critical need for governments and industry to work together and use appropriate and evidence-based science to build capacity and confidence with local communities.

Historically, conservation approaches implemented in the PICTs were often the embodiment of colonial values adopted from European and North American governments. As a consequence, seagrass ecosystems across the Pacific are rarely included in western conservation legislation and policy, possibly a consequence of lacking information and colonial attitudes. In some PICTs, traditional knowledge is playing a greater role in managing local marine resources, which include seagrass ecosystems. The use of traditional protocols and knowledge as part of conservation measures is recognised as having a profound impact on the management of marine resources. There is now a growing recognition to "decolonise" conservation approaches across the Pacific Islands and empower local peoples with the assistance of western science to help influence and implement policy. In some PICTs, such as the Solomon Islands, community-based resource management is well embedded in government policies and plans. As such, establishment of LMMAs is one of the best ways to encourage conservation of coastal ecosystems such as seagrass habitats.

An essential conservation consideration for seagrass ecosystems is for management to set reference conditions and desired state targets (Collier et al., 2020). Although we have presented the current state and identified trends in seagrass condition within the PICTs, we have insufficient information to determine the desired state for these ecosystems. The desired target state for seagrass ecosystems ideally would be that which maintains ecosystem services (Madden et al., 2009). Key attributes that can be assessed which underpin ecosystem target state include both condition and resilience (O'Brien et al., 2018), but determining and setting desired state in the dynamic and diverse tropical habitats of the Pacific Islands presents multiple challenges. First,

adequate historical data which covers temporal and spatial variability that can be used as reference data is generally lacking. Without a clear baseline, it is not possible to determine if the current seagrass ecosystem condition meets a desired state (Collier et al., 2020). Second, setting target state requires informed decisions, in conjunction with exploratory analysis, be made by experienced scientists familiar with the data and area of interest (Collier et al., 2020). Lastly, it requires matching the assessment scale to target state scale. Seagrass assessment programs are generally lacking across the PICTs, and regional or PICT-wide seagrass ecosystem state targets may not be applicable for some individual PICTs, requiring targets to be refined to increase the spatial resolution.

To resolve these challengers and respond to the pressures faced by seagrass ecosystems across the PICTs, the following broad actions are recommended:

- Establishing well-designed protected areas with an ambitious target of 30% of the overall marine coastal areas;
- Providing greater support for local communities that wish to sustainably manage their seagrass ecosystems;
- Promoting seagrass conservation through development of locally relevant educational and outreach materials;
- Encouraging collaboration between research institutions and build scientific capacity within PICTs by implementing well-funded long-term regional projects and supporting postgraduate scholarships;
- Building research collaborations between management agencies and research institutions;
- Increasing funding support for scientific research and collection of data to underpin evidence-based policy;
- Undertaking a detailed Risk and Vulnerability assessment within each PICT and PICT-wide to ensure effective management of anthropogenic threats and to update future projections;
- Undertaking spatial mapping of seagrass meadows within and across data depauperate regions;
- Investigating incidences of presumed local extinction of species with PICTs, to verify possible species loss and provide greater confidence in biodiversity measures;
- Supporting seagrass citizen science initiatives which significantly contribute to science, education, society and policy;
- Supporting and building the capacity of local PICT herbaria to store and database herbarium collections, including the capacity to contribute specimen records to regional and global data aggregators (e.g. the Australasian Virtual Herbarium (AVH) and the Global Biodiversity Information Facility (GBIF)), and encourage distribution of duplicate specimens to regional and other herbaria in New Zealand and Australia, e.g. State Herbarium of South Australia;
- Encouraging citizen scientists to conduct spot checks to fill information gaps and validate seagrass species occurrence, using SeagrassSpotter;
- Expanding seagrass ecosystem health monitoring programs such as Seagrass-Watch across the PICTs
- Encouraging seagrass scientists across the Pacific Islands to participate in established networks (e.g. Indo-Pacific Seagrass Network, World Seagrass Association) to foster collaboration and knowledge exchange.

These actions will help significantly with conservation planning decisions, and environmental law and policy development and implementation throughout the PICTs. Effective conservation of seagrass ecosystems will also require novel and strategic investments, such as providing legal support to local communities, and by holding extractive industries and government agencies accountable. It is likely that individual countries and territories will need to include additional actions to address specific or localised pressures/issues, and to prioritize the broader actions depending on their capacity and/or their area of jurisdiction (e.g. number of islands, length of coastline).

5. Conclusions

Diverse and extensive seagrass ecosystems predominate in Melanesia region compared to Micronesia and Polynesia. Seagrass diversity also attenuates towards the east of the Pacific Ocean, with some PICTs having no recorded seagrass species. Human activities are threatening seagrass ecosystems globally. It has been estimated that rates of seagrass loss globally, accelerated from 0.9% yr^{-1} in the 1940s to 7% yr^{-1} towards the end of the 20th century (Waycott et al., 2009). These losses were primarily the result of overexploitation, physical modification, nutrient and sediment pollution, introduction of non-native species, and global climate change (Waycott et al., 2009). Of concern, is that these losses are threatening millions of people who depend on seagrass ecosystems for their food security and livelihoods. Although this presents a worrying picture, from the evidence provided in our review, it appears the seagrass ecosystems of the PICTs display features of high resilience to anthropogenic pressures and may represent a "bright spot" among the world's seagrass ecosystems. Bright spots are not necessarily pristine, or immune to human activity, but are ecosystems fairing much better under pressure. This may be similar to coral reefs globally, where the bright spots were mainly in the Pacific, including populated countries like the Solomon Islands, Papua New Guinea and Kiribati (Cinner et al., 2016). Coral reef bright spots displayed crucial characteristics, including: strong local sea traditions, which include ownership rights and/or customary practices to manage fisheries; high levels of participation in management by local people; and high levels of dependence on fishing (Cinner et al., 2016). Pacific Island countries and territories, which often do not have funds for conservation, have a close social connection to the health of their oceans (McKenzie et al., 2021). We believe that the PICTs may offer some hope and possible solutions that can be applied more broadly across the world's seagrass ecosystems. By fostering and involving local peoples in the management of nearshore resources, and reducing destructive practices provides significant opportunities to enhance seagrass ecosystems resilience. Empowering local communities to have stewardship over the resources, will allow the development of culturally sensitive and creative solutions to support conservation measures.

CRediT authorship contribution statement

Len J. McKenzie: Conceptualization, Methodology, Investigation, Formal analysis, Visualization, Writing – original draft, Writing – review & editing. **Rudi L. Yoshida:** Conceptualization, Methodology, Investigation, Data curation, Visualization, Writing – original draft, Writing – review & editing. **John W. Aini:** Writing – original draft. **Serge Andréfouet:** Investigation, Writing – original draft, Writing – review & editing. **Patrick L. Colin:** Investigation, Writing – original draft. **Leanne C. Cullen-Unsworth:** Writing – original draft, Writing – review & editing. **Alec T. Hughes:** Writing – original draft. **Claude E. Payri:** Investigation, Writing – original draft, Writing – review & editing. **Manibua Rota:** Writing – original draft. **Christina Shaw:** Investigation, Writing – original draft, Writing – review & editing. **Posa A. Skelton:** Writing – original draft. **Roy T. Tsuda:** Investigation, Writing – original draft. **Veikila C. Vuki:** Writing – original draft, Writing – review & editing. **Richard K.F. Unsworth:** Conceptualization, Writing – original draft, Writing – review & editing.

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.2021.112308. These data include the Google map of the most important areas described in this article.

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