

National-scale marine bioregions for the Southwest Pacific

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ABSTRACT

Existing marine bioregions covering the Pacific Ocean are conceptualised at spatial scales that are too broad for national marine spatial planning. Here, we developed the first combined oceanic and coastal marine bioregionalisation at national scales, delineating 262 deep-water and 103 reef-associated bioregions across the southwest Pacific. The deep-water bioregions were informed by thirty biophysical environmental variables. For reef-associated environments, records for 806 taxa at 7369 sites were used to predict the probability of observing taxa based on environmental variables. Both deep-water and reef-associated bioregions were defined with cluster analysis applied to the environmental variables and predicted species observation probabilities, respectively to classify areas with high taxonomic similarity. Local experts further refined the delineation of the bioregions at national scales for four countries. This work provides marine bioregions that enable the design of ecologically representative national systems of marine protected areas within offshore and inshore environments in the Pacific.

1. Introduction

The global decline of marine biodiversity and ecosystem services

requires better ocean management (Beger et al., 2015; Jackson et al., 2001; Klein et al., 2015; Mora, 2008; Worm et al., 2006). Pacific Island countries and territories have large and highly biodiverse ocean spaces

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within their Exclusive Economic Zones (EEZs). They are moving towards more sustainable management of their marine and coastal resources (e.g. see Pratt and Govan, 2011, Pacific Island Country Voluntary Commitments at the United Nations Ocean conference) and many are party to the Convention on Biological Diversity (CBD). Through the CBD Pacific Island countries and territories have committed to protecting 10 percent of their marine environment in national ecologically representative systems of marine protected areas (MPAs) and/or other effective area-based conservation measures (Woodley et al., 2012).

Many Pacific Island countries and territories have applied marine spatial planning, especially for the design of marine protected areas at local community scales or in coastal areas (Dalleau et al., 2010; Green et al., 2009; Gurney et al., 2015; Weeks and Jupiter, 2013). A number of Pacific Island countries and territories are now implementing national-scale marine spatial planning to help, amongst other things, achieve their CBD and Sustainable Development Goal targets for marine protected areas and sustainable use throughout their ocean waters (United Nations Ocean Conference Voluntary Commitments). Marine spatial planning is a public process of analysing and allocating the spatial and temporal distribution of human activities in the ocean to achieve ecological, economic, and social objectives that are usually specified through a political process (Ehler and Douvère, 2009). Despite their best efforts, marine spatial planning in Pacific Island countries and territories is hindered by many challenges, including a paucity of spatially explicit data that adequately captures the marine biodiversity patterns and processes in ocean spaces (Division for Ocean Affairs and Law of the Sea, 2016; PIFS, 2018; SPREP, 2016).

Adequately representing marine biodiversity in national marine spatial planning is difficult, particularly in data-poor regions such as the Pacific Ocean (Álvarez-Romero et al., 2018; Beger et al., 2015; Division for Ocean Affairs and Law of the Sea, 2016; PIFS, 2018; SPREP, 2016). There are three issues: some ecosystem and habitat types are not accurately mapped in the Pacific (e.g. seagrasses, mangroves, seabed geomorphology, offshore pelagic habitats) (Bhattarai and Chandra, 2011; Harris et al., 2014; Torres-Pulliza et al., 2013), species assemblages and habitats can vary substantially at local scales, and comprehensive habitat and species information is subject to constant change as new technologies are applied and new information emerges (Intergovernmental Oceanographic Commission, 2017). For these reasons, environmental descriptors used in planning must be robust to uncertain, inadequate, and changing information.

Data challenges in marine spatial planning can be overcome by the use of biological proxies (Sutcliffe et al., 2014, 2015), such as environmental conditions (Grantham et al., 2010), non-comprehensive data collected at different spatial scales (Mellin et al., 2009), surrogate species (Beger et al., 2015; Olds et al., 2014), marine community classifications (Green et al., 2009), expert decision-making (Brewer et al., 2009), regional-scale remote sensing studies (Purkis et al., 2019) or some combination of these (Kerrigan et al., 2011). In particular, the classification of the marine environment into spatial units that host similar biota (i.e. marine bioregions) can serve to provide spatially explicit surrogates of biodiversity for decision-making in marine conservation and management (Fernandes et al., 2005, 2012; Foster et al., 2013; Last et al., 2010; Rickbeil et al., 2014; Terauds et al., 2012) (Fig. 1). Bioregions define areas with relatively similar assemblages of biological and physical characteristics, without requiring complete data on all species, habitats and processes (Costello et al., 2017; Spalding et al., 2007). Since assemblages of marine species with similar life histories often respond similarly to environmental conditions (Elith and Leathwick, 2009), these species can be grouped for biogeographical predictions or ecological modelling (Tremblay and Halpin, 2012). The probability of occurrence of such species groupings is often determined by the unique combinations of environmental parameters that are likely to drive the distribution of these groups. Classification of such combinations of environmental variables can thus serve as surrogates for

marine biodiversity that is otherwise unrecorded (Sutcliffe et al., 2015).

There are many marine biogeographical regions and also smaller marine regions or provinces that have been described for the oceans of the world, or parts thereof, including the Pacific (Brewer et al., 2009; Costello et al., 2017; Green et al., 2014; Kerrigan et al., 2011; Lourie and Vincent, 2004; Sayre et al., 2017) (Fig. 1). These include schemes based on shallow coral reef fishes (Kulbicki et al., 2013) (Fig. 1c) or scleractinian corals (Keith et al., 2013, 2015) (Fig. 1d). Others use a mix of species distributions, environmental parameters, and expert opinion (Kerrigan et al., 2011; Spalding et al., 2007; Terauds et al., 2012) (e.g. Fig. 1b). Many schemes do not explicitly classify offshore areas. Where they do, they describe large swathes of ocean as largely homogeneous and classify the ocean into very large-scale ecoregions, particularly in the Pacific (Costello et al., 2017; Longhurst, 2006; Sherman et al., 2009; Spalding et al., 2012; Sutton et al., 2017; Watling et al., 2013) (Fig. 1). Specifically, Longhurst (2006) described four global pelagic provinces (three in Oceania) and 51 sub-provinces (9 in Oceania) from a global database of chlorophyll profiles (Fig. 1f). A scheme by UNESCO (2009) and Watling et al. (2013) divides the ocean beyond the continental shelf into biogeographical provinces based on both environmental variables and the available data on species composition. Further, the biogeography of benthic bathyal ophiuroid fauna can be characterised into latitudinal bands (O'Hara et al., 2011), of which three are in the tropical southwest Pacific (Fig. 1g). A recent bioregionalisation of the ocean's mesopelagic zone (200–1,000 m) resulted in ten biogeographic provinces (six in the tropical southwest Pacific) (Proud et al., 2017) (Fig. 1i). Lastly, the distribution of tuna and billfish communities form nine well-defined communities across the global ocean, four of them in the southwest Pacific (Reygondedeau et al., 2012).

These offshore bioregions typically span whole ocean basins or their subsections. Such broad characterisation of offshore environments is particularly problematic, because environmental variability occurs at much smaller scales and drives biodiversity patterns. Offshore environmental dynamics at a subregional scale influence the distributions of biota (e.g. for tuna) to a large degree (Lehodey et al., 2008; Senina et al., 2008). For example, changes in thermocline characteristics affect the productivity, distribution and abundance of marine fishes (Devney et al., 2009; Kitagawa et al., 2007; Schaefer et al., 2007), and the depth of the 20 °C thermocline predicts bigeye tuna catches (Howell and Kobayashi, 2006). Temperature also predicts phytoplankton size, structure, and taxonomic composition (Heather et al., 2003), and temperature across pelagic ocean habitats is spatially and temporally highly variable. A metric of sea surface temperature (SST), the annual SST range, predicts tunas and billfishes, krill, and to a lesser degree oceanic sharks (Tittensor et al., 2010). Bluefin tuna (*Thunnus maccoyii*) feeding success is predicted by SST mean, SST variability, and the SST colour anomaly (Bestley et al., 2010). Zooplankton can respond strongly to temporally and spatially dynamic El Niño–Southern Oscillation (ENSO) patterns (Mackas et al., 2001), and phytoplankton abundance is predicted by the photosynthetically available radiation (PAR, i.e. a measure of light) and nitrate concentrations (Edwards et al., 2013). It follows that spatially dynamic environmental regimes across the Pacific likely drive biodiversity patterns at smaller scales than that of ocean basins typically recorded by offshore bioregionalisations.

Aside from patterns that may be detected in the surface waters of ocean habitats, deep-water ocean habitats are also characterised by multiple deeper water layers and the seabed (Ceccarelli et al., 2017a; Harris et al., 2014). Deep open ocean water varies dramatically with increasing depth, in respect to physical (especially light, temperature and pressure), biological and ecological characteristics, across at least five major layers or vertical zones (Herring, 2002). Within each zone, there are horizontal patterns that differ in physical and biological characteristics with latitude and longitude, at various spatial scales, which may or may not overlap vertically (Benoit-Bird et al., 2016; Craig et al., 2010). Furthermore, the linkages between surface and deeper zones have a substantial influence on deep ocean dynamics. For

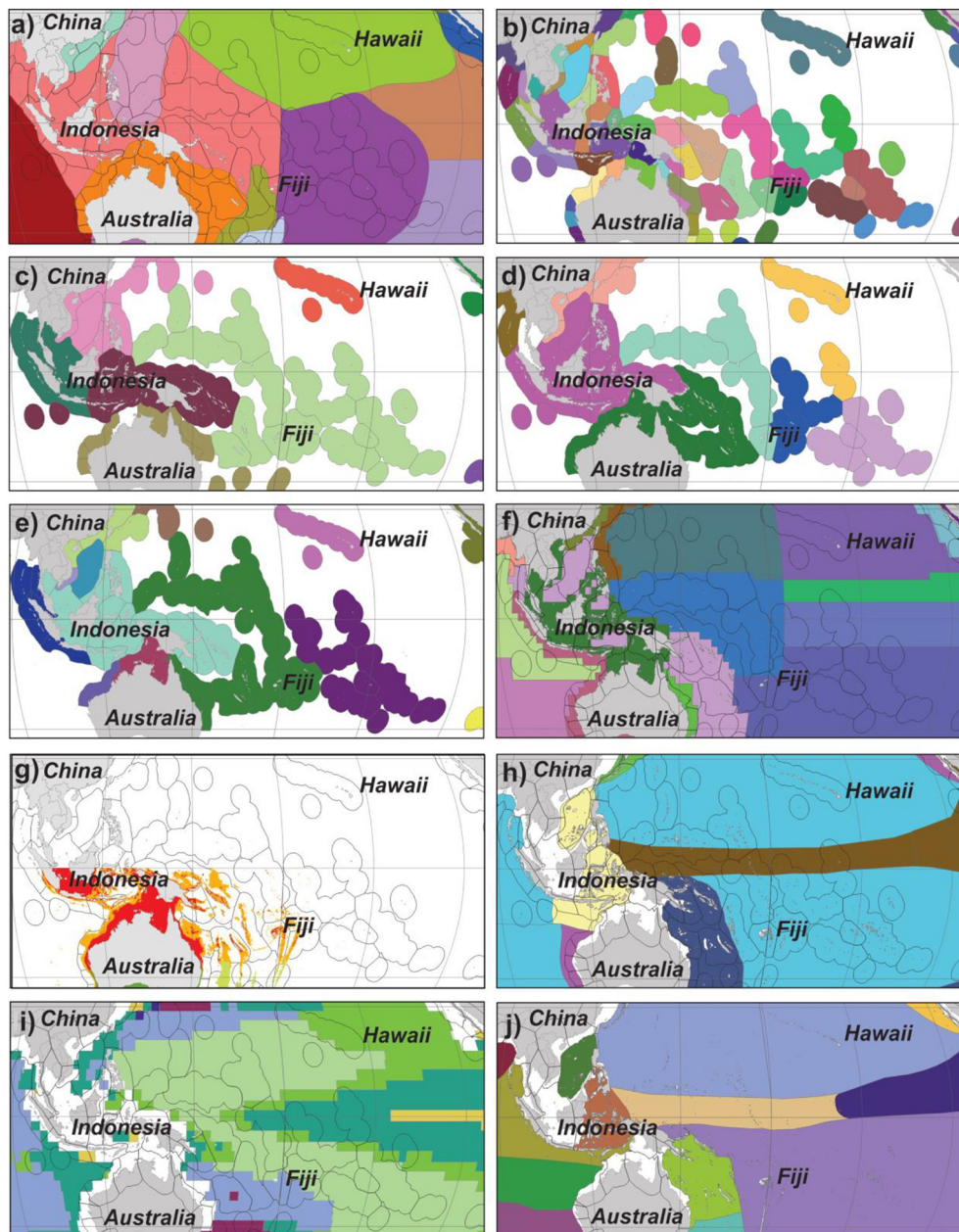


Fig. 1. Map of Pacific Island countries' EEZs and their position within selected existing classification schemes: a) global marine (Costello et al., 2017); b) MEOW (Spalding et al., 2007); c) coral reef fishes (Kulbicki et al., 2013); d) scleractinian corals (Keith et al., 2013); e) scleractinian corals (Veron et al., 2015); f) biogeochemical provinces (Longhurst, 2006); g) Deepwater ophiuroids (O'Hara et al., 2011); h) MEOW pelagic (Spalding et al., 2012); i) Indo-Pacific mesopelagic bioregions (Proud et al., 2017); j) refined mesopelagic bioregions (Sutton et al., 2017).

instance, primary productivity at the surface can influence the habitat and species communities that occur within much deeper oceanic layers (Ban et al., 2014; Graf, 1989; Rex et al., 2006; Woolley et al., 2016). Also, offshore species, at least partly because of the above-described features of the open ocean, do not move randomly through either surface or deep oceanic waters. Instead, they tend to follow predictable pathways and/or aggregate within sites with particular characteristics (Ban et al., 2014). As part of these behaviours, oceanic species such as tuna interact with nearshore environments through preying on its species (Allain et al., 2012).

The currently existing broad-scale bioregionalisations of marine environments (both coastal and offshore) are too coarse to inform most national planning processes. This is because the large exclusive economic zones (EEZs) of Pacific Island countries and territories are often classified into three, two or even one marine region, despite known

variability within and across the marine environment (Ceccarelli et al., 2017b, 2018a, 2018b; Sykes et al., 2018). The entire ocean of Fiji, for example, is often contained within one or two bioregions in the bioregionalisations mentioned above (Fig. 1). This level of assumed national and regional homogeneity is incorrect, and cannot differentiate marine assemblages at the spatial scales relevant for ocean management, such as marine protected areas at km scale. Reef-associated marine habitats are known to vary within the scale of Pacific Island countries and territories with changing environment and coastal morphology (Chin et al., 2011). Offshore environments are also highly variable, and are shaped by oceanographic and biophysical factors (Game et al., 2009; Sutcliffe et al., 2015) that drive open ocean population dynamics. Therefore, existing marine bioregions in the Pacific are too coarse to inform ecological representativeness (i.e. accommodating differences in biotic assemblages within marine protected area system

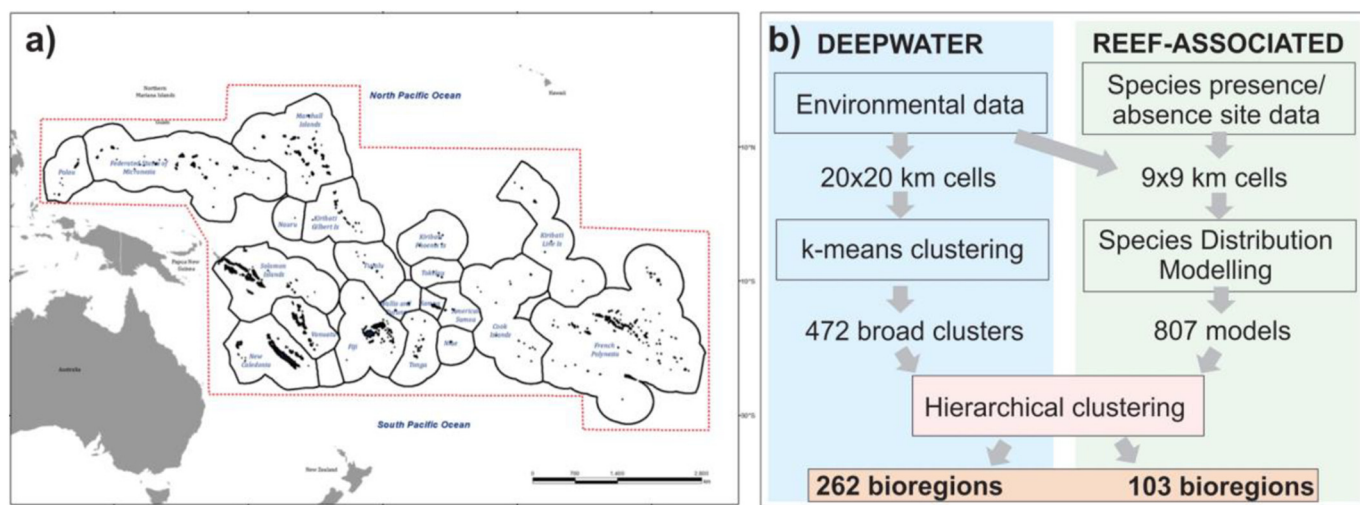


Fig. 2. Project set-up, depicting a) a map displaying the study area in the southwest Pacific (red dotted line) and indicative provisional EEZs (black solid lines), and b) a flow diagram summarising the methods used to delineate deep-water and reef-associated bioregions. EEZ data from (Flanders Marine Institute, 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

design).

Here, we use a data-driven approach to identify and map marine bioregions across the southwest Pacific, distinguishing deep-water and reef-associated environments. Our marine bioregionalisation is designed to support national marine spatial and marine protected area planning processes in Pacific Island countries and territories (Wendt et al., 2018a, b, c, d). We develop these bioregions at a spatial scale that will be suitable for national planning across the southwest Pacific, whilst providing a biological and environmental basis for representing nearshore and offshore marine biodiversity across the region.

2. Methods

Recognising the cross-jurisdictional nature of ecological and biological processes, we defined the area of interest for the analysis as all the countries and territories in the southwest Pacific with the exception of Australia, New Zealand and Papua New Guinea, for which other, existing, scale-appropriate marine bioregionalisations already exist, or are in development (Department of Conservation and Ministry of Fisheries, 2011; Department of the Environment and Heritage, 2006; Green et al., 2014) (Fig. 2a). Our area of interest extends from Palau and the Commonwealth of the Northern Mariana Islands to French Polynesia (130°W to 127°E, 34°S to 20°N) and includes the areas beyond national jurisdictions (ABNJ).

To meet the needs of EEZ-wide marine spatial planning, we developed separate deep-water and reef-associated bioregionalisations to account for different types and resolution of available data (Fig. 2b). The deep-water environments were broadly classified based on environmental data as surrogates for species distributions (Table 1). Reef-associated bioregions were delineated using modelled distributions of coral reef-associated taxa. We delineated the inshore boundary of the deep-water analysis as including areas deeper than 200 m depth or 20 km offshore, whichever was the furthest from land. Correspondingly, the reef-associated analysis captured areas between that boundary and land. The appropriate resolution of the analytical units for the deep-water and reef-associated analyses was based upon the data resolution, the scale of information considered in national spatial planning and decision-making, and computing limitations. Thus, we used 140,598 analytical units with a 20×20 km resolution for the deep-water analysis, and 45,106 analytical units with a 9×9 km resolution for the shallower reef-associated areas. The reef-associated areas included coral reef habitats, and other reef-associated habitats such as seagrasses, and mangroves. For each bioregionalisation analysis, we

collated and quality-checked environmental and biological data available from open-access sources (Tables 1 and 2), the author team and data providers (Tables 1 and 2). Data were determined to be adequately comprehensive if they covered the study area with sufficient resolution to enable within-country distinctions of the parameter of interest. Data were also assessed for taxonomic consistency, outliers, and recording errors.

2.1. Deep-water bioregional classification

Classification of the deep-water bioregions was developed with 30 environmental datasets derived from satellite or ship measurements, including factors of depth, salinity, sea surface temperature, and chlorophyll alpha (CHL_a) concentration (Table 1, Supplementary Material S1). Comprehensive data were available at depths up to 1000 m, thus all data for deeper depths were omitted. Because of the disproportionate influence of bathymetry upon deep-water habitats and taxa, the value of the “depth” environmental parameter was weighted by a factor of two in the analysis (Brown and Thatje, 2014; Dunstan et al., 2012; Piacenza et al., 2015). All raster datasets were projected to a Lambert cylindrical equal-area projection with metre measurement units, allowing us to generate analysis units representing equal-sized areas. The datasets were then assigned to analytical units using the QGIS “zonal statistics” algorithm to calculate the mean value of each dataset within each cell. The data were standardised so that all values were between 0 and 1.

Classification of the analytical units used a two-step process that was executed in the R programming language (R Development Core Team, 2017). Data were first clustered into 5000 groups using the k-means algorithm, which optimizes classification of items into clusters based on an initial set of randomly chosen centres (MacQueen, 1967). To avoid incidental bias in the analysis, we repeated the analysis 20 times and then chose the best fit classification determined by the minimum total within-cluster sum of squares. We then utilized a hierarchical clustering approach by calculating a distance matrix using the centre of gravity of each k-means cluster with the *dist* function, followed by generating classes of sites with the hierarchical clustering algorithm *hclust* in R. The hierarchical clustering tree was cut at a height of 0.4 using the *cutree* function, yielding 475 clusters. The cut-off height was determined by assessing the relative variability of the clusters and identifying the natural break between cluster distances. Deep-water bioregions that were entirely located in ABNJs were removed as they were not associated with any country. Finally, we

Table 1
Datasets used to derive deep-water bioregions.

	Dataset name (source)	Parameter
1	Satellite gravimetry & multibeam data (GEBCO)	Depth (m)
2	Aqua-MODIS (BioOracle)	Calcite Concentration (mol/m ³)
3	World Ocean Database 2009 (BioOracle)	Dissolved Oxygen Concentration (ml/l)
4	World Ocean Database 2009 (BioOracle)	Nitrate Concentration (μmol/l)
5	SeaWiFS (BioOracle)	Photosynthetically Available Radiation (Einstein/m ² /day) (maximum)
6	SeaWiFS (BioOracle)	Photosynthetically Available Radiation (Einstein/m ² /day) (mean)
7	World Ocean Database 2009 (BioOracle)	pH (unitless)
8	World Ocean Database 2009 (BioOracle)	Phosphate Concentration (μmol/l)
9	World Ocean Database 2009 (BioOracle)	Salinity (PSS)
10	World Ocean Database 2009 (BioOracle)	Silicate Concentration (μmol/l)
11	Global Administrative Areas (GADM28)	Distance from Land (m)
12	Aqua-MODIS (NASA)	Chlorophyll <i>a</i> Concentration (mg/m ³) (maximum)
13	Aqua-MODIS (NASA)	Chlorophyll <i>a</i> Concentration (mg/m ³) (mean)
14	Aqua-MODIS (NASA)	Chlorophyll <i>a</i> Concentration (mg/m ³) (minimum)
15	Aqua-MODIS (NASA)	Chlorophyll <i>a</i> Concentration (mg/m ³) (range)
16	Aqua-MODIS (NASA)	Sea Surface Temperature (°C) (maximum)
17	Aqua-MODIS (NASA)	Sea Surface Temperature (°C) (mean)
18	Aqua-MODIS (NASA)	Sea Surface Temperature (°C) (minimum)
19	Aqua-MODIS (NASA)	Sea Surface Temperature (°C) (range)
20	Atlas of Regional Seas (CSIRO)	Dynamic height of sea surface with regard to 2000 m (m)
21	Atlas of Regional Seas (CSIRO)	Depth of 20° isotherm (m)
22	Atlas of Regional Seas (CSIRO)	Mixed Layer Depth (m)
23	Atlas of Regional Seas (CSIRO)	Seawater Temperature (°C) (30 m)
24	Atlas of Regional Seas (CSIRO)	Seawater Temperature (°C) (200 m)
25	Atlas of Regional Seas (CSIRO)	Seawater Temperature (°C) (1000 m)
26	Atlas of Regional Seas (CSIRO)	Nitrate (μmol/l) (1000 m)
27	Atlas of Regional Seas (CSIRO)	Dissolved Oxygen Concentration (mg/l) (1000 m)
28	Atlas of Regional Seas (CSIRO)	Phosphate Concentration (μmol/l) (1000 m)
29	Atlas of Regional Seas (CSIRO)	Salinity (PSS) (1000 m)
30	Atlas of Regional Seas (CSIRO)	Silicate Concentration (μmol/l) (1000 m)

applied a spatial smoothing and quality control step to address assigned isolated outliers and to smooth the gridded boundaries between the resulting classified regions (see [Wendt et al., 2018e](#) for details).

2.2. Reef-associated bioregional classification

We executed a finer-scale classification of reef-associated areas based on both biological and environmental data. Reef biodiversity records were collated from the authors, data contributors, and open access databases across the area of interest ([Table 2](#)). Reef biodiversity records came from a variety of shallow, reef-associated habitat surveys from 4804 georeferenced sites for fishes, 863 sites for scleractinian and soft corals, and 1702 sites for other macro-invertebrates. Taxonomic resolution was at species level for fishes, scleractinian corals, and some invertebrates, and genus or higher taxonomic group for soft corals and other invertebrates. Differing sampling methods and species required standardisation of data to survey area and/or conversion to presence/absence records, which was the most common level of data available from all data sources ([Table 2](#)).

We developed species distribution models for all species that occurred at least 30 times across the Pacific to ensure valid models could be built ([Beger and Possingham, 2008](#); [Elith, 2000](#)). We applied generalised additive modelling (GAM) to create models that use major environmental variables and species observations to generate spatial predictions of the probabilities to observe species in sites with no observational data ([Elith et al., 2006](#)). All the environmental variables across the area of interest available from the Bio-Oracle database were initially considered ([Tyberghein et al., 2012](#)). To avoid over-parameterization and multicollinearity, we tested all pairs of variables for correlation and excluded one of each pair of highly correlated predictors ($r > 0.6$) based on their ecological relevance for coral reef-related organisms. The final predictor set consisted of: calcite, mean CHL_a concentrations, mean SST, pH, maximum PAR, mean PAR, and nitrate. These environmental data were similar to those used in previous large-scale coral reef modelling studies ([Stuart-Smith et al., 2013](#)). Using

9 × 9 km analytical units, we modelled species with a binomial distribution and predicted species probability for all coastal analytical units with the *gam* function in the “mgcv” package in R ([R Development Core Team, 2017](#)). We classified reef-associated bioregions with the modelled species observation probabilities based on hierarchical clustering with Ward similarity ([Clarke, 1993](#)) to identify clusters of sites with similar species assemblages ([Procheş and Ramdhani, 2012](#)). As in deep-water bioregions, the data-classified regions derived from clustering were quality controlled and smoothed to derive the final bioregion boundaries.

2.3. Bioregion names and descriptions

A final step in the analytical process was to assign unique code identifiers, names and initial descriptions to the classified bioregions. Whilst codes and names were assigned to all bioregions, descriptions were only provided for deep-water bioregions, drawn from the habitats and environmental variables that influenced the delineation of each bioregion. The naming system for the bioregions was based on: 1) existing geographic place names; 2) geomorphic feature types within each cluster; 3) environmental variables that influenced the delineation of each cluster; and 4) notable key underwater features.

2.4. Reviewing bioregions with in-country specialists

National workshops with in-country experts were held in 2017 and 2018 to review and revise the draft bioregions developed by the above technical analysis. Local expert workshops were held in Fiji, Solomon Islands, Tonga and Vanuatu to: (a) describe the analysis conducted, (b) introduce the draft marine bioregions and the data upon which they were based, and (c) review, revise and finalise the draft marine bioregions in light of in-country knowledge and expertise. Workshops were attended by representatives from government, academia and NGOs with relevant knowledge and expertise in national conditions and planning processes. This process also built local ownership of the

Table 2

Reef biodiversity datasets used to derive reef-associated bioregions. * indicates open access or publicly requestable data.

	Parameter	Source	Countries
1	Reef fish	Khaled bin Sultan Living Oceans Foundation	Fiji, Tonga
2	Reef fish	Marine Ecology Consulting (H Sykes)	Fiji
3	Reef fish	National Oceanic and Atmospheric Administration*	Pacific Remote Island Areas, Samoa
4	Reef fish	Reef Life Survey*	Tonga, Cook Islands, Niue, French Polynesia, American Samoa, Solomon Islands, Pitcairn, Vanuatu, Marshall Islands
5	Reef fish	Secretariat of the Pacific Community*	Fiji, Kiribati, Nauru, New Caledonia, Niue, Solomon Islands, Tonga, Tuvalu, Vanuatu, Wallis And Futuna
6	Reef fish	South Pacific Regional Environment Programme*	Tonga, Nauru
7	Reef fish	The Nature Conservancy	Solomon Islands
8	Reef fish	University of Queensland (Dr M Beger)	Marshall Islands
9	Reef fish	Dr D Ceccarelli	Tuvalu
10	Reef fish	Dr D Ceccarelli, K Stone	Tonga
11	Reef fish	PIPA (Dr S Sandin, Dr R Rotjan)	Kiribati
12	Reef fish	WCS	Fiji
13	Coral	University of Queensland (Dr D Fenner, Dr Z Richards)	Marshall Islands
14	Coral	Dr D Fenner	Tonga, Nauru
15	Coral	PIPA (Dr R Rotjan, Dr S Mangubhai)	Kiribati
16	Coral	University of Queensland (Dr E Turak, Dr Z Richards)	Papua New Guinea
17	Coral	Dr Doug Fenner	American Samoa
18	Coral	TNC Rapid Ecological Assessment (Dr P Houk)	Micronesia (Chuuk)
19	Coral	The Nature Conservancy	Solomon Islands
20	Coral	University of British Columbia (Dr S Donner)	Kiribati
21	Coral	WCS	Fiji
22	Coral	Museum of Tropical Queensland (Dr P Muir)	New Caledonia
23	Invertebrates	Secretariat of the Pacific Community*	Fiji, Kiribati, Nauru, New Caledonia, Niue, Solomon Islands, Tonga, Tuvalu, Vanuatu, Wallis And Futuna
24	Invertebrates	Marine Ecology Consulting (H Sykes)	Fiji
25	Coral reefs	UNEP-WCMC (2010)*	Global distribution
26	Mangroves	Giri C et al. (2011)*	Global distribution

marine bioregions and understanding their use in national marine spatial planning (Wendt et al., 2018a, b, c, d).

3. Results

3.1. Reef-associated species distribution models

The resulting database contained records for 1014 fishes (after excluding fishes with few records or not reliably sampled from the original dataset of 1405 species), 321 coral species, and 300 mobile invertebrates distributed across the project area (for species list see Supplementary Material S2). After excluding species that occurred less than 30 times across the Pacific, we built GAMs for 465 fishes, 259 corals (species level taxonomy for Scleractinian corals, and genus or family level for soft corals), and 82 mobile invertebrate taxa (for all model stats, see Supplementary Material S3). All environmental predictor variables used here were important for some species, but the main drivers of species from all three taxa were nitrate, light (PAR), pH-value, and mean SST (Fig. 3).

3.2. Deepwater bioregional classification

A total of 262 deep-water bioregions were defined across the Southwest Pacific (Fig. 4a,c, Table 3). Many deep-water bioregion boundaries extended beyond Pacific Island countries and territories' EEZs and also into ABNJs (Fig. 4a). Most deep-water bioregions were unitary but some had multiple, non-contiguous parts that were divided where they were more than 1000 km apart. A majority of the deep-water bioregions share boundaries with neighbouring Pacific Island countries and territories, as did many reef-associated bioregions. Names and descriptions of bioregions are provided in Supplementary Material S4.

3.3. Reef-associated bioregional classification

A total of 103 reef-associated bioregions were defined across the southwest Pacific (Fig. 4b,d, Table 3). Names of reef-associated bioregions are provided in Supplementary Material S5.

3.4. Final bioregions after in-country expert review

The marine bioregions derived from the data-driven analyses were modified through local expert review to better encompass local features and patterns that were known but not reflected in datasets and thus could not be represented in our analysis. Reviews were undertaken in Fiji, Solomon Islands, Tonga, and Vanuatu. The workshops had 20 to 50 participants with expertise that included inshore and offshore fish ecology, coral reef ecology and biodiversity, threatened species, seabed geology, mangroves, cetaceans, sea turtle ecology, water quality science and traditional knowledge. Participants included government staff, scientists, consultants and those with traditional knowledge from communities. Participants first explored the deep-water, then reef-associated bioregions. They used a template to guide their review of all the bioregions' locations and boundaries, names and descriptions. They were divided into groups based upon their geographical area of knowledge and those with comprehensive knowledge were asked to move amongst the groups. The participants were provided with approximately 40 hard copy maps of environmental and biological data to reference (posted on the wall) and each break-out group had a GIS expert with 50–60 datasets that could be viewed on the computer. Each break-out group also had a rapporteur and facilitator (Wendt et al., 2018a, b, c, d).

Changes made were typically merging or division of some bioregions, some boundary realignments, and some finer scale description of both deep-water and reef-associated bioregions (Fig. 5) (Wendt et al., 2018a, b, c, d). For example, in country experts suggested reducing the width of the reef-associated bioregions to more accurately represent shallow reef extent which was misrepresented by globally mapped reef

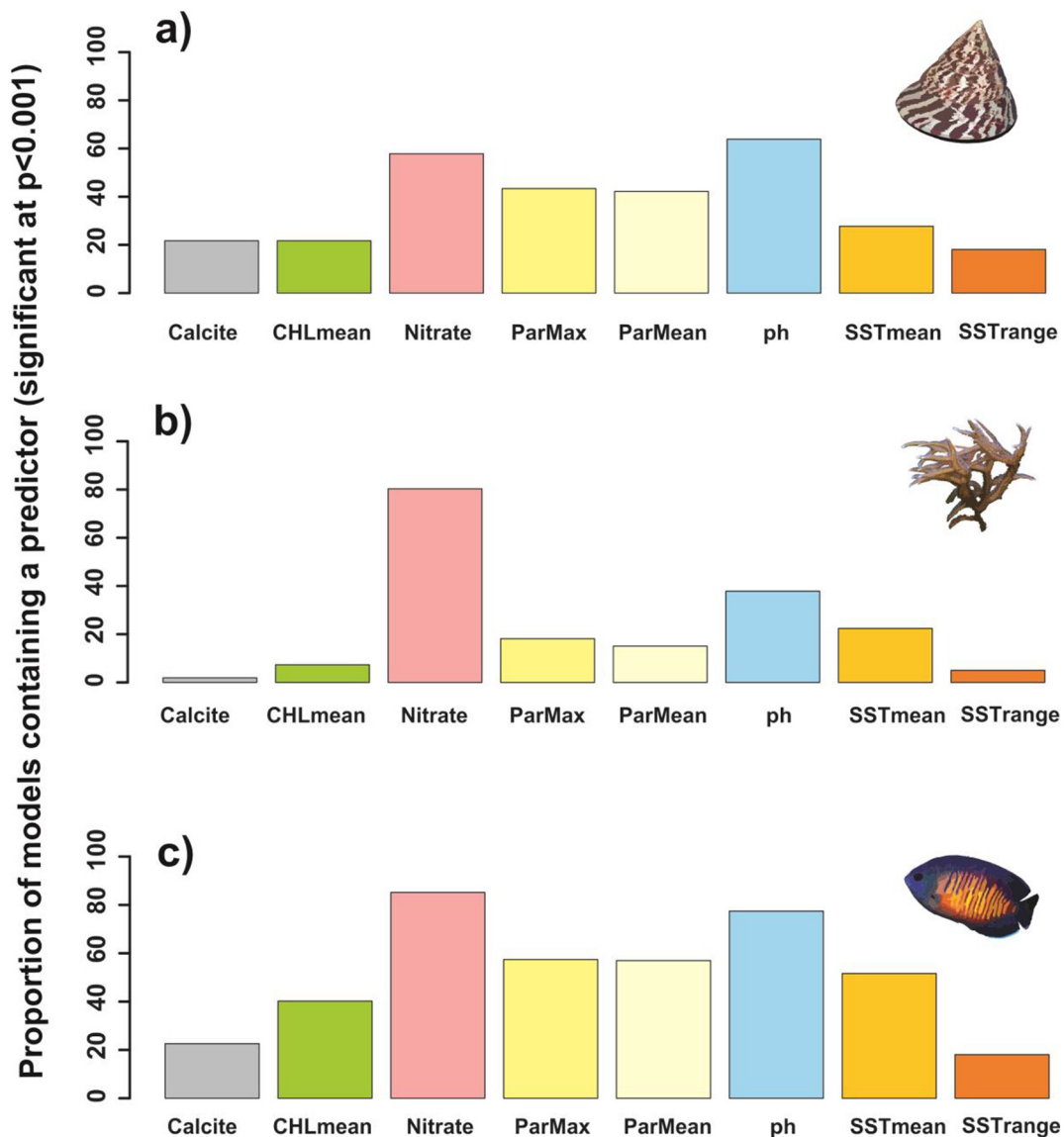


Fig. 3. The proportion of environmental predictors included in models of species distributions for a) invertebrates, b) scleractinian corals, and c) fishes.

extent data in some cases (Fig. 5).

4. Discussion

This work provides the first set of sub-national ocean and coastal marine bioregionalisation for the southwest Pacific, delineating 262 deep-water bioregions and 103 reef-associated bioregions within Pacific Island countries and territories and ABNJs. Importantly, our marine bioregions form a vital first step in providing the biophysical data layer needed to foster and improve effective spatial planning across the southwest Pacific. Countries can now, for example, design ecologically representative systems of marine protected areas by ensuring representation of examples of every marine bioregion in the system. Whilst such spatial planning requires much more than representation of biodiversity, our marine bioregions offer a biophysical dataset to inform a critical step in the process (Lewis et al., 2017). Of course, most natural resource managers also have social, economic, and cultural objectives they wish to achieve in national planning, therefore consideration of human uses and values of marine areas will also be pivotal to developing effective spatial plans and marine protected area systems (Geange et al., 2017; Lewis et al., 2017; Lundquist and Granek, 2005; Mangubhai et al., 2015; Pomeroy and Douvère, 2008).

There has been a recent impetus throughout Pacific nations to fulfil international commitments in ocean conservation, despite the lack of sub-national bioregionalisation to support such efforts. For example, large ocean states in the Pacific, including Fiji, Solomon Islands, Tonga and Vanuatu, have committed to improve their ocean protection (e.g. United Nations Ocean Conference Voluntary Commitments). Most Pacific Island countries, including these four, are party to the CBD and committed to meeting the part of Aichi Target 11 calling for ecologically representative systems of marine protected areas by 2020. Some nations have already protected large proportions of their marine environment (e.g. Kiribati and the Cook Islands, Christie et al., 2017; Rotjan et al., 2014). Others, for example, the countries within the Micronesia Challenge (i.e. Palau, Federated States of Micronesia and the Marshall Islands) and Fiji, are moving towards protecting at least 30% of their marine estate (Houk et al., 2015; Ministry of Economy, 2017). Many of these efforts also include aspects of systematic conservation planning, at least in shallow water ecosystems (Baker et al., 2011). However, 98% of the marine environment of Pacific Island countries lies beyond coastal ecosystems. Recognising this, some countries are aiming towards holistic national systems of marine protected areas which are embedded into wider seascapes through national marine spatial planning across their EEZs (e.g. Vanuatu, Tonga and Solomon

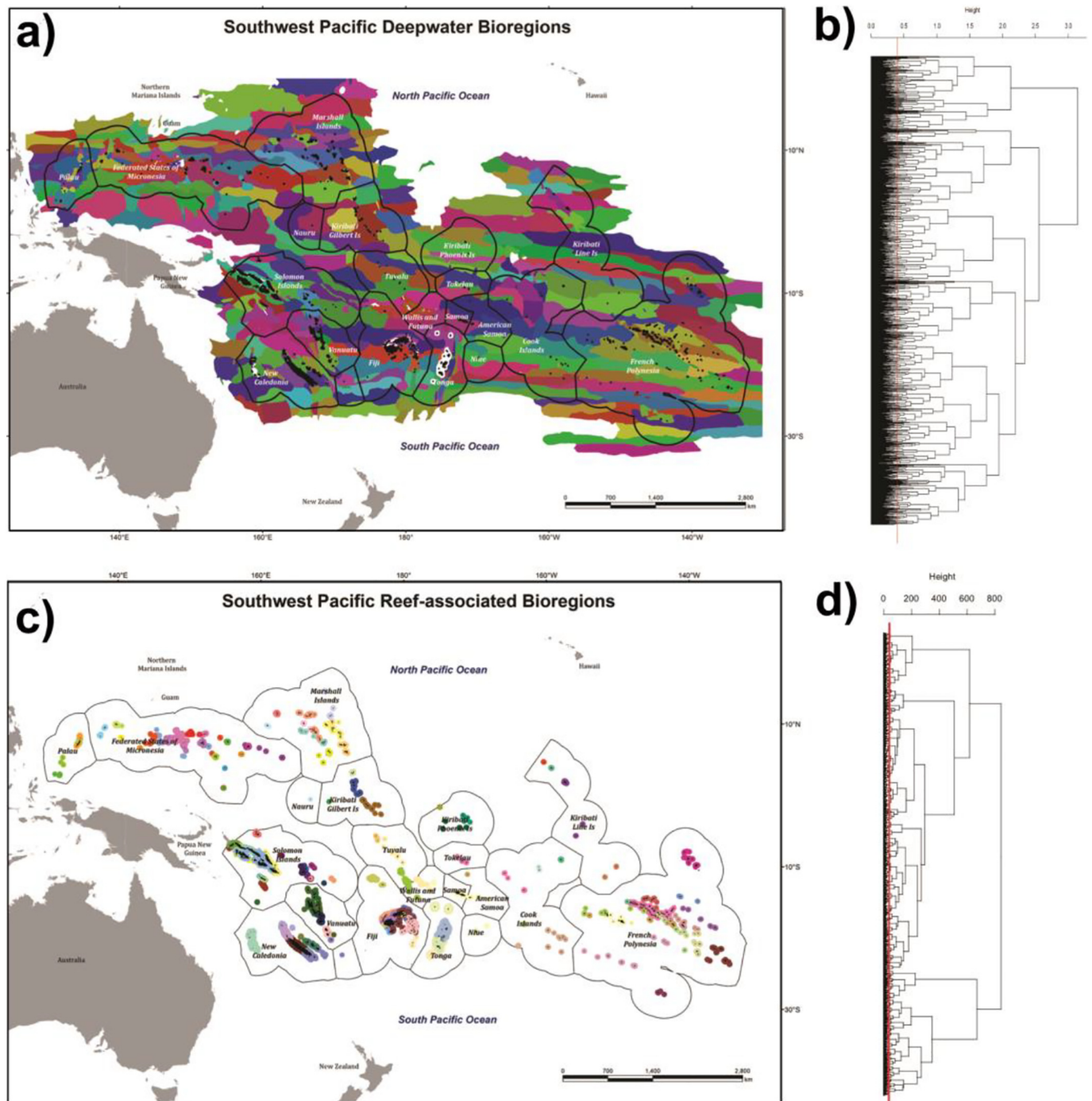


Fig. 4. Map depicting the regions derived from marine classification of the southwest Pacific, for a) deep-water bioregions with b) showing the hierarchical clusters, and c) reef-associated bioregions for the Southwest Pacific with d) showing clusters. Reef areas are exaggerated in this Figure for ease of viewing. EEZ data from (Flanders Marine Institute, 2018).

Islands) (MEIDECC Kingdom of Tonga, 2017; Ocean12 Technical Working Group, 2018; Ocean Sub-Committee of the National Committee for Maritime Boundary Delimitation, 2016). Until now, a mechanism to systematically implement ecologically representative systems of marine protected areas at national scales (i.e. including offshore areas) within Pacific Island countries has not been available.

Our technical analysis provides marine bioregions across the southwest Pacific at a spatial scale suitable for marine spatial planning in Pacific nations. The methodologies used in this study are repeatable, statistically robust, and based on many sets of comprehensive and reliable data available. Our approach here is akin to other data-driven

bioregionalisations (Keith et al., 2013; Kulbicki et al., 2013; Longhurst, 2006; O'Hara et al., 2011; Proud et al., 2017), but informed by multiple taxa and environmental surrogates. However, analytically produced bioregions will still benefit from expert input (Brewer et al., 2015), particularly from people with local or regional biogeographical expertise. This is reflected in several changes suggested by local marine experts that reviewed and revised bioregion names, boundaries and descriptions to ensure they reflect their knowledge of their marine ecosystems. This coupling of technical analysis and expert input ensures that bioregions are based on the best available knowledge and is a relatively unique approach to the creation of bioregions which normally

Table 3

Number of draft deep-water and reef-associated bioregions described per country or overseas territory as an output of this analysis. Because many bioregions cut across national jurisdictions they are listed in more than one country.

Country name	Number of deep-water bioregions	Number of shared deep-water bioregions	Number of reef-associated bioregions	Number of shared reef-associated bioregions
American Samoa	9	9	2	2
Cook Islands	30	27	6	4
Fiji	23	23	12	3
French Polynesia	52	23	16	5
Kiribati	54	47	11	2
Marshall Islands	34	19	9	2
Federated States of Micronesia	41	32	19	4
Nauru	6	6	1	1
New Caledonia	31	24	8	1
Niue	6	6	2	2
Palau	19	18	4	0
Samoa	6	6	1	1
Solomon Islands	33	26	19	6
Tokelau	8	8	2	2
Tonga	35	27	4	3
Tuvalu	13	13	4	3
Vanuatu	20	18	7	3
Wallis and Futuna	9	9	3	3
ABNJ	0	200	0	0

rely on either solely technical (Keith et al., 2013; Kulbicki et al., 2013; Longhurst, 2006; O'Hara et al., 2011; Proud et al., 2017) or expert driven (Green et al., 2014; Spalding et al., 2007; UNESCO, 2009). As new and better information becomes available, the analysis can be rerun to build better defined and more robust marine bioregions of the southwest Pacific.

Defining bioregions is only one step in a much more complex marine spatial planning process, which aims to minimise conflict between environmental protection and a wide range of human uses. Ideally, this process results in marine spatial plans (of which a network of marine protected areas is one component) that guides the management of human activities and is adaptable over time (Ehler and Douvère, 2009). As knowledge is gained about marine ecosystems and their responses to climate change and other human pressures, and the activities themselves change, the plan can be adapted to provide the best solution possible given the information available.

We acknowledge that the epiphotic (or photic), mesophotic, bathyal, abyssal, hadal and benthic ocean zones host assemblages of organisms that may not vertically align. Sayre et al. (2017), for example, used environmental data to create three-dimensional maps of the ocean, leading to a comprehensive set of 37 distinct volumetric region units at various depths across oceans globally. Eleven of these regions were in the tropical southwest Pacific (Sayre et al., 2017). Thus, in an ideal world, one would describe marine bioregions within each vertical ocean “zone” at a scale useful for national management. However, this was not possible given the data constraints at the time of this work. It is also generally impractical from a management perspective to establish protected zones for different depth zones (Venegas-Li et al., 2018), and the scope of current marine spatial planning work in the region does not include such an approach.

We also recognise that the offshore bioregionalisation reflects a suite of physical variables with biological relevance that are grouped with equal weighting (other than depth which is double weighted). This equal weighting will tend to overemphasise the importance of the larger subsets of variables that are highly auto-correlated at the expense of uncorrelated variables, potentially including some with high

biological significance. As the density of species-level information increases for offshore waters, validation of the physical regionalisation using offshore biological data is desirable.

Alternatively, different methods can be used to describe bioregions. For example, Last et al. (2010) present a framework of ten hierarchical layers of “regions” that describe the seabed only, but at different scales from the ocean basin-scale (biogeographic) to the genetic level. Its in-country utility for national-planning purposes in the Pacific has yet to be explored. The clustering of the reef-associated species data could also have been conducted with other methods, for example where species assemblages are tracked together probabilistically (e.g. Foster et al., 2013), or with a network approach (Vilhena and Antonelli, 2015) or, albeit restricted to shallow areas, with reference to regional-scale maps of benthic habitat (Purkis et al., 2019). Each of the many types of methods available has pros and cons; we chose approaches that we considered would best match Pacific Island ocean planning requirements and data constraints.

The marine environment and the organisms that live in the ocean are not bound by national boundaries—in addition to national planning the national-scale bioregions can also inform multi-lateral planning initiative in the region or contribute to the governance of ABNJs. Locally and nationally, marine organisms are also distributed in highly heterogeneous patterns, particularly across the huge EEZs of some Pacific countries. The kilometre-scale bioregions presented here satisfy the need to represent such heterogeneous biodiversity patterns in national planning, whilst also providing a level of robustness to change that reflects local knowledge and diversity in data gathering. Thus, marine bioregions are a key ingredient in marine spatial planning because they offer insurance against ignoring parts of the ocean where data are incomplete or absent. Our results provide a first, unique, and essential step in designing ecologically representative systems of marine protected areas at national scales in southwest Pacific Island countries and territories.

Author contributions

MB & LF led conceptualisation, data curation, analysis, writing, and overall progress of the project, HW, JL, JS, KD contributed to concept refinement, analysed, and wrote, LF, HW, JS, JL, KD, SJ, NY, AH, JR led or assisted with in-country development of ecoregions, JS, JL, and CM analysed data, HW, MB, LF, JS wrote the original draft, AGB, DMC, AD, DAF, GE, HG, SNK, SM, SP, ZTR, RR, RSS, HS, and NY contributed or managed data, and all authors reviewed and edited the draft manuscript. LF provided the original idea and acquired funding.

Data and code

All code and data to rerun the analysis is deposited in <https://github.com/MACBIO/National-scale-marine-bioregions-for-the-Southwest-Pacific>.

The ecoregion files are provided here:

Regional: http://macbio-pacific.info/wp-content/uploads/2018/04/MACBIO_Bioregions_Data.zip.

Fiji: <http://macbio-pacific.info/wp-content/uploads/2018/09/Fiji-Bioregions-Data.zip>.

Solomon Islands: <http://macbio-pacific.info/wp-content/uploads/2018/04/SLB-Bioregions-Data.zip>.

Tonga: http://macbio-pacific.info/wp-content/uploads/2018/04/Tonga_deepwater_bioregions.zip.

Vanuatu: <http://macbio-pacific.info/wp-content/uploads/2018/04/VUT-Bioregions-Data.zip>.

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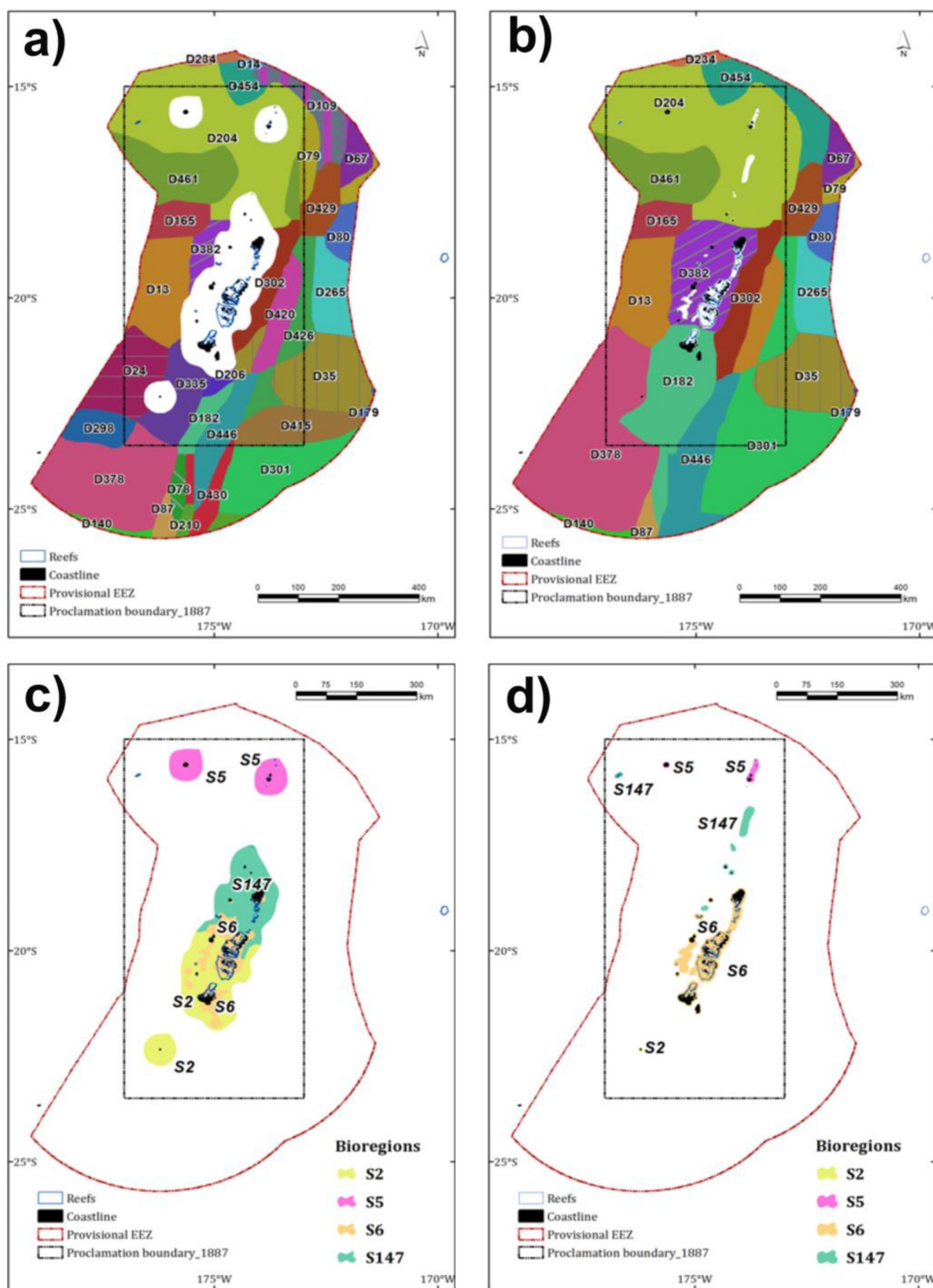


Fig. 5. Alterations to draft bioregions for Tonga after local expert review (Wendt et al., 2018), showing a) draft deep-water bioregions, b) final deep-water bioregions, c) draft reef-associated bioregions; and d) final reef-associated bioregions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marpolbul.2019.110710>.

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