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Spatial assemblage structure of shallow-water reef fish in Southwest Australia

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ABSTRACT: Bioregional categorisation of the Australian marine environment is essential to conserve and manage entire ecosystems, including the biota and associated habitats. It is important that these regions are optimally positioned to effectively plan for the protection of distinct assemblages. Recent climatic variation and changes to the marine environment in Southwest Australia (SWA) have resulted in shifts in species ranges and changes to the composition of marine assemblages. The goal of this study was to determine if the current bioregionalisation of SWA accurately represents the present distribution of shallow-water reef fishes across 2000 km of its subtropical and temperate coastline. Data was collected in 2015 using diver-operated underwater stereo-video surveys from 7 regions between Port Gregory (north of Geraldton) to the east of Esperance. This study indicated that (1) the shallow-water reef fish of SWA formed 4 distinct assemblages along the coast: one Midwestern, one Central and 2 Southern Assemblages; (2) differences between these fish assemblages were primarily driven by sea surface temperature, *Ecklonia radiata* cover, non-*E. radiata* (canopy) cover, understorey algae cover, reef type and reef height; and (3) each of the 4 assemblages were characterised by a high number of short-range Australian and Western Australian endemic species. The findings from this study suggest that 4, rather than the existing 3 bioregions would more effectively capture the shallow-water reef fish assemblage patterns, with boundaries having shifted southwards likely associated with ocean warming.

KEY WORDS: Fish assemblages · Reef fish · Bioregions · Endemic fish · Marine · Sea surface temperature · Southwest Australia

1. INTRODUCTION

1.1. Marine bioregionalisation

'Bioregionalisation', or accurately specifying distinct bioregions, is important for both marine and terrestrial conservation planning. Once defined, these regions can be used to build a planning framework for an area that is representative and comprehensive (e.g. Ray & McCormick-Ray 1992, Salm et al. 2000). Managing an area by bioregions allows for whole ecosystem conservation and management (Olson et al. 2001), which is recognised as an optimal management practice for regions of high biodiversity in terrestrial systems (e.g. Warry & Hanau 1993, Jenkins & Joppa 2009). In contrast to terrestrial bioregional planning, the marine environment is underrepresented in management systems, despite a number of regions having high biodiversity and a high concentration of species and endemics (Phillips 2001). As a consequence of this underrepresentation, a shift towards management strategies that conserve and protect entire marine ecosystems is occurring (Wood et al. 2008, Barr & Possingham 2013). The concept of marine bioregionalisation has been expanding since the late 1990s (Agardy 1999), with it being suggested that these regions should be of a suitable size to assist in managing the dynamic marine environment, encompass multiple

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use and no-take areas and enable the protection of associated habitats (Day 2002, GBRMP Authority 2004). This concept is being adopted globally (Morrone 2015) to balance and manage resource use and conserve marine biodiversity and habitats. For example, the Netherlands are developing a regional management plan and framework to enhance the economic value of the North Sea while protecting and managing the ecology and habitat (IDON 2015). Similarly, the UK has adopted a spatial management plan of their entire marine area via the White Bill, allowing plans for interactions between ecological and economical uses (DEFRA 2007). Australia has also adopted a bioregional approach and aims to have over 35% of its waters protected within this system (Barr & Possingham 2013).

In 1991 (Last et al. 2011), Australia established the National Representative System of Marine Protected Areas based on bioregional marine planning. To facilitate and ensure establishment of this management strategy by 2012, the Integrated Marine and Coastal Regionalisation of Australia (IMCRA) was developed (Commonwealth of Australia 2006). These maps arranged the marine environment into 60 mesoscale bioregions on the Australian continental shelf. In Southwest Australia (SWA), there are 3 identified mesoscale bioregions under the current iteration (Commonwealth of Australia 2006): (1) the Central West Coast; (2) The Leeuwin-Naturaliste; and (3) the Western Australia (WA) South Coast. The goal of IMCRA is to ensure these bioregions are ecologically structured and useful for resource planning and conservation of species and their habitats in Australia (Commonwealth of Australia 2006).

Commercial fisheries in SWA are managed according to slightly different management regions, building upon the IMCRA mesoscale bioregions. In this region, fisheries management utilises the risk-based ecosystem-based fisheries management (EBFM) approach to form a regional management and planning system (Fletcher et al. 2010, 2012), which observes the linkage between fisheries value and individual exploited fish stocks as well as effects on habitat and individual species (Gaughan & Santoro 2018). Currently, SWA commercial fisheries are managed within 2 bioregions: the West Coast and the South Coast. Bioregions in Australia form the basis of marine management and planning to balance biodiversity preservation and sustainable resource use. As a consequence, the bioregions should accurately represent the marine communities within them (Stewart et al. 2003) and be adaptable to consider changes in the distribution of species.

1.2. Australia's biodiversity

Australia's marine biodiversity has long been recognised as unique (Kriwoken 1996, Wernberg et al. 2011), with its waters containing a number of internationally accredited biodiversity marine 'hotspots' (regions with a high biodiversity and concentration of species and endemics) (Phillips 2001, Wernberg et al. 2011). Hotspots are areas usually isolated in space and time and are useful to prioritise the conservation and management of a region. The most famous Australian marine hotspot is the Great Barrier Reef, which is home to approximately 1150 fish species and tropical coral reef communities (Allen 2008, Wood et al. 2008). SWA is also a global biodiversity hotspot (e.g. Lüning 1991, Bolton 1994, Bennett et al. 2016), recognised for its high species richness and endemism and estimated to have 30–40% of the world's macroalgae diversity within its coastal waters (Bolton 1994). The 'Great Southern Reef' of SWA provides substantial socio-economic and ecological value to the surrounding communities that depend on this reef system (Bennett et al. 2016).

SWA has a complex coastline ranging from a subtropical north to a temperate south (Fox & Beckley 2005). The waters contain approximately 3000 species of marine fish (Hutchins 2001), with 19.5% of these species estimated to be short-range endemics (Fox & Beckley 2005), defined as species that occur naturally across small areas less than 10 000 km^2 (Harvey 2002). The coastline of SWA is highly heterogeneous, with abundant rocky coasts, kelp forests and sandy beaches, and is subjected to oceanographic influence, such as ocean currents that may facilitate the migration of species (Adey & Steneck 2001, Phillips 2001). The southward flowing Leeuwin Current has a major influence on SWA coastal waters, transporting warmer water from the north and ensuring the survival of tropical fauna along the coast (Pearce & Walker 1991). The Leeuwin Current and the corresponding sea surface temperature (SST) gradient from north to south makes SWA an ideal area to study the distribution and assemblage structure of shallow-water reef fish (Wernberg et al. 2010, Langlois et al. 2012). Algal assemblages and canopy-forming macroalgae (Levin & Hay 1996, Galaiduk et al. 2017), substratum type (Jenkins & Wheatley 1998), vertical relief (Harman et al. 2003) and SST (Pörtner et al. 2010, Langlois et al. 2012) all contribute to creating distinct ecological habitats and niches that give rise to unique fish assemblages within a geographic area. The relationship between species, habitat and SST, along with other environmental variables can aid in defining bioregions, which can be used in conservation and management, allowing prioritisation of resources and funding (Ward et al. 1999, Valavanis et al. 2004, Moore et al. 2010).

Bioregions in SWA were identified by studies completed in the early 2000s (e.g. Hutchins 1994, 2001, Fox & Beckley 2005, Commonwealth of Australia 2006). However, in the past 2 decades, climatic variations including changes in salinity, ocean currents and temperature have been predicted and documented (Hobday & Lough 2011, Cheung et al. 2012), which has resulted in regime shifts (Bennett et al. 2015b, Wernberg et al. 2016), shifts in species ranges, changes in the composition of fish and other marine assemblages (e.g. Bennett et al. 2015b, Shalders et al. 2018, Parker et al. 2019) and changes in fishing effort (Gaughan & Santoro 2018). To adequately manage and protect species and habitats in a changing environment, it is important to determine if the current bioregionalisation of SWA represents the present distribution of shallow-water reef fish communities.

The goal of this study was to determine whether the defined bioregionalisation of SWA accurately represents the current distribution of shallow-water reef fish communities. Quantifying the accuracy of SWA's bioregionalisation can inform management to ensure bioregions accurately represent shallow-water reef fish assemblages and contribute to accurate protection of hotspot regions. The aims of this study were to (1) assess whether 7 regions sampled each represent distinct fish assemblages or group into a smaller number of clusters representing bioregions; (2) assess whether any distinct bioregions observed align to the established SWA IMCRA and fisheries management regions; and (3) identify the primary environmental variables that influence the distribution of shallow-water reef fish and the fish species that characterise the fish assemblages within the distinct bioregions in SWA.

2. MATERIALS AND METHODS

2.1. Study area and experimental design

Surveys of shallow-water reef fish assemblages were completed across SWA following a hierarchical experimental design (Saunders et al. 2014, Shalders et al. 2018, Parker et al. 2019). A total of 7 coastal regions in SWA were sampled, designed to incorporate the subtropical to warm temperate transition, and warm temperate SWA coastline. Locations were selected to ensure they encompassed the temperature gradient that exists along the coast and the heterogeneous habitats of SWA. The 7 regions spanned 2000 km of coastline, ranging from Geraldton (28.7797° S, 114.6144° E) in the north, through Jurien Bay (30.3070° S, 115.0372° E), Perth (31.9505° S, 115.8605° E), South-West Capes (34.0887° S, 114.9975° E), Albany (35.0269° S, 117.8837° E) and Bremer Bay (34.3979° S, 119.1897° E), to Esperance (33.8613° S, 121.8914° E) in the southeast of WA (Fig. 1). In total, 4 locations were selected within each region, 4 reef sites were chosen within each location and 12 transect lines (25 m long × 5 m wide) were surveyed within each reef site. This resulted in data being collected from 1344 transects across 112 reef sites between December 2014 and July 2015. While collecting data over a 6 mo period may have resulted in seasonal changes in the recorded fish assemblages, most reef-dwelling fish species are site-associated (Sale 1991), and therefore the recorded assemblages were likely to be stable between seasons (Holbrook et

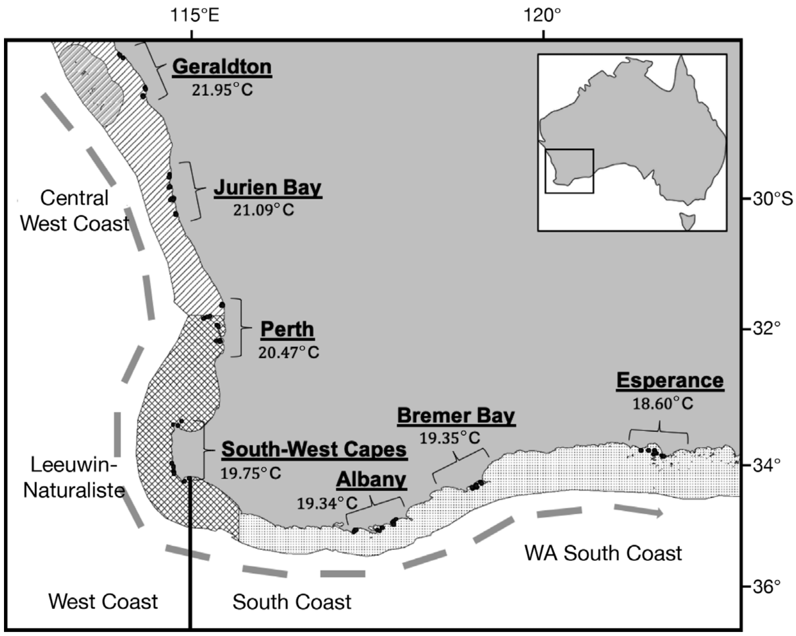

Fig. 1. Survey design in Southwest Australia (SWA) showing the 7 regions (1: Geraldton; 2: Jurien Bay; 3: Perth; 4: South-West Capes; 5: Albany; 6: Bremer Bay; 7: Esperance) and mean sea surface temperature for each region during the study period. Within each region the locations of each reef site (n = 112) are illustrated. Grey arrow along the coast: direction of the Leeuwin Current and the corresponding temperature gradient; hatching and shading: the 3 Integrated Marine and Coastal Regionalisation of Australia mesoscale regions: Central West Coast, Leeuwin-Naturaliste and the Western Australia (WA) South Coast; dark line heading south from the South-West Capes: the 2 fisheries management areas of SWA

al. 1994). Samples were separated by distance based on a hierarchical spatial scale. The 7 regions were separated by 1000s to 100s of km, locations within each region by 10s of km and reef sites within each location by kilometres to 100s of metres. Transects within each reef site were separated by at least 10 m. Sampling targeted shallow, complex reefs between 4 and 12 m deep and encompassed a coastline spanning 7° of latitude and 10° of longitude.

2.2. Survey method

To record and survey the shallow-water reef fish and benthic habitats, SCUBA divers maneuvered a diver-operated stereo-video system (stereo-DOV) along the 25 × 5 m transects. The use of 25 m transect lengths was chosen due to the patchiness of the complex shallow-water reefs sampled. Each transect was swum by a pair of SCUBA divers with one diver operating the stereo-DOV. Stereo-DOVs were designed to improve the precision of length and distance estimates and minimise inter-observer variability (Harvey & Shortis 1995, Harvey et al. 2002, Harvey et al. 2004, 2010). The stereo-video system used in this research was constructed from 2 Sony HDR CX700 video cameras in underwater housings, fixed 700 mm apart and inwardly converged at 8° to maximise the area for measurement (Shalders et al. 2018, Parker et al. 2019). The system was calibrated before and after each set of field work using the software CAL (Seager 2014), which ensured accurate calculation of transect dimensions and length measurements throughout the entire study area (Harvey & Shortis 1998, Shortis & Harvey 1998, Harvey et al. 2004).

2.3. Video analysis

Video recordings created a permanent record of each transect, allowing for post-survey analysis of fish and benthic habitat. The video footage was analysed using the software package Event-Measure (stereo) (www.seagis.com.au) with an observer identifying, counting and measuring the lengths of fish seen within each transect. Rules established within the software prevented fish that were more than 7 m away from the camera or 2.5 m away from the centre of the transect line (outside the transect) from being counted or measured (Harvey et al. 2004). Fish that were only visible in one camera, due to obstruction of the field of view by algae or substrate, were still counted if the analyst was certain that the fish were within transect boundaries.

2.4. Habitat analysis

The same video footage was also used to quantify the benthic habitat. Video imagery was analysed in a Visual Basic program in Microsoft Excel modified from that described by Holmes (2005). Following the procedures from Saunders et al. (2014), 5 equally spaced frames were selected within each 25 m transect and analysed. Each frame was non-overlapping and showed an extensive view of the habitat, which allowed categorisation as a horizontal image. It was then assigned a reef type, either limestone or granite, and reef cover was approximated and assigned a categorical value from 1–6 within each frame: (1) 0–25% reef and 75–100% sand, (2) 21–50% reef and 50–75% sand, (3) 50% reef and 50% sand, (4) 50–75% reef and 25–50% sand, (5) 75–100% reef and 0–25% sand or (6) 100% reef. Reef height was also estimated from the field of view and categorised with a value from 1–4: (1) platform reef, (2) small (<1 m in height boulders or outcrops), (3) large (1–3 m in height boulders or outcrops), or (4) massive (>3 m in height outcrops). Reef slope was estimated and assigned a value from 1–5 based on (1) gentle slope (<30°), (2) steep slope (30–70°), (3) vertical wall (70–110°), (4) overhanging wall (>110°) and (5) overhead overhanging reef or cave. Benthic habitat was also estimated at each frame for *Ecklonia radiata* Canopy, non-*E. radiata* (canopy) cover, understorey algae cover (foliose and turfing algal forms) and hard coral cover, and were given a rank from 0–6, with (0) no cover, (1) <1%, (2) 1–10%, (3) 10–25%, (4) 25–50%, (5) 50–75% and (6) >75% cover. Seagrass presence or absence was also recorded for each frame. The Australian Ocean Data Network (AODN) open access to ocean data portal AODN (2020) was used to determine mean SST at each study location. The AODN uses a single-sensor, multi-satellite 'SSTfnd' product that is derived from observations on all available NOAA satellites to produce a 0.02° grid. The mean temperature value was calculated from all available temperature recordings to give a single temperature value for each location over the year 2015.

2.5. Statistical analysis

A species list was generated, and the geographic affiliation and endemism of each species compiled.

Geographic affiliation information was gathered primarily from the literature (e.g. Fairclough et al. 2011) (see Table S1 in the Supplement at www.int-res.com/articles/suppl/m649p125_supp.pdf) with additional data obtained from FishBase (Froese & Pauly 2019). Endemism data were collected from Fishes of Australia (Museums Victoria) (Bray et al. 2017–2020) with supplementary information from FishBase (Froese & Pauly 2019). Species that could not be accurately distinguished to species level with high certainty were grouped to family level for statistical analysis. These included *Pempheris* spp., *Siphonognathus* spp. and *Trachinops* spp. *Kyphosus* species could be differentiated via video but were classified into 2 distinct groups based on their morphology: *K. cornelli/biggibus/vaigiensis* and *K. sydneyanus/gladius.*

2.5.1. SWA's faunal structure and endemism

For each of the 28 locations, the overall abundance of fish was represented graphically. Temperature affiliation of each species (temperate, subtropical and tropical), along with the contribution of WA and Australian endemics, Indo-Pacific species and 'other' species (species with global distributions) were illustrated using stacked bar plots.

2.5.2. SWA's distinct shallow-water reef fish assemblages

Multivariate statistical analysis was used to analyse the spatial distribution patterns of shallow-water reef fish in SWA and was performed using the PRIMER v.7.0 software package (Anderson et al. 2008). Prior to transformation, raw transect assemblage data were summed to site level (n = 112 across the SWA coast; Fig. 1). Dispersion-weighting was then applied to transform and down-weight overly dispersed species and those with large abundance fluctuations in the data set. This transformation gave species with similar abundances within each site (i.e. stable species) greater weight in the analysis but still ensured that the data remained quantitative by allowing all species to contribute to overall patterns (Clarke et al. 2006). A Bray-Curtis similarity coefficient was implemented in a resemblance matrix constructed using the site data, as it does not consider species with joint absences evidence for similarity (Bray & Curtis 1957, Clarke 1993). To determine if an overall significant difference in the shallow-water reef fish assemblages occurred across regions and locations along the SWA coast, the resemblance matrix was tested using a 2-factor permutational multivariate analysis of variance (PERMANOVA) (Anderson 2001). This design included region (fixed factor; 7 levels) and location (random factor, nested in region; 28 levels). Prior to the PERMANOVA analysis, the Bray-Curtis resemblance matrix was tested for homogeneity of multivariate dispersions on the factor 'region' using the 'PERMDISP' function in PRIMER, as PERMANOVA models are sensitive to these dispersions (Anderson 2004).

A canonical analysis of principal coordinates (CAP) was used to project each site (n = 112) into high-dimensional space using the 7 regions of SWA as a factor for groups. The CAP procedure is constrained to hypotheses described *a priori* and is used to show maximum differences between levels of a chosen factor. This procedure may have more power than PERMANOVA in certain situations in multivariate space where the overall dispersion in the data conceals real dispersion among groups (Anderson & Willis 2003). The resulting leave-one-out allocation success of observations (region) table was used to analyse which regions were clearly separated from others. CAP was also used to assess alternative ways by which the fish assemblages of the 7 sampled regions could be arranged into 'assemblage structures'. The 'assemblage structures' arrangements assessed were (1) the 2 fisheries management zones, (2) the 3 mesoscale regions of SWA (Fig. 1) and (3) assemblages comprising 3, 4, 5 and 6 distinct groupings. CAP analyses were implemented for each of these 6 different assemblage structures and the resulting plots and leave-one-out allocation success tables were examined to determine which structure best represented the distinct assemblages of shallow-water reef fish species in SWA. To directly compare and support the results of the 6 CAP analyses, corrected Akaike's information criterion (AIC_C) was calculated for each assemblage structure using the equation:

$$N \log (SS_{residual} / N) + 2v [N / (N - v - 1)] \quad (1)$$

where N is the sample size (i.e. 112 sites) and v is the number of groups within each assemblage structure. The AIC_C results are directly comparable between the 6 CAP analyses, and the assemblage structure with the lowest AIC_C was considered to be the best representation of the current distribution of shallow-water reef fish assemblages along the SWA coastline.

Species that typified each distinct region as determined by the CAP analysis with the lowest AIC_C value were examined using SIMPER (Clarke & Warwick 2001) and ranked by their percentage contribution (% contrib).

2.5.3. Contribution of habitat and SST to SWA's distinct shallow-water reef fish assemblages

To analyse the contribution of habitat (reef cover, reef type, reef height, reef slope, *E. radiata* cover, non-*E. radiata* canopy cover, understorey algal cover, hard coral cover and seagrass presence) and SST on distinct fish assemblage structures, a distance-based multivariate linear model (DISTLM) analysis was run using the PERMANOVA+ package (Anderson 2004, Anderson et al. 2008). This procedure selected habitat and temperature variables that best explained the variation in shallow-water reef fish assemblages along the SWA coast. Prior to analysis, the mean for categorical variables was calculated for each site to give measures of habitat at each of the 112 study sites. Correlations between explanatory variables were viewed in Draftsman Plots, as models based on regression are sensitive to these correlations. All correlations were <0.9, allowing all variables to be available for inclusion in the analysis. Normality was assessed visually via histogram plots, and as a result, reef height was log transformed. The final DISTLM model was constructed using the BEST selection procedure (fits all possible models) and the AIC_C selection criterion (Chambers & Hastie 1992). The BEST selection procedure was used to formulate the optimum model, as this evaluated selection criteria for all possible combinations of variables (Anderson et al. 2008). AIC_C was the most suitable for this procedure, as it reduced the bias from linear regression (Sugiura 1978) and refined model selection by correcting for small sample sizes (Hurvich & Tsai 1989). Analysis using DISTLM was based on the Bray-Curtis resemblance matrix of the dispersion-weighted shallow-water reef fish assemblage data. A distance-based redundancy analysis (dbRDA) was used to present the optimum model created by the DISTLM, with the dbRDA performing an ordination of the assemblage data that is constrained to the significant habitat and temperature variables.

3. RESULTS

3.1. SWA's faunal structure and endemism

Across the 28 locations, the most speciose family was the Labridae, with 28 species comprising 26% of the total number of fish recorded, followed by Pomacentridae (14 species) with 12% of the total number of fish. Of the 119 species recorded, 32% (38 species) had an Indo-Pacific distribution, 66% (79 species) were endemic to Australia and 2% (2 species) were categorised as 'other' having global distributions. Of the 79 Australian endemic species, 21% (25 species) were short-range endemics only occurring in WA. Overall, 29% (34 species) had a tropical affiliation, 17% (20 species) were subtropical and 54% (65 species) had a temperate distribution. All locations contained species from each climatic affiliation and each endemic category. The full species list can be found in Table S1, along with the abundance of each species across the entire survey area, observation frequency (% of sites present), temperature affiliation and endemism level.

Across the ~2000 km survey area, species richness remained relatively stable, with no significant increases or decreases in any location. Numbers of Indo-Pacific species were higher in the Midwest and Central regions of Geraldton, Jurien Bay and Perth (9–22 species) than in the lower West Coast and Southern locations of South-West Capes, Albany, Bremer Bay and Esperance (4–13 species) (Fig. 2B). Australian endemic species showed the opposite trend, with a higher number of species in Southern and lower West Coast locations (10–24 species) than in Midwest and Central locations (4–12 species) (Fig. 2A). WA endemics did not appear to follow any pattern, with numbers remaining relatively stable across all locations (7–14 species).

3.2. SWA's distinct shallow-water reef fish assemblages

PERMANOVA showed a significant difference in shallow-water reef fish assemblages across the 7 regions and 28 locations (Table 1: $\text{Location(Region)}_{21,84}$, MS = 3432, Pseudo-$F$ = 1.61, $p < 0.001$). This indicated distinct groupings of fish assemblages across the ~2000 km coast of SWA. CAP analysis also showed significant differences in fish assemblages across the 7 regions (Fig. 3A; trace statistic = 4.53, $p < 0.001$) which supported the results from the PERMANOVA test. The percentage of overall correct classification was high (83%), and the leave-one-out allocation success rates were >93% for the regions of Geraldton and Esperance, indicating that the composition of the shallow-water reef fish assemblages of these regions is unique (Table 2). Misclassification of sites occurred between Jurien Bay and Perth, show-

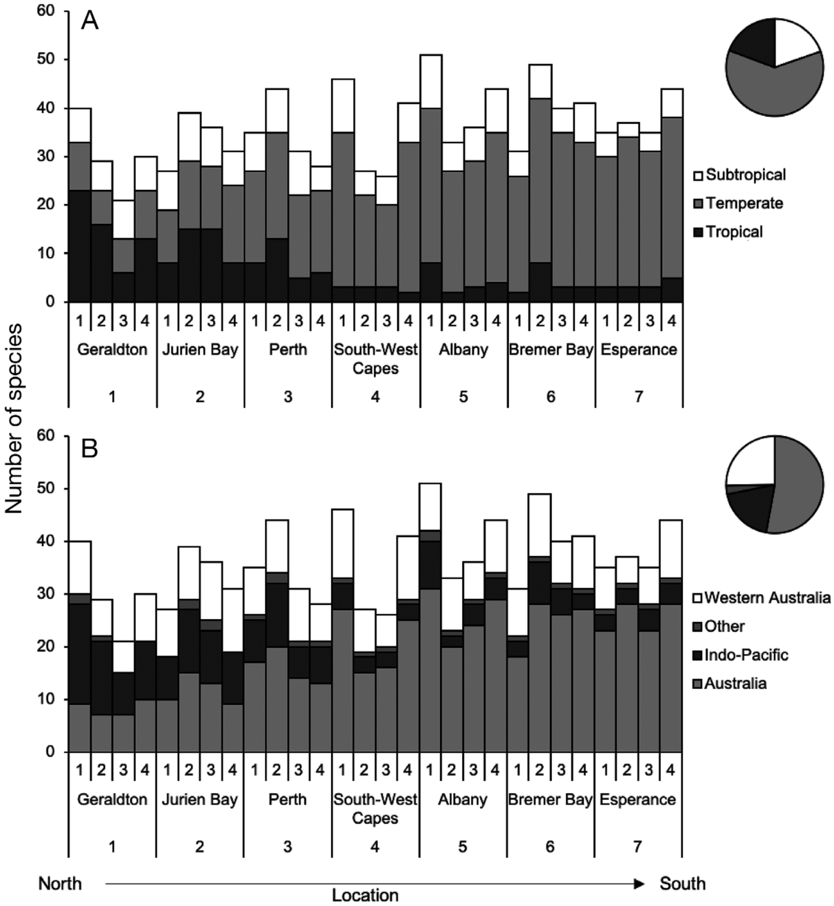

Fig. 2. (A) Temperature affiliation (tropical, subtropical, temperate) and (B) endemism (Australia, Western Australia, Indo-Pacific and Other) of shallow-water reef fish species in each of the 28 locations along the Southwest Australian (SWA) coast (n = 119 species); insets show the percentage of temperature affiliation (A) and endemism (B) within the total fish fauna of SWA

ing a similarity of fish assemblage composition between these 2 regions (Table 2). The South-West Capes, Albany and Bremer Bay had a lower allocation success rate (<87.5%) and sites were misclassified across these 3 regions, suggesting that the composition of the fish assemblage at these regions is similar (Table 2). These groupings were supported by the CAP plot (Fig. 3A), which showed a distinct separation of sites within the Geraldton and Esperance regions, grouped together the regions of Jurien Bay and Perth, and showed no distinction between the South-West Capes, Albany and Bremer Bay regions.

Further CAP analyses were performed to determine which of the 6 'assemblage structures' arrangements (the fisheries management zones, IMCRA mesoscale regions and assemblages with 3, 4, 5 and 6 groupings) best represented the current distribution of shallow-water reef fish assemblages (Figs. 3, S1 & S2). The resulting plot and leave-one-out allocation success rates (Tables 3 & 4, Figs S1 & S2) indicated that the distribution of SWA's shallow-water reef could be arranged into at least 3 distinct assemblages along the coast (Fig. 3B, trace statistic = 1.64, $p < 0.001$; Fig. 3C, trace statistic = 2.29, $p < 0.001$).

AIC_C results compared among each assemblage arrangement supported the results of the CAP analysis. The lowest AIC_C value was calculated for the '3 assemblage' structure (AIC_C = 387.879), closely followed by the '4 assemblage' structure (AIC_C = 387.955). These 4 assemblages are the Midwest, which contains the Geraldton region, the Central assemblage, which consists of Jurien Bay and Perth, a Southern region that contains the South-West Capes, Albany and Bremer Bay and a second Southern assemblage that consists of the Esperance region.

It was also of interest to analyse how well the 2 fisheries management zones and 3 IMCRA mesoscale regions represented the current distribution of shallow-water reef fish in SWA (Figs. S1 & S2). The leave-one-out allocation success rates were low, indicating that the fish assemblage composition did not conform well to the management areas (Figs. S1 & S2), and the AIC_C values were higher compared to the '3 assemblage' and '4 assemblage' arrangement (fisheries AIC_C = 391.024; IMCRA AIC_C = 389.889).

The top 5 species in each assemblage, ranked by their percentage contribution (% contrib), were identified by the SIMPER analysis (Table 5). The Midwest assemblage contained the region of Geraldton and

Table 1. Results of a 2-factor nested permutational multivariate analysis of variance on dispersion-weighted transformed densities of shallow-water reef fish species across the 7 regions in Southwest Australia (SWA). Region is a fixed factor; location is nested within region

Source	df	MS	Pseudo-*F*	Unique perms	p
Region	6	18184.0	5.2986	9873	0.0001
Location(Region)	21	3431.9	1.6051	9564	0.0001
Residuals	84	2138.1			
Total	111				

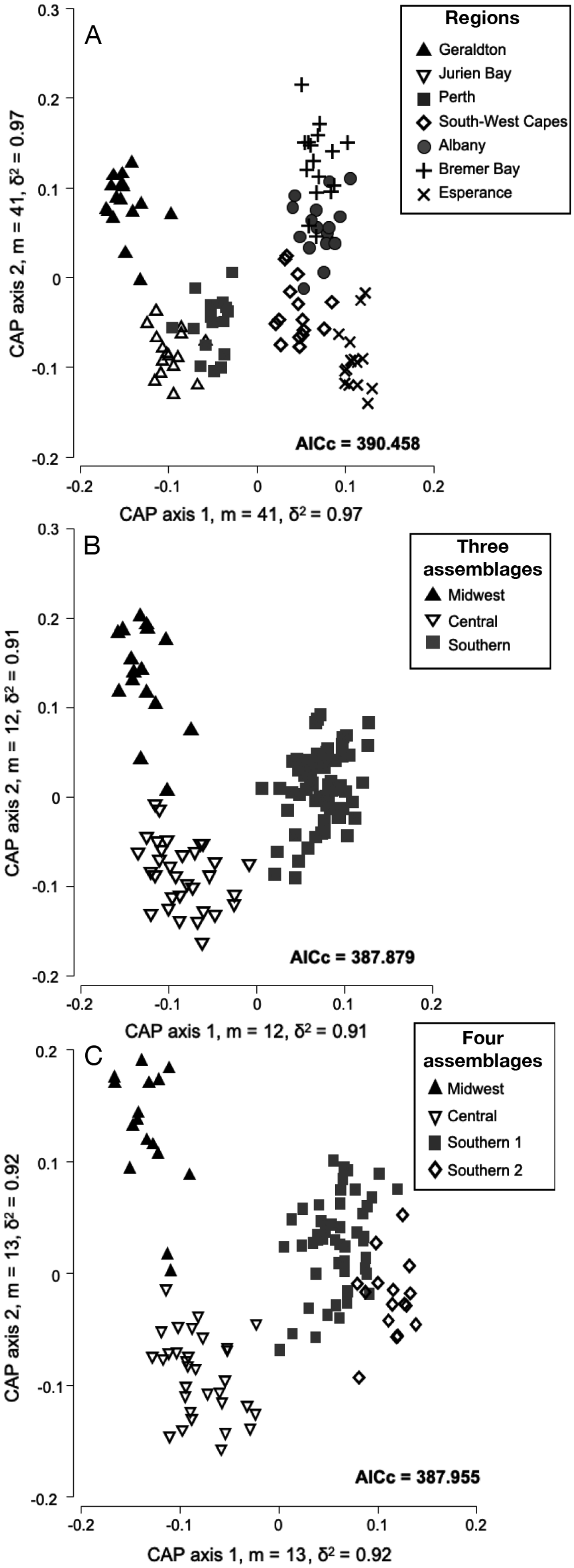

Fig. 3. Canonical analysis of principal coordinates (CAP) plots of shallow-water reef fish assemblages using (A) the 7 regions of Southwest Australia (SWA): Geraldton, Jurien Bay, Perth, South-West Capes, Albany, Bremer Bay, Esperance (m [number of PCO axes] = 41, n [sample size] = 112) as a factor of groups; (B) the 3 assemblage structure: Midwest (Geraldton), Central (Jurien Bay and Perth) and Southwest (South-West Capes, Albany, Bremer Bay and Esperance) (m = 12, n = 112) as a factor of groups; and (C) the 4 assemblage structure; Midwest (Geraldton), Central (Jurien Bay and Perth), Southwest 1 (South-West Capes, Albany and Bremer Bay) and Southwest 2 (Esperance) (m = 13, n = 112) as a factor of groups. Ordinations are based on the Bray-Curtis resemblance matrix using dispersion-weighted shallow-water reef fish abundance data; assemblage structures (3 or 4) were based on corrected Akaike's information criterion (AIC_C) values and the leave-one-out allocation success to observation values

was characterised by mostly tropical- and subtropical-affiliated species. The highest percentage contributor was the tropical Indo-Pacific species *Plectorhinchus flavomaculatus* (goldspotted sweetlips), followed by the subtropical WA endemics *Parma occidentalis* (western scalyfin) and *Choerodon rubescens* (baldchin groper). Jurien Bay and Perth made up the Central assemblage and were characterised by a combination of subtropical and temperate species. The greatest contributing (%) species was *Notolabrus parilus* (brownspotted wrasse), a temperate Australian endemic, followed by the temperate WA endemic *Parma mccullochi* (Mcculloch's scalyfin) and the subtropical *Coris auricularis* (western king wrasse, a WA endemic). The Southern assemblage consisted of the South-West Capes, Albany and Bremer Bay regions and was predominantly characterised by temperate species such as the Australian endemic *Olisthops cyanomelas* (herring cale) and the WA endemics *P. mccullochi* and *Pseudolabrus biserialis* (red-banded wrasse).The Esperance region formed the second Southern assemblage, which also consisted mainly of temperate Australian endemic species including *N. parilus* and *Achoerodus gouldii* (western blue groper).

3.3. Contribution of habitat and SST to SWA's distinct shallow-water reef fish assemblages

DISTLM analysis generated a final model that explained 25.5 % of the variation in shallow-water reef fish assemblages using 6 environmental variables ($R^2 = 0.255$, $AIC_C = 886.820$): SST, *Ecklonia radiata* cover, non-*E. radiata* canopy cover, understorey algae cover, reef type and reef height. Individual marginal

Table 2. Leave-one-out allocation success rate (%) of observation to Region (m [number of PCO axes] = 41, n [sample size] = 112), for 7 regions of Southwest Australia (SWA)

Region	Geraldton	Jurien Bay	Perth	South-West Capes	Albany	Bremer Bay	Esperance	Total	Success (%)
Geraldton	15	0	1	0	0	0	0	16	93.75
Jurien Bay	0	12	4	0	0	0	0	16	75.00
Perth	0	1	14	1	0	0	0	16	87.50
South-West Capes	0	0	2	12	1	1	0	16	75.00
Albany	0	0	1	3	11	1	0	16	68.75
Bremer Bay	0	0	0	0	2	14	0	16	87.50
Esperance	0	0	0	1	0	0	15	16	93.75

Table 3. Leave-one-out allocation success rate (%) of observations to Assemblage (m [number of PCO axes] = 12, n [sample size] = 112), for 3 assemblages of Southwest Australia (SWA): Midwest (Geraldton), Central (Jurien Bay and Perth) and Southern (South-West Capes, Albany, Bremer Bay and Esperance)

Assemblages	1	2	3	Total	Success (%)
Midwest	15	1	0	16	93.75
Central	0	32	0	32	100.00
Southern	0	1	63	64	98.44

tests showed that SST explained the highest proportion of variation (15.5%), followed by reef type (11.6%) and reef height (6.9%). The best model resulting from DISTLM is illustrated in Fig. 4A, using the dbRDA procedure overlaid with partial correlations of the explanatory environmental variables. The strength and direction of the correlation of each of the 6 variables included in the final model to the dbRDA axes are shown by the length and direction of the vectors. The first 2 dbRDA axes explained 61.9 and 14.8% of the variation in the fitted model, respectively and together accounted for 19.6% of total variation in the distribution and density of SWA's shallow-water reef fish (Fig. 4A). SST was positively correlated to the first dbRDA axes (Fig. 4A, Table 6) in a similar direction to the species *P. occidentalis*, *C. rubescens*, *P. flavomaculatus* and *K. cornelli/biggibus/vaigiensis*; *Ophthalmolepis lineolatus*, *Scorpis aequipinnis*, *O. cyanomelas* and *P. biserialis* were negatively correlated to this axis (Fig. 4B, Table 6) as was non-*E. radiata* (canopy) cover. *Cheilodactylus rubrolabiatus* was negatively correlated to the second dbRDA axis (Fig. 4B, Table 6) while *N. parilus* was positively correlated. Understorey algae cover, reef type and *E. radiata* cover was also positively correlated to the second dbRDA axis (Fig. 4B, Table 6).

Table 4. Leave-one-out allocation success rate (%) of observation to Assemblage (m [number of PCO axes] = 13, n [sample size] = 112), for 4 assemblages of Southwest Australia (SWA): Midwest (Geraldton), Central (Jurien Bay and Perth), Southern 1 (South-West Capes, Albany and Bremer Bay) and Southern 2 (Esperance)

Assemblage	Midwest	Central	Southern 1	Southern 2	Total	Success (%)
Midwest	15	1	0	0	16	93.75
Central	0	31	1	0	32	96.88
Southern 1	0	1	45	2	48	93.75
Southern 2	0	0	1	15	16	93.75

4. DISCUSSION

The shallow-water reef fish of SWA formed 4 distinct assemblages along the ~2000 km coastline: a Midwestern, a Central and 2 Southern assemblages (Fig. 5). The differences between these assemblages were predominantly driven by 6 environmental variables: SST, *Ecklonia radiata* cover, non-*E. radiata* (canopy) cover, understorey algae cover, reef type and reef height. Along the SWA coastline, the fauna composition changed from one with a high number of tropical and subtropical species to one dominated by warm temperate species. Each of the 4 assemblages were characterised by species endemic to both Australia and WA.

The spatially fine-scale quantitative data collected here suggest that intricate distributional patterns exist within the assemblages of shallow-water reef fish along the SWA coastline. These assemblages form unique regions and are composed of a high number of short-range endemic species, with ranges less than 10 000 km^2 (Harvey 2002). Shallow-water reef fish of SWA can be clustered into 4 distinct fish assemblages (see Section 3.2 and Fig. 5). Hutchins (2001) however, grouped the SWA fish fauna

Table 5. Species identified by SIMPER as characteristic of each of the 4 distinct groups (Midwest, Central, Southern 1, Southern 2) defined in the canonical analysis of principal coordinates of shallow-water reef fish in Southwest Australia (SWA)

Species	Average abundance	Average similarity	Similarity/ SD	Contribution (%)	Cumulative abundance (%)
Midwest assemblage					
Average similarity: 28.37					
Plectorhinchus flavomaculatus	1.00	5.64	0.90	19.87	19.87
Parma occidentalis	0.83	4.16	1.27	14.67	34.53
Kyphosus cornelii / bigibbus / vaigiensis	0.66	2.95	0.95	10.40	44.94
Choerodon rubescens	0.65	2.89	0.92	10.17	55.11
Cheilodactylus rubrolabiatus	0.53	2.52	0.78	8.90	64.01
Central assemblage					
Average similarity: 32.67					
Notolabrus parilus	1.96	10.28	2.22	31.48	31.48
Parma mccullochi	1.42	5.59	1.22	17.12	48.59
Coris auricularis	0.86	3.20	1.33	9.81	58.40
Chelmonops curiosus	0.65	2.50	0.81	7.66	66.06
Kyphosus cornelii / bigibbus / vaigiensis	0.69	2.05	0.77	6.27	72.33
Southern assemblage 1					
Average similarity: 25.18					
Parma mccullochi	0.98	3.62	1.12	14.38	14.38
Notolabrus parilus	0.87	2.87	1.10	11.40	25.78
Ophthalmolepis lineolatus	0.59	2.52	0.75	10.02	35.81
Pseudolabrus biserialis	0.82	2.50	1.08	9.92	45.73
Olisthops cyanomelas	0.59	1.72	0.75	6.84	52.57
Southern assemblage 2					
Average similarity: 39.18					
Notolabrus parilus	1.33	6.80	1.88	17.35	17.35
Achoerodus gouldii	1.13	3.99	1.52	10.19	27.54
Ophthalmolepis lineolatus	0.83	2.78	1.03	7.09	34.63
Scorpis aequipinnis	0.79	2.70	0.84	6.89	41.52
Chelmonops curiosus	0.56	1.74	0.83	4.44	66.46

into one continuous region, while Fox & Beckley (2005) further divided this region into 2 distinct faunal groupings with a division south of Perth. The results of this study confirmed these and further divisions of the SWA coast. The AIC_C values were essentially equivalent for the 'assemblage structure' arrangement with 4 or 3 groupings, which indicated that 3 groups were also a good representation of the distribution of shallow-water reef fish. The 3 grouping arrangement included a Midwest (Geraldton), Central (Jurien Bay and Perth) and Southern assemblage (South-West Capes, Albany, Bremer Bay and Esperance). However, the clear distinction of sites within Esperance, supported by the leave-one-out allocation success table and previous studies (Harvey et al. 2013), demonstrated the separation of assemblages within this region. Harvey et al. (2013) noted the uniqueness of the Esperance region with its diverse Monacanthidae and Labridae fauna, coupled with long-lived '*K*-selected' species. These species have a heightened vulnerability to fishing and bycatch pressures due to their large body size, late maturity and longevity (Le Quesne & Jennings 2012). The characteristic species within the Esperance region highlights the importance of independent management of this assemblage, which is taken into consideration within the '4 assemblage structure' bioregional arrangement.

4.1. Bioregional management

Bioregionalisation as a management tool has been adopted not only in Australia (Heap et al. 2005, Last et al. 2005, Commonwealth of Australia 2006), but also internationally in the UK and other parts of Europe (DEFRA 2007, Raakjær et al. 2012) for fisheries management (Fletcher et al. 2010, 2012), reserve selection (Fox & Beckley 2005, Last et al. 2011) and resource allocation (Day 2002). The continuing development of bioregions has highlighted the importance of high-quality, accurate, distributional data on marine biota worldwide. However, movement of species ranges and changes to species interactions have been documented both globally (Perry et al. 2005, Vergés

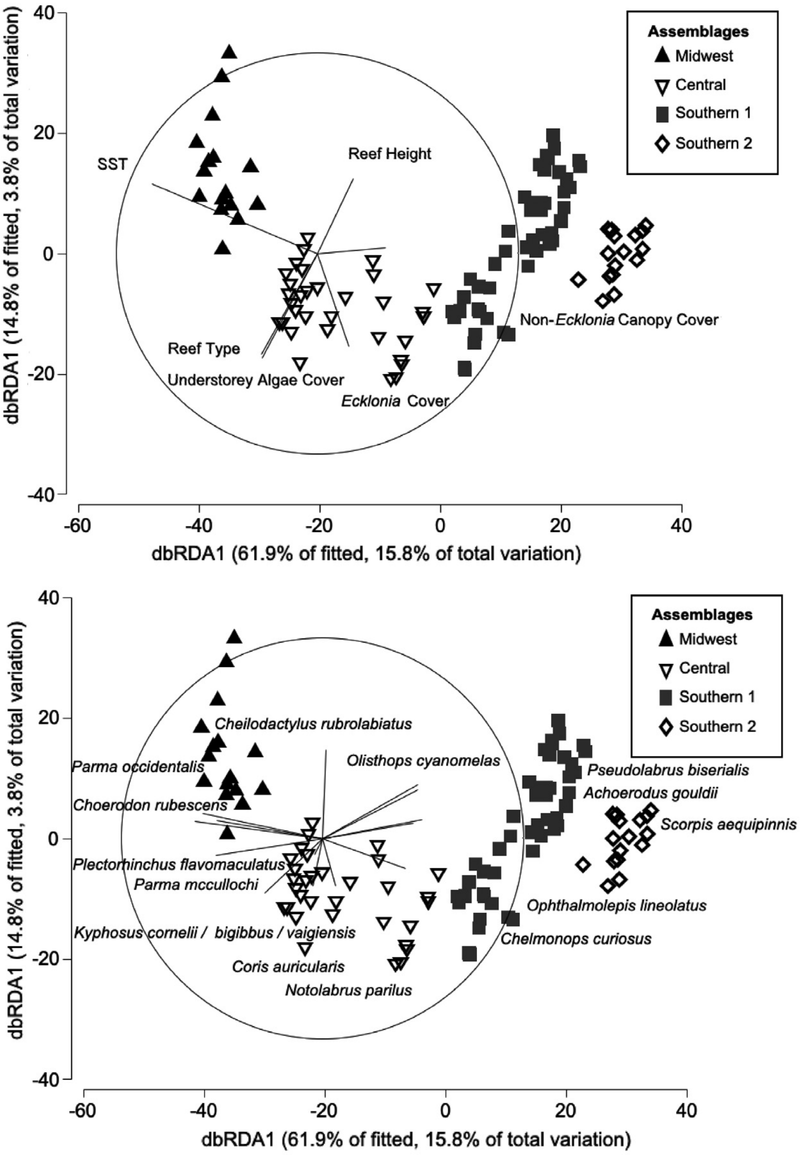

Fig. 4. Distance-based redundancy analysis (dbRDA) ordination of first and second fitted axes relating to (A) environmental variables and (B) characterising species of shallow-water reef fish over the entire study area in Southwest Australia (SWA). Vectors: strength and direction of multiple partial correlations for the environmental variables and Pearson's correlations for characterising species, to the first and second RDA axes. The first and second axes explained 61.9 and 14.8% of variation in the fitted model, respectively

et al. 2014) and locally in SWA (Wernberg et al. 2016). Changes in the composition of fish and other marine assemblages have also been recorded along the SWA coast (e.g. Cure et al. 2018, Shalders et al. 2018, Parker et al. 2019). The length of the SWA coastline, along with climatic changes and increasing SST, make this region an ideal area to study changes in the distribution of fish assemblages, with corresponding implications for management being globally applicable (Day 2002, DEFRA 2007, Morrone 2015). Environmental and climatic changes are occurring globally (e.g. Perry et al. 2005), and continued monitoring of the distribution of fish assemblages worldwide is essential to inform bioregional management, planning and to manage resource allocation.

The existing IMCRA (Commonwealth of Australia 2006) and fisheries management (Gaughan & Santoro 2018) regions in SWA do not effectively align with the current distribution of shallow-water reef fish assemblages, and this may have a negative impact on their practicality (Fig. 5). The data showed that the South-West Capes region formed a group within the Southern assemblage, but currently it is managed within the West Coast fisheries bioregion. IMCRA defines this region individually due to the unique oceanic currents occurring in this area (Commonwealth of Australia 2006). The Esperance region contained a unique assemblage of shallow-water reef fish, yet it is currently managed as part of the broader WA South Coast region. Aspects of this uniqueness may be compromised by managing this region at the broader scale. Whilst the results illustrated the current assemblage patterns of SWAs' shallow-water reef fish, it is important to note that IMCRA considers a larger area, and holistically considers all marine species and geological data from both the continental shelf and slope (Commonwealth of Australia 2006).

4.2. Environmental variables

This study also identified that SST, *E. radiata* cover, non-*E. radiata* (canopy) cover, understorey algal cover reef type and reef height were the most important drivers of fish assemblages on shallow, rocky reefs in SWA, with SST being the primary driver. Previous international and local studies have documented SST as a dominant environmental driver of the distribution and composition of marine assemblages (Lüning 1984, Dayton et al. 1999), and have demonstrated tropicalisation and movement of species poleward correlated with a change in SST (Dornelas et al.

Table 6. Correlations to the first, second and third distance-based redundancy analysis (dbRDA) axes of selected environmental variables (multiple partial correlations) and characterising shallow-water reef fish species (Pearson correlations) of Southwest Australia (SWA)

Environmental variable	dbRDA1	dbRDA2	dbRDA3
Reef type	0.278	0.482	0.522
Reef height	−0.175	−0.362	0.179
Ecklonia cover	−0.160	0.451	0.262
Non-*Ecklonia* cover	−0.340	−0.056	−0.412
Understorey algae cover	0.271	0.510	−0.666
2015 Mean sea surface temperature	0.821	−0.345	−0.031
Species variable			
Achoerodus gouldii	−0.498	−0.094	−0.072
Cheilodactylus rubrolabiatus	−0.018	−0.444	−0.022
Choerodon rubescens	0.527	−0.091	−0.078
Kyphosus cornelii / bigibbus / vaigiensis	0.530	0.087	−0.115
Notolabrus parilus	0.048	0.238	−0.388
Olisthops cyanomelas	−0.473	−0.267	−0.151
Ophthalmolepis lineolatus	−0.415	0.152	0.136
Parma occidentalis	0.594	−0.126	0.002
Plectorhinchus flavomaculatus	0.634	−0.085	−0.150
Pseudolabrus biserialis	−0.473	−0.241	−0.173
Scorpis aequipinnis	−0.453	−0.077	−0.021

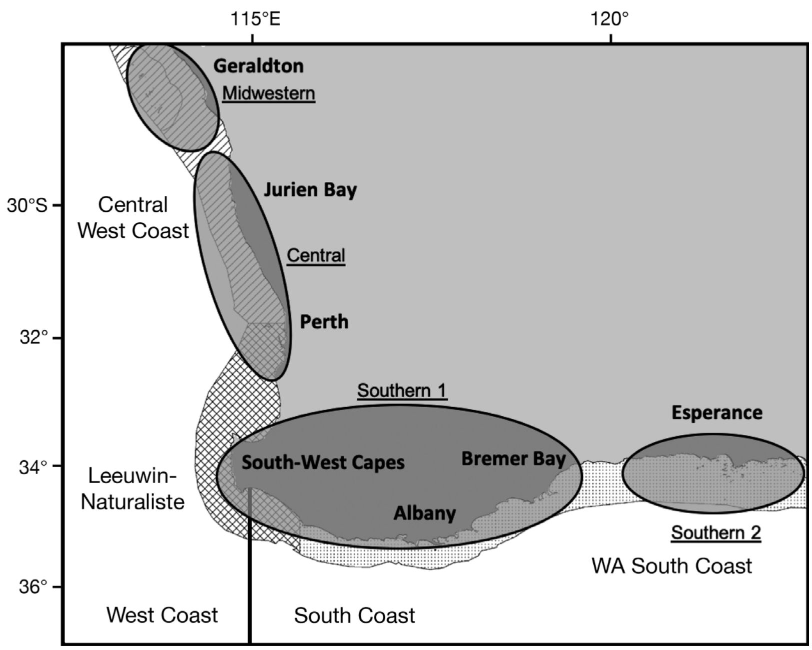

Fig. 5. Proposed improved bioregional boundaries according to the distribution of shallow-water reef fish in Southwest Australia (SWA) with the 4 bioregions: Midwestern, Central, Southern 1 and Southern 2. For reference, the 3 Integrated Marine and Coastal Regionalisation of Australia mesoscale regions (Central West Coast, Leeuwin-Naturaliste and WA South Coast) are illustrated by hatching and shading, and the 2 fisheries management areas of SWA are delineated by the dark line heading south from the South-West Capes

2014, Vergés et al. 2014). For example, Perry et al. (2005) described the shifting distributions of North Sea fishes in both latitude and depth as a response to changing SSTs, and with the predicted change in climate, this movement is expected to continue.

Locally in SWA, the Leeuwin Current has a major influence along the coast, which maintains a consistent temperature gradient from north to south. This current is also responsible for the transition from tropical through to subtropical- and temperate-affiliated marine species (Hutchins 2001). Furthermore, it facilitates the extension and survival of tropical fauna further south than their usual range (Pearce & Walker 1991). However, with increasing SST the Leeuwin Current may further aid this poleward shift of warm-water species, increasing the vulnerability of cool-water species with geographical range restrictions (Shalders et al. 2018, Parker et al. 2019). In 2011, SWA experienced a marine heatwave which increased SSTs across the study area. Studies following this rise in temperature documented rapid regime shifts to tropical- and subtropical-affiliated seaweeds, fish and other marine organisms (Bennett et al. 2015a,b, Wernberg et al. 2016). The shifting boundaries of shallow-water reef fish reported in this study may be driven by disturbances such as the 2011 heatwave, as the Leeuwin Current promotes distributional changes of fish assemblages and their associated habitats. Increasing SSTs may also act as a surrogate for changes in habitat; e.g. a shift from kelp forests to one dominated by turfs and other algal forms (Bennett et al. 2015a), and therefore habitat variables are also important for defining species distributions (Harvey et al. 2013, Saunders et al. 2014, Galaiduk et al. 2017).

Macroalgae, especially *E. radiata* and other canopy cover, was also a prominent driver of the distribution of shallow-water reef fish assemblages. This result was similar to previous studies along this coastline (Harvey et al. 2013, Galaiduk et al. 2017). For example, using a multivariate regression tree model, Galaiduk et al. (2017)

found macroalgae to explain 13% of the variation of fish assemblages, while earlier work in the Esperance region also found these organisms to be a driver of fish assemblage structure (Harvey et al. 2013). With changing climate, the effect on canopy seaweeds in SWA is uncertain, and they may undergo rapid and irreversible changes (Wernberg et al. 2011, Bennett et al. 2015b). Effects may be magnified due to their sessile nature, limited reproductive movement and hence recovery potential (Wernberg et al. 2016). Understorey algae cover was also defined in our model as a driver of fish assemblage distributions, and a shift from canopy to understorey algae dominance may benefit certain fish species while hindering others. An increase in understorey algae has been correlated with a shift in species characteristic of subtropical and tropical waters (Wernberg et al. 2016), as this algae may increase food and habitat availability for grazing herbivores such as pomacentrids (Norman & Jones 1984, Jones & Norman 1986, Saunders et al. 2013) and parrotfishes (Bennett et al. 2015b). In contrast, a shift from canopy to understorey algae may have detrimental effects on temperate species such as *Olisthops cyanomelas* that rely on canopy seaweeds for food and habitat (Shepherd & Baker 2008). The changing climate and associated effects on habitat may have a current and continued impact on the distribution of fish species, particularly short-range endemic habitat specialist species such as *Parma mccullochi* and *O. cyanomelas.*

4.3. Climatic affiliation and endemism

Over the 2000 km of coastline studied, the shallow-water reef fish assemblages of SWA changed from one with a large number of tropical, Indo-Pacific species in our northern study sites to one dominated by short-range temperate Australian endemics in the southern study sites. This pattern of affiliation and endemism is supported by other studies along this coastline (Wilson & Allen 1987, Hutchins 1994, 2001, Fox & Beckley 2005). This high level of endemism may be attributed to the long isolation of the Australian continent and unique oceanography, such as the Leeuwin Current, which characterises the area (Adey & Steneck 2001, Phillips 2001). The 4 distinct shallow-water reef fish assemblages described in this study were dominated by species endemic to Australia, with many being confined to only WA.

While the demography of many fish species in SWA is unknown or unstudied, individual families and species have been examined due to their longevity and vulnerability to climate change. *Choerodon rubescens* (baldchin groper), characteristic of the Midwest assemblage, and *Achoerodus gouldii* (western blue groper), found in the Southern assemblage, are wrasses of the Labridae family and are notable due to their importance in both commercial and recreational fishing. However, as targeted species with slow growth and high longevity (max. 70 yr), they are vulnerable and susceptible to overfishing (Nardi et al. 2006, Coulson et al. 2009). Labridae species were abundant in this study, with many being short-range endemics. A recent study detailed the increase of tropical and subtropical SWA Labridae species in 2015 that were absent or rare in 2006, which was correlated with a change in climate and a marine heatwave in 2011 (Parker et al. 2019). Similarly, several long-lived Pomacentridae species are also only found in WA, such as *Parma occidentalis* and *P. mccullochi*, and these species have been affected by climatic changes with an increasing abundance of warm-water species (Shalders et al. 2018). Endemic species of WA are abundant and characteristic of the distinct assemblages, but as endemics, these species are more vulnerable to extinction than wider ranging species. It is important that changes in their distribution and abundance are monitored, especially given the geographic constraints of the SWA coastline to further southern shifts of South Coast species and assemblages.

4.4. Conclusions and recommendations

The shallow-water reef fish fauna of SWA is species-rich, and this study identified that it has a spatial structure that forms 4 distinct assemblages along the coast. This key finding is in contrast with both the current IMCRA and Southwest Australian Fisheries Management bioregions, indicating that the present bioregionalisation of SWA may not be the best representation of the current distribution of shallow-water reef fish species. Determining the spatial structure of assemblages can support and inform bioregional and EBFM for any area worldwide (Browman & Stergiou 2004). Bioregions can also aid in conserving entire ecosystems and monitoring distributional changes and extinctions, particularly of small-range endemic species (Briggs & Bowen 2012, Colton & Swearer 2012). Both ecological and fisheries bioregionalisation of any region should accurately represent the current distribution of species that inhabit the area. This adaptable approach will improve management and protection of valuable and dynamic marine ecosystems and the vulnerable, unique marine species.

SWA is experiencing species movements and environmental changes that correspond with changes occurring in other regions worldwide (e.g. Perry et al. 2005, Parker et al. 2019). The survey and statistical methods of this study were designed to be replicable, and the approach can be applied to any marine area to determine the effectiveness of current regional planning and conservation. This study illustrates that changes in the distribution of fish assemblages has implications for bioregional boundaries, and similar changes are likely to continue to occur globally (Hobday & Lough 2011). It also demonstrates that continued monitoring, alongside adaptive and flexible management, is key to ensure that bioregions and protected areas are effectively placed. Correct placement of these areas will improve the conservation of species and their habitats and allow managers in any region worldwide to allocate resources optimally.

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