

Species pools and habitat complexity define Western Australian marine fish community composition

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ABSTRACT: Previous studies describing Western Australian marine fish fauna have been either (1) broad-scale biogeographical descriptions or (2) considered smaller spatial extents and assessed the influence of local habitat variation on fish assemblage structure. This study simultaneously considered the relative effects of geographical distance and environment in structuring the Western Australian ichthyofaunal assemblages across spatial scales. Abundances of 440 species were estimated from baited underwater video sampling. Kruskal-Wallis tests were used to test for changes in species richness among locations. Changes in community composition relating to environmental and spatial gradients were analysed using multivariate regression trees. Species richness displayed a non-monotonic decrease along the expected north–south geographical gradient. At the broadest scale, 2 distinct assemblages were detected, the Indo-Pacific tropical ichthyofauna and a temperate assemblage with varying degrees of local endemism. Space was the greatest influence on the structure of fish assemblages in tropical localities, but local habitat properties were more important in temperate locations. At the biogeographic scale, in Western Australia, the elsewhere widespread Indo-Pacific ichthyofauna has a restricted distribution, while temperate species have greater geographical ranges. This difference may be attributed to the greater environmental heterogeneity seen among tropical locations in this study, creating less continuous suitable habitat for species. Within locations, habitat was found to be the greatest driver of assemblage structure, suggesting the importance of habitat filtering as a process structuring ichthyofaunal assemblages at smaller spatial scales.

KEY WORDS: Biogeography · Ecological community · Marine fish · Habitat complexity · Environmental gradients · Spatial gradients

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INTRODUCTION

Ecological communities often demonstrate structural changes along environmental and geographic gradients (Gaston 2000), and understanding the cause of these changes is one of community ecology's central goals. One of the strongest patterns found in ecological and biogeographical studies is a decrease in species richness from low to high latitudes (Rohde 1992, Gray 2001). In agreement with this global pattern, Western Australia's marine ichthyofauna

displays an overall poleward decrease in species richness (Hutchins 2001, Last et al. 2011), but this decrease is not monotonic, with Fox & Beckley (2005) noting increased richness in the Abrolhos Islands, in the Perth region, and around Rottnest Island. Endemism is richest in the south and decreases northward (Hutchins 2001, Fox & Beckley 2005), with similar patterns recorded for fishes, corals, molluscs, and algae (Hutchins 2001, Phillips 2001, Fox & Beckley 2005, Last et al. 2011, Wernberg et al. 2011), likely reflecting a common marine influence.

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The major oceanographic feature in this region is the Leeuwin Current, an anomalous, non-reversing poleward current on the eastern boundary of an ocean (Waite et al. 2007). This current suppresses any significant upwelling, creating an oligotrophic marine environment (Pearce 1991). The low productivity is further augmented by the lack of significant terrigenous nutrient input due to typically low rainfall and few large river systems (Caputi et al. 1996). The Leeuwin Current also promotes movement of tropical fish faunas south, mixing the typically widespread tropical Indo-Pacific fish species with endemic southern Australian forms, which in part accounts for high species richness in the Abrolhos Islands and at Rottnest Island.

Diversity in southwestern Australian endemic marine fish communities reflects a long period of continental isolation since the breakup of Gondwanaland and subsequent tectonic stability in southwestern Australia. The southern Australian endemic species evolved in a region consisting of a relatively homogeneous environment which experienced little or no tectonic activity or glaciation during the Cenozoic and Pleistocene periods, resulting in a coevolved endemic ichthyofauna with similar environmental niches. The high levels of diversity and endemism are thought to have originated as a result of the pulsing nature of the Leeuwin Current since the Eocene; fluctuations in sea level, creating new habitats or splitting ranges; and larval supply from 2 distinct ichthyofaunas (Poore 1995, McGowran et al. 1997, Phillips 2001): (1) globally distributed Indo-Pacific fish faunas found in tropical northwestern Australia and (2) southern endemic faunas.

Sharp faunal breaks in the fish communities occur as a result of abrupt changes in environmental attributes along Western Australia's tropical and subtropical coastlines. These steep gradients are superimposed over the expected north to south declines in temperature and changes in broad climate types (Barry & Dayton 1991). This is in contrast to patterns observed in the Great Barrier Reef on the eastern coast of Australia, where Cappo et al. (2007) reported slight latitudinal changes in marine vertebrate communities over 14 degrees of latitude. Along the Western Australian coast, Dampier and Barrow Island are characterised by a turbid macrotidal environment, receiving little wave energy (Jones & Syms 1998). Ningaloo Reef, with its northern tip ~160 km southwest of Barrow Island, is characterised by clear waters, high wave energy, and a mesotidal regime (Cassata & Collins 2008). Shark Bay possesses a distinct environment; water within the bay is often

hypersaline with a microtidal regime (<1 m), and much of the bay is not subject to swell (Walker et al. 1988). The Abrolhos Islands, located ~60 km offshore from the coast at the continental shelf break, are strongly influenced by the Leeuwin Current and contain the Indian Ocean's most southern true coral reefs (Watson et al. 2009, Watson & Harvey 2009). This feature results in the Abrolhos having a flora and fauna very different from mainland coastal sites at comparable latitudes, though the Abrolhos also support some temperate macroalgae, e.g. *Ecklonia radiata* (Johannes et al. 1983). In contrast, the Western Australian marine environment from Jurien Bay to Esperance is relatively homogeneous, with rocky reefs dominated by *E. radiata*. These reefs are composed of limestone on the western coast and limestone and granite along the southern coast (Kendrick 1999, Wernberg et al. 2003).

While past studies of the Western Australian ichthyofauna have established broad biogeographic trends in marine fish community structure, the effects of habitat complexity and abundances of species were not used to explain the trends observed (e.g. Hutchins 2001, Fox & Beckley 2005, Last et al. 2011). When environmental features were taken into account, the spatial extent of these studies was relatively restricted (e.g. Fitzpatrick et al. 2012, Harvey et al. 2013, McLean et al. 2016), habitat was coarsely defined (e.g. Travers et al. 2010, Smith et al. 2014), or only a single family of fishes was considered (e.g. Tuya et al. 2009).

Patterns of diversity in marine fishes have been demonstrated to be related to changes in the physical complexity of the associated substrate (e.g. Pérez-Matus et al. 2007, Hackradt et al. 2011), with richness generally increasing with habitat complexity and assemblage composition changing with both structural complexity of the substrate and the species composition of the benthos (Gratwicke & Speight 2005, Friedlander et al. 2007). The incorporation of species abundances, as opposed to presence/absence measures or species richness, into explanations of changes in diversity with gradients in habitat complexity provides greater detail of the habitat preferences of the observed species, helping define the preferred habitat of each species (Morris 1988, Brown et al. 1995, Fulton et al. 2016).

This study was performed to test the predictions that, as a result of the differing evolutionary histories of the temperate and tropical Western Australian ichthyofauna, the patterns of habitat association and spatial distribution of the faunas within Western Australian waters will differ; specifically, (1) habitat complexity will be a strong driver of community composi-

tion in both temperate and tropical faunas; (2) the relative homogeneity of the temperate marine environment will result in greater spatial ranges of temperate endemic fish species, with overlapping habitat affinities among these species; and (3) tropical ichthyofauna will demonstrate greater spatial structuring due to rapid changes in local environmental conditions, with the effect of habitat complexity superimposed on this feature within locations.

MATERIALS AND METHODS

Sampling

Fish abundances were estimated from 12 locations spanning tropical to temperate marine environments along the Western Australian coastline (Esperance [34.02° S, 123.34° E] to Dampier [20.46° S, 116.72° E]) from April 2006 to March 2010 (Table 1, Fig. 1). Abundances of fishes were estimated from 2336 samples taken using stereo baited remote underwater video systems (stereo BRUVS). While species selectivity differs among sampling methods, Cappo et al. (2004) identified that changes in the structure of fish communities were comparable between trawl and BRUVS methods, with BRUVS sampling a greater size spectra of families.

Video cameras were deployed at least 250 m apart on the seafloor and collected after 1 h. Bait was ~800 g of crushed pilchards *Sardinops sagax*, placed in a bait bag in front of each unit. Using EventMeasure (SeaGIS) to analyse the footage, fish were identified to species level where possible, and the maximum number of individuals within a given footage frame (MaxN) was calculated for each species to avoid re-counting the same individual (Cappo et al. 2004). De-

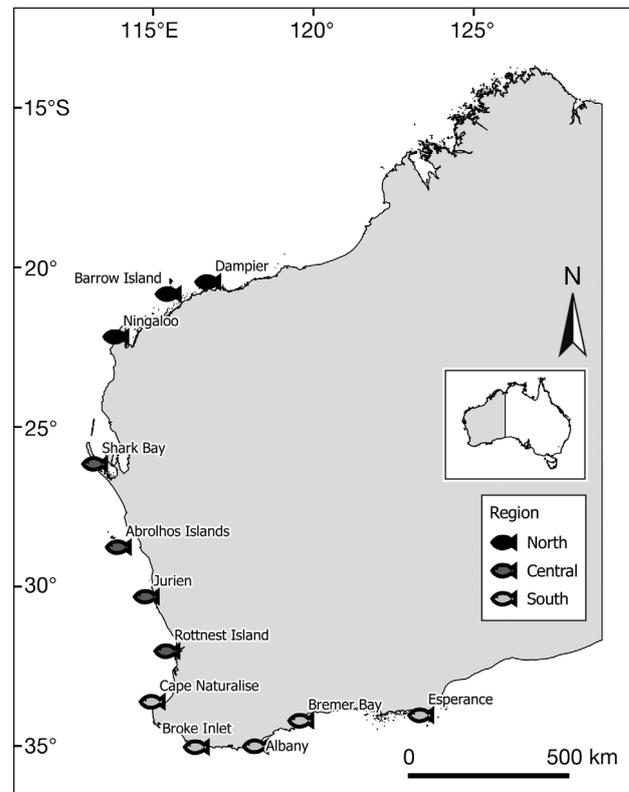


Fig. 1. Locations sampled along tropical to temperate marine environments of Western Australia. Regions follow Last et al. (2011)

tails of stereo BRUVS and footage analyses procedures are outlined in other studies (e.g. Harvey & Shortis 1996, 1998, Langlois et al. 2012, McLean et al. 2016).

Depth and position of each sample were recorded using an on-board depth sounder and GPS. Sample depths ranged from 0.5 to 109 m (see Supplement 1 at www.int-res.com/articles/suppl/m574p157_supp.pdf).

Samples in southern regions were generally deeper than those in northern regions, with the exception of samples collected at Ningaloo (Supplement 1).

Habitat characteristics were categorised in the laboratory from BRUVS imagery. Relief was categorised as either high-profile reef (HPR), medium-profile reef (MPR), low-profile reef (LPR), sand-inundated reef (SIR), or flat (FLAT). Benthos was categorised as either canopy-forming algal assemblages (CA), coral (CO), foliose algal assemblages (FO), sand (SA), seagrass (SG),

Table 1. Summary of sampling design and study location attributes

Location	No. of samples	Date sampled (mm/yyyy)	Latitude range (°S)	Longitude range (°E)
Dampier	393	08/2008	20.35°–20.58°	116.83°–116.54°
Barrow Island	172	03/2010	20.65°–20.94°	115.60°–115.37°
Ningaloo	222	04,05,07/2006	21.89°–22.64°	113.97°–113.57°
Shark Bay	287	09/2009	26.00°–26.18°	113.29°–113.16°
Abrolhos Islands	165	05/2007	28.65°–28.87°	114.05°–113.87°
Jurien	144	05,08/2007	30.19°–30.36°	114.97°–114.64°
Rottneest Island	168	09/2007	31.97°–32.06°	115.54°–115.32°
Cape Naturaliste	138	02,03/2007	33.48°–33.72°	115.03°–114.91°
Broke Inlet	139	02/2008	34.96°–35.10°	116.43°–116.25°
Albany	164	11/2007	34.92°–35.07°	118.30°–118.10°
Bremer Bay	180	11/2007	34.14°–34.31°	119.75°–119.56°
Esperance	164	11/2007	33.95°–34.12°	123.42°–123.23°

or sessile invertebrates (SI). Details of the distribution of samples across relief and benthos categories at each location are given in Supplement 1.

Statistical analyses

Species accumulation curves created using the *vegan* package in R version 2.13.1 (R Development Core Team 2011) were calculated for each location and confirmed that sampling had captured an adequate representation of fish assemblages present (Fig. S2.1 in Supplement 2). To test for differences in species richness among locations, Kruskal-Wallis tests were performed, followed by false discovery rate corrected pairwise comparisons (Benjamini & Hochberg 1995) using the *coin* package (Hothorn et al. 2008) and supplementary code provided by Mangiafico (2015).

Multivariate regression trees (MRTs) (De'ath & Fabricius 2000, De'ath 2002) were used to assess the effect of spatial and environmental variables on fish assemblage structure. The minimum cross-validated relative error (De'ath 2002) was used to determine the number of terminal nodes. The resulting trees were then interactively pruned (Andersen et al. 2000).

MRT analysis was conducted using the *mvpart* package (Therneau & Atkinson. 2011). The relative abundance data were Hellinger transformed (Legendre & Gallagher 2001) to decrease the influence of abundant species and account for the large number of zeros in the data (Borcard et al. 2011), which is appropriate for least squares methods such as regression trees (Legendre & Gallagher 2001). The transformed data were then used to analyse the effect of space and environment on the fish assemblage structure at 2 spatial scales. Location (categorical), latitude, and longitude were included in these analyses to account for spatial effects on assemblage structure. Environmental variables were relief and benthos as categorical variables, while depth was a continuous variable. To investigate changes in ecological patterns with changes in spatial scale of observation, subsequent MRT analyses were performed on Hellinger-transformed abundance data at each location.

Indicator species were identified using the *IndVal* index (Dufrene & Legendre 1997), calculated via the *labdsv* package (Roberts 2010). This procedure identifies species associated mostly with a particular group based on a species' fidelity and specificity to the group (Borcard et al. 2011), in this case, the groups being terminal nodes of the MRT. Permutation tests were then used to test for significant differences (Borcard et al. 2011).

To compare the distribution (number of sampled locations a species was detected in) of species observed among locations, a 2-sample Cramer-von Mises test was performed using the *CvM2SL2Test* package (Xiao & Cui 2010). All analyses were performed using R version 2.13.1 (R Development Core Team 2011).

RESULTS

Overall description

In total, 115 972 individuals from 440 species and 75 families were used in the analyses. Labridae was the family most often observed at most locations. At Broke Inlet, Albany, and Esperance, Monacanthidae was the dominant family. Other common families in southern locations were Carangidae, Kyphosidae, Pomacentridae, and Serranidae. Acanthuridae, Carangidae, Chaetodontidae, Lethrinidae, Lutjanidae, Pomacentridae, Scaridae, and Serranidae were common in the northern locations. *Nelusetta ayraudi* was the most abundant species, with 12 559 individuals observed, followed by *Trachurus novaezelandiae* (9068), *Coris auricularis* (6101), and *Pentapodus vitta* (6033). Following this, total abundance counts rapidly decreased due to the large geographical range of the study and the large number of rare species found in Western Australian marine fish assemblages. The majority of species identified in samples were rare, being observed in less than 100 samples (Fig. S2.2 in Supplement 2).

Species richness

Species richness differed among locations (Fig. 2; Kruskal-Wallis test, $p < 0.001$). Although species richness declined along the geographical gradient sampled (e.g. mean of 11.094 at Dampier significantly higher than mean of 4.390 at Esperance; Kruskal-Wallis test, $H = 4.390$, adjusted $p < 0.001$), this decrease was not monotonic. A spike in richness was observed at Rottneest Island (mean of 10.696) and Cape Naturaliste (mean of 11.072; Fig. 2).

Geographical patterns in assemblage structure

Regression tree analysis split the samples into 2 distinct groups associated with temperate and tropical faunal boundaries (Fig. 3). Samples from locations in the western coast overlap zone (Abrolhos Islands

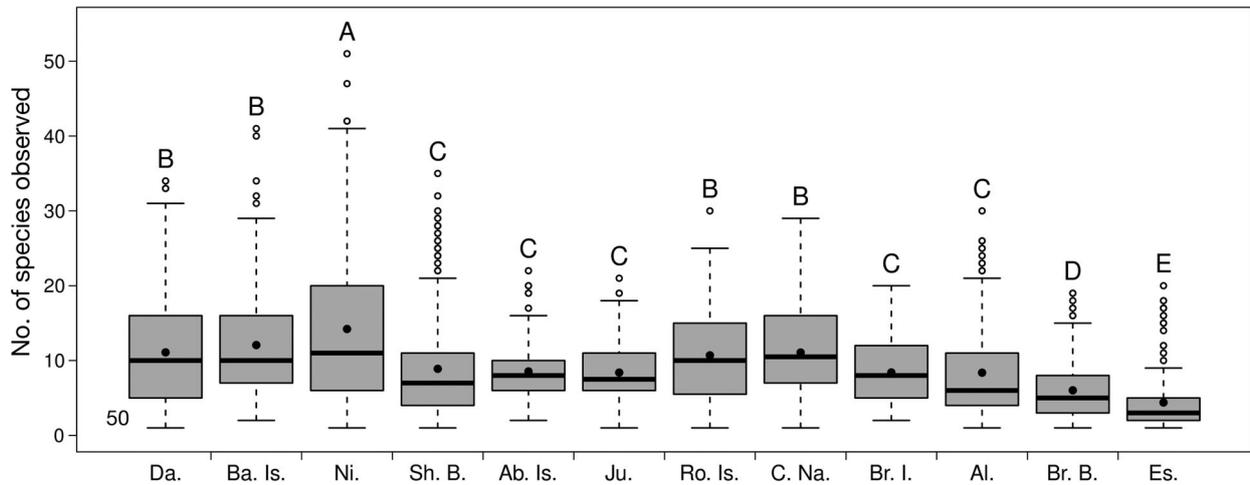


Fig. 2. Number of species observed in samples for each of the locations along a circa latitudinal gradient (from left to right) at the Western Australian coast (see Fig. 1). Letters above boxes correspond to locations not significantly different through pairwise tests. Solid lines represent medians; boxes represent first and third quartiles; whiskers indicate minimum and maximum values; open points represent outliers. Filled points indicate mean values. Da.: Dampier; Ba. Is.: Barrow Island; Ni.: Ningaloo; Sh. B.: Shark Bay; Ab. Is.: Abrolhos Islands; Ju.: Jurien; Ro. Is.: Rottnest Island; C. Na.: Cape Naturaliste; Br. I.: Broke Inlet; Al.: Albany; Br. B.: Bremer Bay; Es.: Esperance

and Shark Bay) (Fox & Beckley 2005) grouped with the tropical samples. Samples falling within the temperate grouping were further divided into 2 distinct subgroups based on topography (Fig. 3). Within the

subgroup defined by soft substrates, the 160 samples from Bremer Bay were distinct from the samples from all of the other temperate locations. Within the subgroup defined by hard substrate, samples from

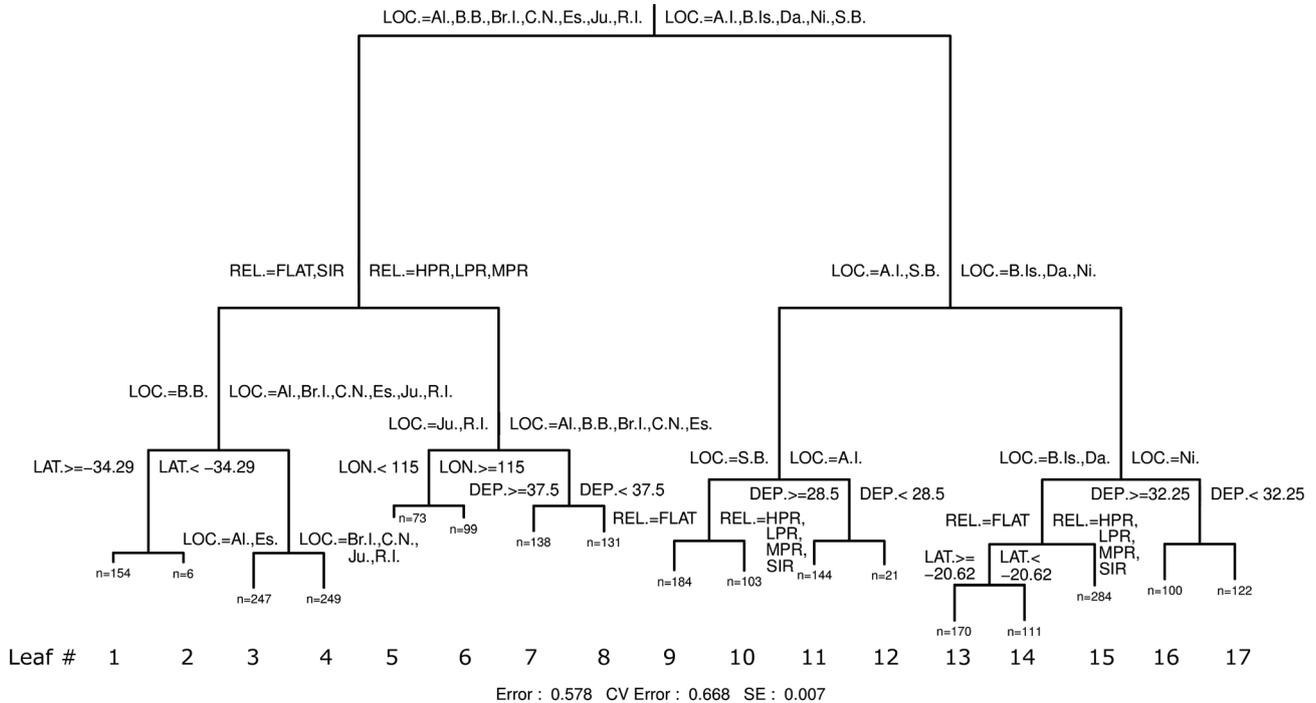


Fig. 3. Coarse-scale multivariate regression tree (see 'Statistical analyses' for details) displaying the effects of space and environment on the fish assemblages along the tropical and temperate coast of Western Australia. Tropical — Da.: Dampier; B.Is.: Barrow Island; Ni.: Ningaloo; S.B.: Shark Bay; A.I.: Abrolhos Islands. Temperate — Ju.: Jurien; R.I.: Rottnest Island; C.N.: Cape Naturaliste; Br.I.: Broke Inlet; Al.: Albany; B.B.: Bremer Bay; Es.: Esperance. LOC.: location; REL.: relief; HPR: high-profile reef; MPR: medium-profile reef; LPR: low-profile reef; SIR: sand-inundated reef; FLAT: flat substrate; DEP.: depth; LAT.: latitude; LON.: longitude

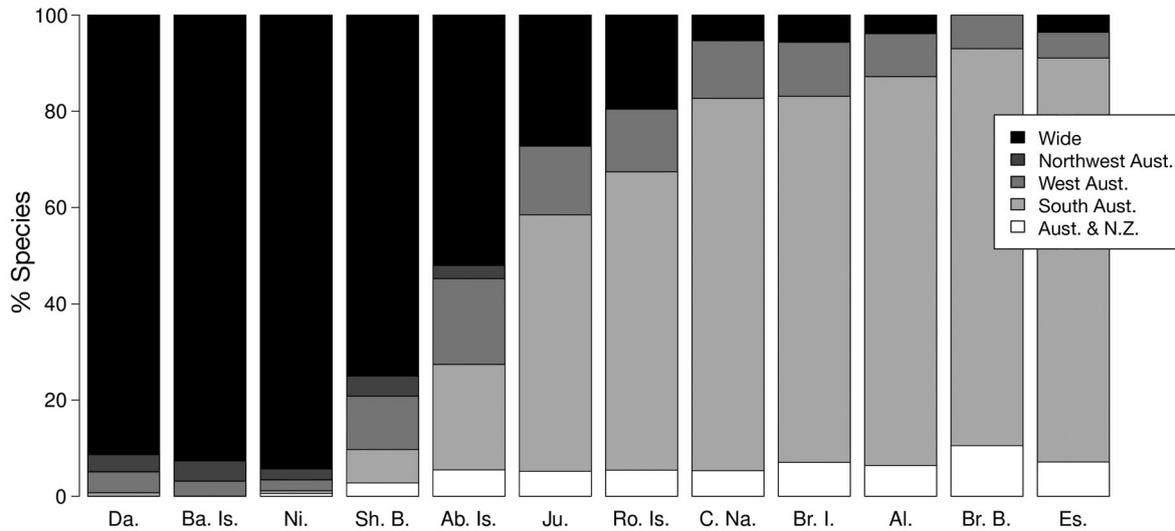


Fig. 4. Percentage of species from each location (abbreviations as in Fig. 2) classified as either widely distributed or endemic to northwestern Australia, Western Australia, southern Australia or Australia and New Zealand

Jurien Bay and Rottnest Island were distinct from the other samples in this temperate subgroup.

The tropical group was divided into 2 subgroups based on geographical location (Fig. 3), resulting in the separation of Shark Bay and Abrolhos Islands samples from those taken at Dampier, Barrow Island, and Ningaloo. Samples taken from Shark Bay were distinct from those collected from the Abrolhos Islands. Similarly, samples from Ningaloo were distinct from those from Barrow Island and Dampier, confirming the importance of geographical location for explaining variability in tropical species assemblages in Western Australia.

Geographical patterns in species distributions

Our analysis identified 288 indicator species (Table S3.1 in Supplement 3) associated with 17 terminal nodes in the MRT (Fig. 3). A large proportion of the indicator species defining the terminal nodes in the temperate grouping were endemic to Western Australia and/or southern Australia. The proportion of endemic species at each location reflected the results obtained for the indicator species (Fig. 4). These endemics were generally widely distributed among the temperate locations (Fig. 5), with the highest number of Western Australian endemics found at

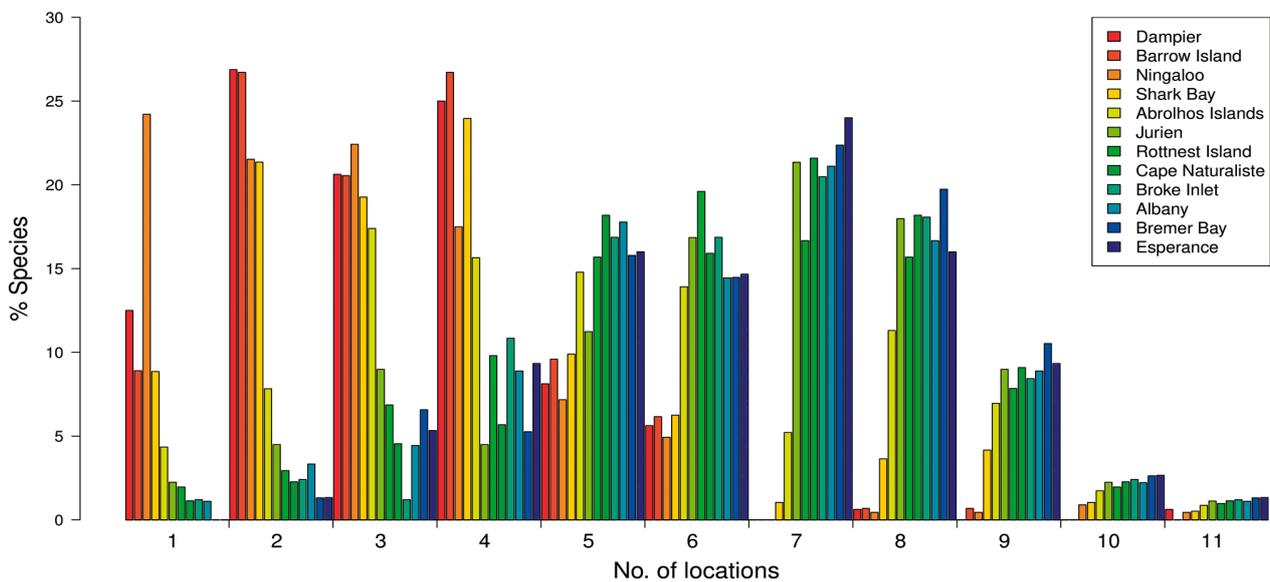


Fig. 5. Distribution of species observed at each location across all 12 locations sampled (see Fig. 1), expressed as the percentage of species from a particular location also occurring at 1 to 11 of the other locations

Jurien and the highest number of southern Australian endemic species found from Cape Naturaliste to Esperance. For most of the southern locations, the greatest proportion of species was observed in 7 locations in total, while Rottnest Island's greatest proportion of species was observed in 6 locations (Fig. 5). The distinctness of the assemblages among northern locations is further demonstrated by Dampier, Barrow Island, Ningaloo, Shark Bay, and Abrolhos Islands having their greatest proportion of species found in 1 (Ningaloo), 2 (Dampier and Barrow Island), 3 (Abrolhos Islands), or 4 (Shark Bay) locations (Fig. 5, Table S3.2 in Supplement 3). Concerning the degree of similarity among locations with respect to the geographical distribution of species observed at each location, all of the northern locations were found to be significantly different in all pairwise comparisons, with the exception of the Abrolhos Islands (Table S3.2 in Supplement 3). The Abrolhos Islands were found to differ only from Broke Inlet, Bremer Bay, and Esperance, while the southern locations differed from northern locations, but no differences were detected among the southern locations (Table S3.2 in Supplement 3).

Microgeographical patterns in assemblage structure

At the microgeographical scale, assemblages were less predictable than the broad geographical patterns observed in the coarse-scale MRT (Fig. 3). This is demonstrated by the reduced variability explained by the fine-scale MRTs (Table 2, Figs. S2.3 to S2.14 in

Supplement 2). However, the first split of the fine-scale trees often explained more variability than the first split at the coarse scale. This result reflects the dominating effect of a particular environmental variable at the microgeographical scale. Within locations, habitat complexity appears to be the major determinant of the fish assemblages, manifesting itself through relief or benthos, but with depth being the major determinant of the assemblages at 3 locations (Ningaloo, Abrolhos Islands, and Broke Inlet) (Table 2).

DISCUSSION

The Western Australian ichthyofaunal assemblages were separated into 2 main groups in the coarse-scale MRTs (Fig. 3), supporting the expected finding of 2 regional species pools along this coastline (Hutchins 1994, 2001, Fox & Beckley 2005). The northern tropical locations (Dampier, Barrow Island, Ningaloo, Shark Bay, and Abrolhos Islands) were generally populated by Indo-Pacific ichthyofauna. The southern temperate fish assemblages, inhabiting the Jurien, Rottnest Island, Cape Naturaliste, Broke Inlet, Albany, Bremer Bay, and Esperance locations, were characterised by southern endemic species.

Comparable to studies from other regions, we found habitat complexity to influence the structure of marine fish assemblages in both temperate and tropical regions (Pérez-Matus et al. 2007, Hackradt et al. 2011). Increased habitat complexity is thought to increase resources including food, shelter, and suitable environments for larval settlement and nesting sites (Holbrook et al. 1990, Garcia Charton & Perez Ruzafa 1998, Jones & Syms 1998, Steele 1999, Angel & Ojeda 2001). As habitat complexity was an observational measure rather than a manipulated variable in this study, the means by which it influenced the ichthyofaunal assemblages and the relative importance of this influence can only be inferred (Hothorn et al. 2011).

The southern location ichthyofauna varied less among locations than tropical faunas but also possessed a greater proportion of endemic species than northern localities (Figs. 3 & 4). Southwestern Australia has been found to be a hotspot for both diver-

Table 2. Summary of fine-scale multivariate regression trees describing the variability in fish community composition at 12 locations along the Western Australian coast

Location	Total variability explained	Variability explained by primary split	Total variability explained by primary split (%)	Primary split variable	Total no. of splits
Dampier	13.10	6.08	46.41	Relief	5
Barrow Island	16.70	9.06	54.25	Benthos	8
Ningaloo	21.50	10.27	47.77	Depth	7
Shark Bay	26.00	8.9	34.23	Relief	10
Abrolhos Islands	22.50	12.12	53.87	Depth	4
Jurien	22.90	12.24	53.45	Relief	4
Rottnest Island	30.80	8.95	29.06	Relief	9
Cape Naturaliste	24.60	12.37	50.28	Relief	6
Broke Inlet	17.60	10.33	58.69	Depth	4
Albany	24.60	11.45	46.54	Relief	6
Bremer Bay	52.80	16.13	30.55	Relief	7
Esperance	20.30	11.07	54.53	Benthos	4

sity and endemism in the marine realm (Phillips 2001, Fox & Beckley 2005). The southern endemic species coevolved in a region of relatively spatially homogeneous environments: they have greater geographic ranges and more niche overlap than their tropical counterparts. The occurrence of southern species was primarily defined by substrate relief, i.e. reef or not reef, throughout the southern locations shown by the major branch within the temperate (left) side of the MRT (Fig. 3). Understanding exactly how these species have evolved requires the marriage of these data on habitat use and specialisation with phylogenetic approaches that define both relationships and the temporal history of diversification. Using molecular clock patterns of diversification can be tied to historic climate shifts and topography but generally lack any associated ecological resolution (e.g. Catullo & Keogh 2014). Fraser et al. (2009) made a limited contribution in the marine realm analysing diversification in kelps between western and eastern Tasmania. A prominent southward-flowing eastern coast tropical current and a western coast temperate current maintained isolation between populations likely initially separated by Pleistocene sea level fluctuations, but considered only 1 kelp species and gave no clues to how differences observed might be adaptively related to ecological and environmental differences.

The high location specificity of the Indo-Pacific ichthyofauna in tropical Western Australia reflects rapid change in the marine environment of Western Australia's northwestern region over small geographical distances. The fish assemblages within the area identified as the western coast overlap zone (Shark Bay and Abrolhos Islands) (Walker et al. 1988, Fox & Beckley 2005) were included with the more northern locations in the first branch of the MRT (Fig. 3) yet were distinct enough to separate in the next branch. The species which constitute the ichthyofauna in the tropical locations sampled are a subset of the diverse Indo-Pacific fauna which have evolved in other tropical regions and have colonised northern Australia. The structure of the tropical communities differs from that of the temperate assemblages in that the gradients in coarse environmental variables (i.e. turbidity, wave exposure) result in distinct subsets of the tropical fauna at locations, likely reflecting the environments they evolved in. Within these locations, habitat complexity then defines assemblage composition.

Building on earlier studies (e.g. Hutchins 2001, Fox & Beckley 2005), this study has improved our understanding of broad-scale ecological patterns of Wes-

tern Australian marine fish assemblages. In contrast to other biogeographical studies of Western Australian marine fish, this study concurrently incorporated measures of abundance, multiple environmental characteristics, and spatial scale. Incorporation of abundance and environmental data provided greater insight into the habitat associations of species and the scale at which coarse or fine environmental variables structure the communities. Integration of environmental characteristics and abundances elucidated the coarse environment filtering seen in the tropical species, e.g. turbid tidal waters at Dampier or clear oceanic waters at Ningaloo, with finer-scale habitat complexity structuring communities within the locations. Conversely, the temperate assemblages are primarily structured by the presence or absence of hard substrate, with less-defined changes in the communities over broad spatial gradients. These results demonstrate that processes which structure fish assemblages in Western Australia differ between temperate and tropical environments, with the scale at which these processes act also differing.

Effective management of marine resources and their conservation values demands an understanding of (1) how those resources are distributed and how the fish fauna use the environment, (2) the unique and general historical patterns they illustrate at both continental and global scales, and (3) run-on unique ecological attributes which particular species or assemblages possess. Our results provide a useful contribution to the understanding of these issues in a region where there are well-established fisheries, and serious attempts to develop good management strategies across the whole region considered by this study (e.g. Fletcher et al. 2010, McClanahan et al. 2011).

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