The relative influence of local to regional drivers of variation in reef fishes

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In this study, fishes and habitat attributes were quantified, four times over 1 year, on three reefs within four regions encompassing a c. 6° latitudinal gradient across south-western Australia. The variability observed was partitioned at these spatio-temporal scales in relation to reef fish variables and the influence of environmental drivers quantified at local scales, *i.e.* at the scale of reefs (the number of small and large topographic elements, the cover of kelp, fucalean and red algae, depth and wave exposure) and at the scale of regions (mean and maximum nutrient concentrations and mean seawater temperature) with regard to the total abundance, species density, species diversity and the multivariate structure of reef fishes. Variation in reef fish species density and diversity was significant at the regional scale, whereas variation in the total abundance and assemblage structure of fishes was also significant at local scales. Spatial variation was greater than temporal variation in all cases. A systematic and gradual species turnover in assemblage structure was observed between adjacent regions across the latitudinal gradient. The cover of red algae within larger patches of brown macroalgae (a biological attribute of the reef) and the number of large topographic elements (a structural attribute of the reef) were correlated with variation observed at local scales, while seawater temperature correlated with variation at the scale of regions. In conclusion, conservation efforts on reef fishes need to incorporate processes operating at regional scales with processes that shape local reef fish communities at local scales. © 2011 The Authors

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Key words: Australia; diversity; macroecology; reef fish assemblages; spatial patterns; variability.

INTRODUCTION

Identifying the scales of spatial and temporal variation relevant to patterns of distribution and abundance of species is a first step in the process of understanding the forces that govern community structure (Underwood *et al.*, 2000). Advances in sampling techniques, coupled with the refinement and computational simplicity of statistical routines, are increasingly enabling the analysis of spatio-temporal patterns, from small to large scales, and have enhanced the ability to explore a broad range of natural phenomena with increasing sophistication (Fraschetti *et al.*, 2005).

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Reef-associated fish assemblages respond to changes in environmental conditions with fluctuations in abundance at different spatial and temporal scales (Connell & Kingsford, 1998; Anderson & Millar, 2004; García-Charton *et al.*, 2004; Malcolm *et al.*, 2007). Understanding the processes underlying such variation is a central aim of fish ecologists and requires identifying the patterns of distribution and abundance of fishes over ecologically and biogeographically relevant spatial and temporal scales. Few studies (Anderson & Millar, 2004; Malcolm *et al.*, 2007), however, have examined spatial variability in fish communities over scales >100 km using hierarchically nested designs which allow a complete partitioning of variation. Indeed, the extent to which the amount of small-scale variability (from metres to >10 km but <100 km) compares to large-scale variation (>100 km) affecting patterns in reef fish abundance, diversity and assemblage structure remains largely unexplored. Even less understood is the extent to which any spatial pattern remains consistent through time. For example, seasonal patterns of fish recruitment can change between adjacent islands within an archipelago as a result of oceanographic differences (Tuya *et al.*, 2006).

At large spatial scales (>100 km), variability in mesoscale oceanographic conditions can affect reef fishes (Leathwick *et al.*, 2006; Wellenreuther *et al.*, 2008), for example *via* control over larval dispersal and recruitment patterns of fishes that have pelagic larvae which disperse over long distances (Kinlan *et al.*, 2005). Indeed, patterns of abundance of reef fishes can follow different biogeographical models across their distribution ranges, *e.g.* 'normal' *v.* 'ramped' patterns (Tuya *et al.*, 2008). At small spatial scales (from metres to >10 <100 km), on the other hand, the physical structure of the reef plays a key role in the organization of fish assemblages, affecting protection from predators and accessibility to food (Jones & Syms, 1998; Tuya *et al.*, 2009), as well as local recruitment patterns (Tolimieri, 1995). In fact, the relationship between reef habitat and fish assemblages is becoming a major tool for the sustainable management of fisheries and marine park planning (Anderson & Millar, 2004; García-Charton *et al.*, 2004). Studies examining the distribution and abundance of fishes in relation to habitat structure are particularly common from tropical coral reefs (Luckhurst & Luckhurst, 1978; Newman & Williams, 1996; Friedlander & Parrish, 1998; Jones & Syms, 1998), but have been also conducted more recently from temperate reefs (Willis & Anderson, 2003; García-Charton *et al.*, 2004; Ordines *et al.*, 2005; Tuya *et al.*, 2009). Local scale reef habitat attributes that can determine the distribution and abundance of reef fishes include substratum type (Guidetti *et al.*, 2004), vertical relief (Luckhurst & Luckhurst, 1978; Yoklavich *et al.*, 2000) and the cover of different types of algal assemblages (Levin, 1994; Tuya *et al.*, 2009). On temperate reefs, one of the main habitats is provided by laminarian and fucalean canopy-forming algae, with smaller foliose algae interspersed in the gaps (Connell & Irving, 2008). Fish assemblages associated with algal habitats are affected by the physical structure of the algal canopies (Ebeling & Laur, 1985; Anderson & Millar, 2004), which influence environmental conditions and the intensity of biological processes (*e.g.* predation pressure, Levin, 1994).

Western Australia is one of the 18 major centres of endemism of the world's reefs (Roberts *et al.*, 2002). The south-west region (Fig. 1) is a transition zone between the Damperian (tropical) and Flindersian (temperate) biogeographical provinces. The high species diversity and endemism of demersal fishes (Williams *et al.*, 2001) is largely attributed to a long period of isolation from other continents (*c.* 80 million
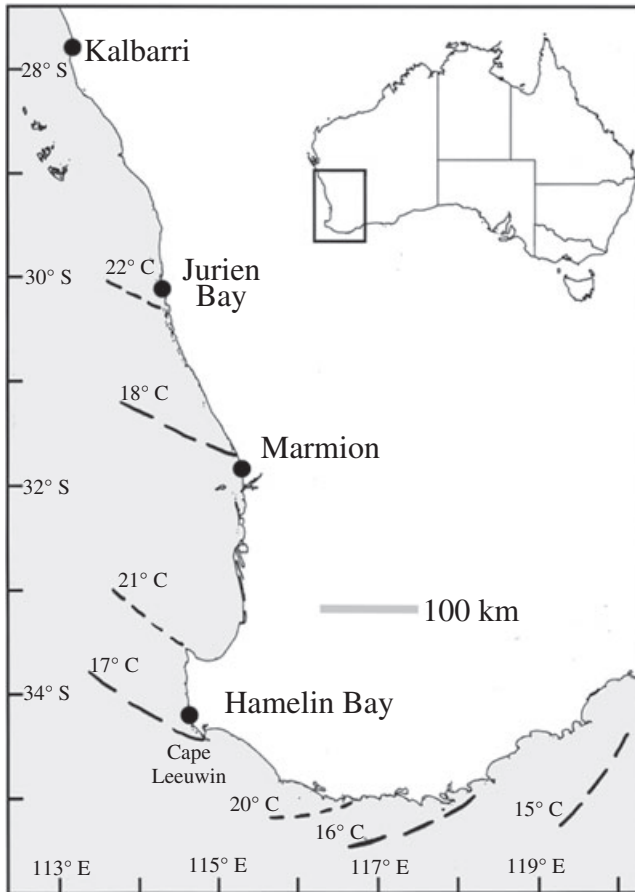
FIG. 1. Map of south-western Australia, showing the four regions included in this study. Summer (‑ ‑ ‑ ‑) and winter (▬ ▬) isotherms are indicated.

years), the moderating influence of the warm Leeuwin Current over the past *c*. 50 million years and the lack of mass extinctions associated with unfavourable conditions, such as glaciations, over the recent geological past. Rocky reefs are a predominant feature along >1600 km of coastline, where they run almost continuously from Shark Bay to Cape Leeuwin. On most of these reefs, the dominant alga is the canopy-forming kelp *Ecklonia radiata* that creates habitats extending from metres to >100 km, interspersed with frondose fucalean algae and smaller foliose red algae (Wernberg *et al.*, 2003). South-western Australia, as a result of its latitudinal gradient in temperature (Smale & Wernberg, 2009; Wernberg *et al.*, 2010), is an ideal candidate to disentangle the effect of different scales of spatial and temporal variations over reef fishes. In this study, a multiscale sampling design was used to partition the variability observed at several spatial and temporal scales over reef fishes. This variability was correlated with a variety of environmental drivers operating at different scales. Specifically, it was assessed how patterns in the abundance, species density, species diversity and multivariate assemblage structure of reef fishes vary on

multiple spatio-temporal scales, and the possible influence of various environmental drivers was quantified.

MATERIALS AND METHODS

STUDY AREA AND SAMPLING DESIGN

This study included four regions across south-western Australia: Hamelin Bay (HAM), Marmion (MAR), Jurien Bay (JUR) and Kalbarri (KAL) (Fig. 1). These regions are evenly spaced across *c*. 6° of latitude (*c*. 800 km, adjacent regions are *c*. 150–200 km apart), encompassing a temperature gradient of 3–4° C (Smale & Wernberg, 2009; Wernberg *et al*., 2010); each region encompasses a stretch of coast between 10 and 20 km. Within each region, shallow-water reef fishes were surveyed at three sites (*i.e.* reefs, 1–20 km apart, 8–12 m depth). Sampling was repeated four times over the course of 1 year (October 2006, March, June and October 2007); sampling times were randomly selected, with successive times separated by between 3 and 5 months. All reefs were outside areas under any protection (*i.e.* no-take areas). At each site and time, three replicate, randomly oriented, 25 m × 5 m belt transects were sampled by the same scuba diver, identifying and counting all adult and sub-adult fishes (moving bits) on the way out (Tuya *et al*., 2008) and the number of large (>1 m) and small (<1 m) topographic elements (hereafter large and small 'drops') of the rocky substrata (*i.e.* cracks, crevices, caves and holes per 125 m^2) when rolling up the transect (non-moving bits). Another diver visually estimated the per cent cover of kelp, fucalean algae and red algae, following standardized procedures for the study region (Wernberg *et al*., 2010). These environmental drivers were considered to operate at the scale of reefs. For each reef the following were recorded: the depth (using a scuba depth gauge), wave exposure (rank from 1 to 12; qualitatively based on >100 dives on each reef under various hydrodynamic and climatic conditions over the last 10 years), the mean and maximum nutrient concentrations [NO_2 or NO_3 analyses of water samples collected *c*. 1 m above the bottom; (Wernberg *et al*. 2010)], and the mean seawater temperature [Tidbit loggers, logging *c*. 5 cm above the reef; (Smale & Wernberg, 2009)]. Mean and maximum nutrient concentrations and mean sea water temperature do not vary significantly among reefs within regions, but among regions along the latitudinal gradient (Wernberg *et al*., 2010); therefore, these environmental drivers were considered to operate at the scale of regions.

DATA ANALYSES

Univariate attributes of the reef fish assemblage included fish abundance, species density (number of species per area; Gotelli & Colwell, 2001) and species diversity (Shannon–Wiener index). These univariate attributes were expressed per transect (125 m^2). Permutation-based ANOVA was used to partition variation in reef fishes into spatial and temporal components. The ANOVA model incorporated, in all cases, the random factors: 'regions', 'times' (orthogonal to 'regions') and 'sites' (nested within 'regions'). ANOVAs were performed on the species density, diversity and total abundance of fishes, as well as abundance of the 20 most common species. Before analysis, Cochran's test was used to test for homogeneity of variances. The α value was set at the most conservative 0·01 level, instead of the traditional 0·05 value, to reduce the probability of type I errors when variances remained heterogeneous despite transformation (Underwood, 1997). A partitioning of multivariate variability (all species with their corresponding abundances) was carried out, using the same model as outlined before, *via* a permutational multivariate ANOVA (Anderson, 2001). Pair-wise comparisons between each pair of regions were executed when significant differences were detected at the regional scale. The contribution of each scale to explain the total variation in univariate and multivariate fish responses was estimated by calculating their variance components and expressing the outcomes as percentages of total explained variation (Graham & Edwards, 2001; Anderson & Millar, 2004).

Multiple regression models, using the DISTLM routine (Anderson, 2001), tested whether variation in the environmental drivers operating at the scale of reefs (the number of small and large topographic elements and the cover of the three types of algal canopies, depth and wave exposure) and regions (mean and maximum nutrient concentrations and the mean seawater temperature) affected variation in the total abundance, species density, species diversity and assemblage structure of reef fishes across the study area (times were pooled for each site) by fitting a linear model. To retain variables (*i.e.* environmental drivers in each case) with good explanatory power, the Akaike information criterion routine was used as a selection criterion [the smaller the value the better the model (Anderson & Legendre, 1999)].

A canonical analysis of principal co-ordinates (CAP; Anderson & Willis, 2003) was used, as a constrained ordination procedure, to visualize differences in the assemblage structure of reef fishes. Two separate canonical analyses were carried out: one to visualize differences among regions (pooling sampling times for each region) and the other to visualize differences among times (pooling regions for each time). Distance-based redundancy analysis (db-RDA; Legendre & Anderson, 1999) was used to visualize whether variation in the environmental drivers of each reef affected variation in the assemblage structure of reef fishes across the study area (times were pooled for each site). In all analysis, fish abundances were $\ln(x + 1)$ transformed to down-weigh the influence of abundant small schooling fishes over larger, more solitary, fishes. Trends in serial correlation (seriation) in assemblage structure among regions were tested *via* the RELATE routine. All multivariate analyses were based on Bray−Curtis similarities. *P*-values were calculated from 4999 permutations of the residuals under the reduced model. All data analyses were done on PRIMER and PERMANOVA 1.0.1 (Anderson *et al*., 2008).

RESULTS

PATTERNS IN TOTAL ABUNDANCE, SPECIES DENSITY AND DIVERSITY OF REEF FISHES

A total of 6111 reef fishes, belonging to 47 taxa, were observed during the study. Twenty species dominated the assemblage in terms of abundance (*c*. 85% of total individuals), and were present in >20% of the censuses (Fig. 2). Total abundance, species density and species diversity of reef fishes were dominated by spatial rather than temporal variation (Table I and Fig. 3). Total abundance of individuals [Figs 3(a) and 4(a)] changed from site to site within each region inconsistently among times [(Fig. 3(a) and Table I, 'sites (region) × time', ANOVA, $P = 0.024$]. Indeed, the lowest levels of variation ['sites (region) × time' and the residual term] accounted for almost 80% of the total variation. Significant variation in species density was found among regions [Figs 3(b) and 4(b) and Table I, ANOVA, $P = 0.004$, *c*. 23% of total explained variation], despite significant differences among sites within regions [Fig. 3(b) and Table I, ANOVA, $P = 0.024$, 13·8% of total explained variation]. Species diversity only differed significantly among regions [Figs 3(c) and 4(c) and Table I, ANOVA, $P = 0.011$, 21·1% of total explained variation]. Pairwise comparisons indicated that Kalbarri had lowest species density and diversity, but not total abundance, of reef fishes than the other three regions [Fig. 4(b) and (c)]. Sampling time did not have any effects over these three attributes (total abundance, species density and species diversity of reef fishes) on its own (Fig. 3 and Table I, ANOVA, d.f. = 3, $P > 0.07$ in all cases) and generally accounted for a small proportion of variation (<12·3%). In all cases, the residual (*i.e.* variation among replicate transects) accounted for a large amount of variation (30·6−51·5%, Table I).
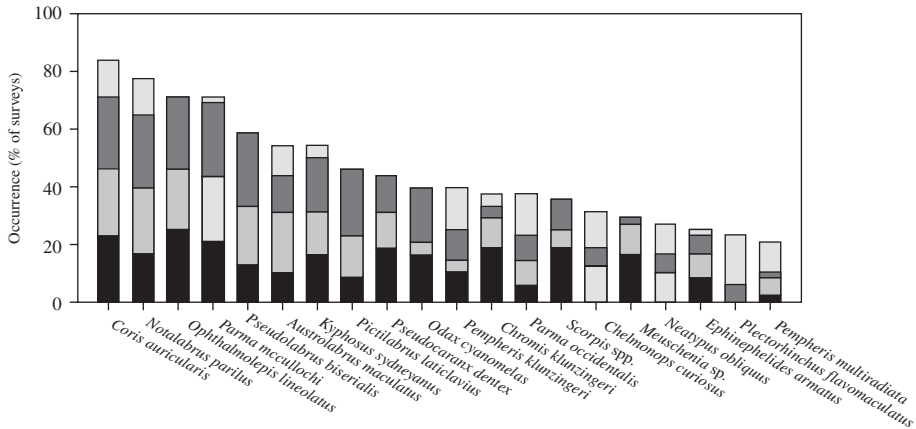
FIG. 2. Occurrence of the 20 most commonly observed fish species across the study area: Hamelin Bay (■),
Marmion (□), Jurien Bay (▨) and Kalbarri (□).

Patterns in the abundance of individual fish species (Fig. 5) were also dominated
by spatial rather than temporal variation, *i.e.* only one (the western talma *Chelmonops
curiosus* Kuiter 1986) of the 20 species showed a significant difference among sam-
pling times. Twelve species varied significantly in abundances among regions across
the latitudinal gradient (Fig. 5); 'regions' accounted for 10–40% of total variation for
these species. Again, the residual term accounted for the largest amount of variation
(Fig. 5).

PATTERNS IN THE ASSEMBLAGE STRUCTURE OF REEF FISHES

Variation in reef fish assemblage structure was complex with almost 80% of vari-
ation attributable to combinations of temporal and spatial components (Table I).
Despite small-scale spatial variability [*i.e.* the residual plus 'sites (regions) × time'
and 'sites'; Fig. 3(d) and Table I] which accounted for 66·1% of total variation
in assemblage structure, spatial variation at the scale of regions (20·5%) dominated
over purely temporal variation (0%) and spatial variation at the scale of sites [13·7%;
Fig. 3(d) and Table I]. These effects were also clearly identifiable in the constrained
ordinations, where there was a clear grouping of regions [Fig, 6(a); $\delta_1^2 = 0.83$,
$P < 0.01$], but no identifiable groupings of sampling times [Fig. 6(b); $\delta_1^2 =
0.32$, $P > 0.05$]. Kalbarri separated from the three other regions along CAP1 (97·22%
of allocation success in the ordination space), whereas HAM, MAR and JUR sepa-
rated along CAP2, with MAR intermediate to JUR and HAM (allocation success for
these locations was <80%). Pair-wise comparisons supported these patterns: KAL
was significantly different from all other regions (pair-wise comparisons, $P < 0.011$),
JUR differed only from HAM (pair-wise comparisons, $P = 0.044$), but MAR did
not differ from either JUR or HAM (pair-wise comparisons, $P > 0.196$). There was
a trend for serial correlation between adjacent regions, and thus a systematic and
gradual species turnover in assemblage structure from KAL in the north to HAM in
the south (RELATE, $\rho = 0.62$, $P = 0.172$).

TABLE I. Results of uni- and multi-variate ANOVA testing the effects of 'regions', 'times' and 'sites' on patterns of species density, total abundance, diversity and assemblage structure of reef fishes, respectively, across south-western Australia

| Source of variation	d.f.	MS	Pseudo-F	P	Denominator MS	Per cent of total explained variation
Species density						
Regions	3	150·2	4·39	0·004	Region × times + sites (region)	23·0
Times	3	47·9	3·63	0·079	Region × times	12·3
Sites (region)	8	22·9	2·76	0·024	Sites (region) × times	13·8
Region × times	9	13·2	1·59	0·176	Sites (region) × times	9·2
Sites (region) × times	24	8·3	1·39	0·134	Residual	11·0
Residual	96	6·0				30·6
Total abundance						
Regions	3	8443	1·68	0·150	Region × times + sites (region)	13·1
Times	3	1334	0·49	0·693	Region × times	0
Sites (region)	8	4595	1·18	0·341	Sites (region) × times	8·6
Region × times	9	2731	0·70	0·696	Sites (region) × times	0·0
Sites (region) × times	24	3878	1·81	0·024	Residual	26·8
Residual	96	2143				51·5
Diversity						
Regions	3	3·568	3·48	0·011	Region × times + sites (region)	21·1
Times	3	1·079	1·49	0·268	Region × times	7·5
Sites (region)	8	0·398	1·16	0·372	Sites (region) × times	5·2
Region × times	9	0·725	2·12	0·055	Sites (region) × times	15·6
Sites (region) × times	24	0·343	1·63	0·051	Residual	15·9
Residual	96	0·210				34·7
Assemblage structure						
Regions	3	28699	2·87	0·001	Region × times + sites (region)	20·5
Times	3	4895	0·96	0·504	Region × times	0·0
Sites (region)	8	5955	2·05	0·001	Sites (region) × times	13·7
Region × times	9	5073	1·75	0·001	Sites (region) × times	13·4
Sites (region) × times	24	2901	1·77	0·001	Residual	17·6
Residual	96	1637				34·8
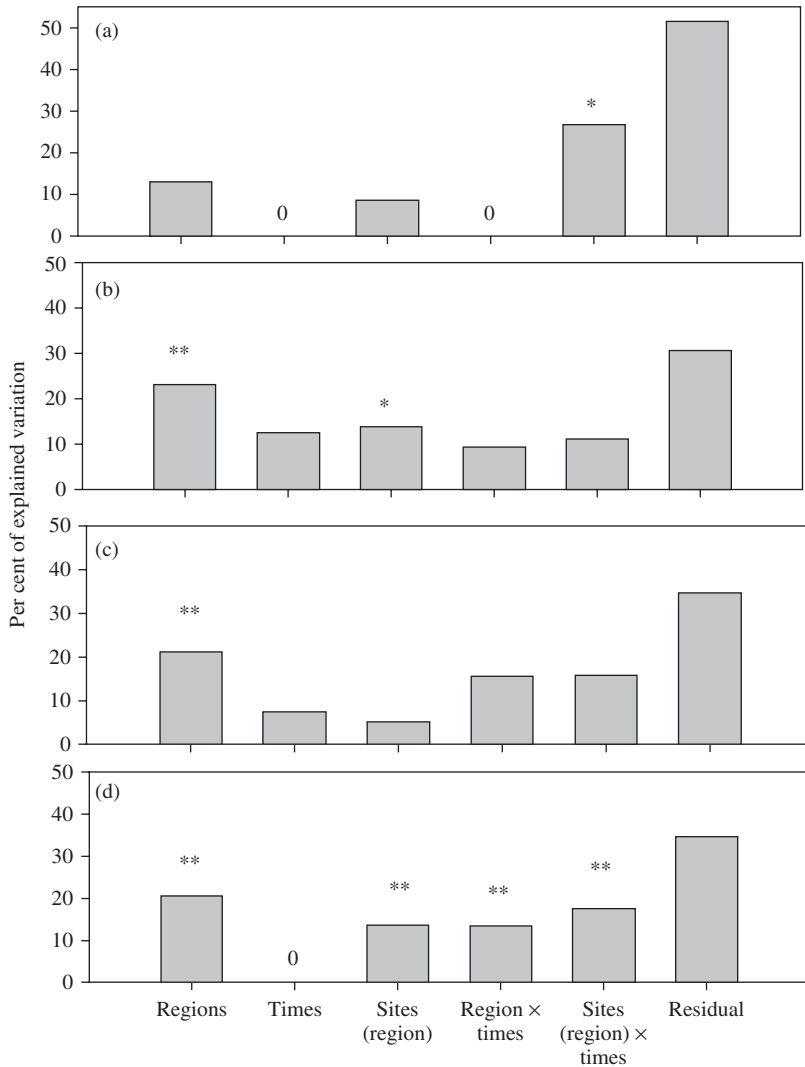
FIG. 3. Components of variation in (a) total abundance, (b) species density, (c) species diversity and (d) assemblage structure at different spatio-temporal scales. Total variation was partitioned among scales and expressed as a percentage of the total. Significant variations are indicated (*, $P < 0.05$; **, $P < 0.01$).

THE EFFECT OF ENVIRONMENTAL DRIVERS ON REEF FISHES

Mean seawater temperature was the environmental factor that explained most variation in the total abundance of reef fishes (*c.* 18% of total variation, sequential tests in the univariate multiple regression, Table II), though its influence was not significant ($P = 0.1087$; Table II). Variation in both species density and species diversity was explained by environmental drivers at the scale of reefs (Table II), including the cover of red algae (*c.* 42 and 48% of total variation, respectively, Table II) and the number of large topographic elements (*c.* 26 and 11% of total variation,
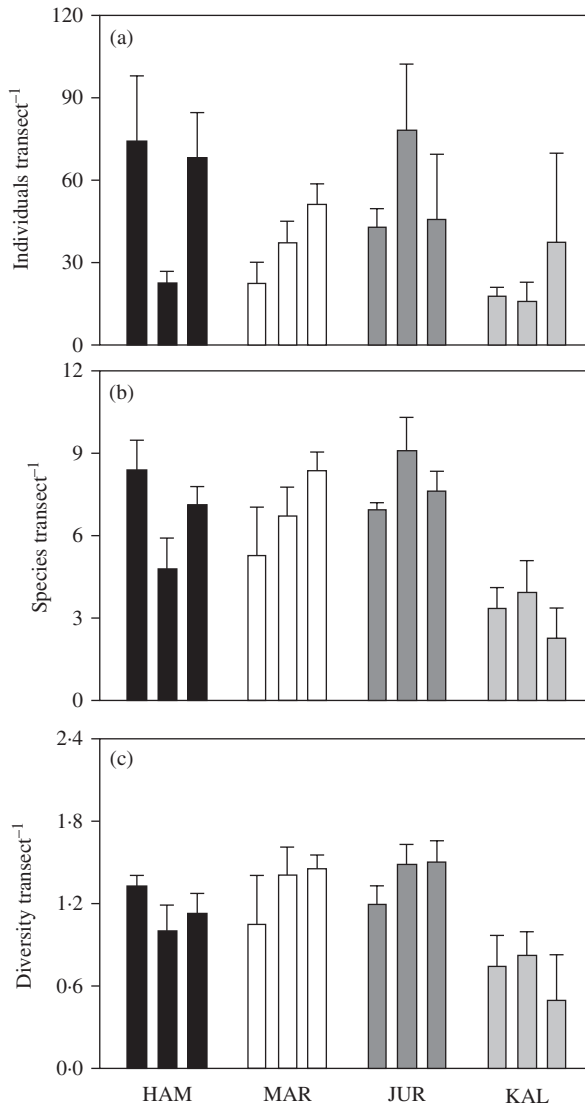
FIG. 4. (a) Total abundance, (b) species density and (c) species diversity of reef fishes (mean + s.e., $n = 12$; four sampling times × three transects) at three reefs within Hamelin Bay (HAM), Marmion (MAR), Jurien Bay (JUR) and Kalbarri (KAL).

respectively, Table II). Mean seawater temperature, an environmental driver operating at the scale of regions, also explained a substantial variation in species density and species diversity (c. 17 and 15%, respectively, Table II).

The first two axes from the db-RDA explained c. 54% of the total variation in reef fish assemblage structure (Fig. 7). Three environmental drivers were selected to explain variability in reef fish assemblage structure (Fig. 7; sequential tests in the multivariate multiple regression, Table I). Mean seawater temperature was, by far, the most important environmental driver of reef fish assemblage structure, accounting
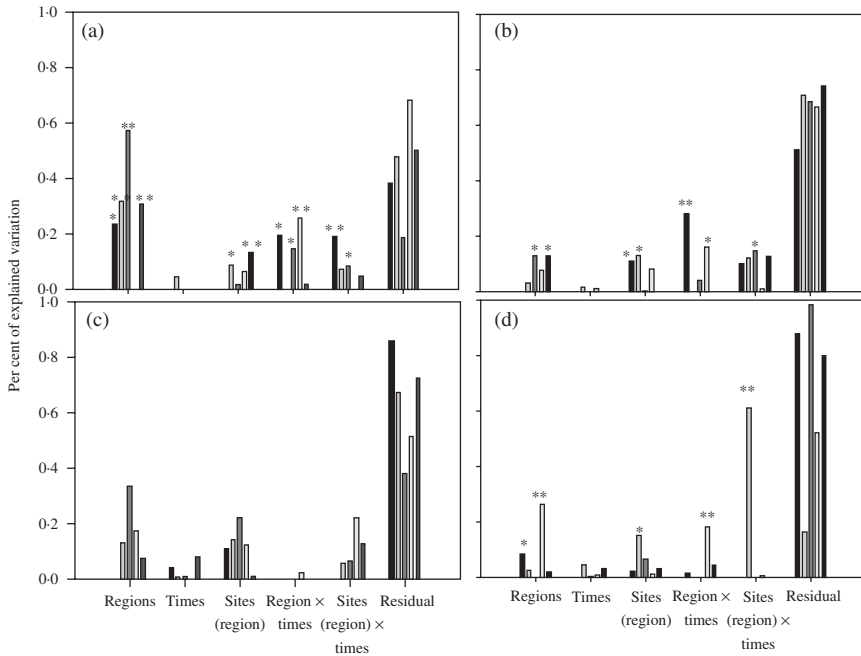
FIG. 5. Components of variation in the abundance of (from left to right) (a) *Coris auricularis, Notolabrus parilus, Ophthalmolepis lineolatus, Parma mccullochi* and *Pseudolabrus biserialis,* (b) *Austrolabrus maculatus, Kyphosus sydneyanus, Pictilabrus laticlavius, Pseudocaranx dentex* and *Odax cyanomelas,* (c) *Pempheris klunzingeri, Chromis klunzingeri, Parma occidentalis, Scorpis* spp. and *Chelmonops curiosus* and (d) *Meuschenia* sp., *Neatypus obliquus, Ephinephelides armatus, Plectorhinchus flavomaculatus* and *Pempheris multiradiata,* at different spatio-temporal scales. Total variation was partitioned among scales and expressed as a percentage of the total. Significant variations are indicated (*, $P < 0.05$; **, $P < 0.01$).

for *c*. 33% of the total multivariate variation (Table I). Additionally, two variables operating at the scale of reefs (the % coverage of red algae and the number of large drops) accounted for an additional *c*. 24% of total variation in reef fish assemblage structure (Table I).

DISCUSSION

Around the world, efforts to protect and conserve local reefs have increased dramatically in the past few decades. To make these efforts more efficient, it is necessary to understand the relative contribution of local *v*. regional processes shaping reef fish assemblages and assessing whether patterns over space are consistent over time. For example, local conservation effort may be of limited value if the fish assemblages are overwhelmingly controlled by regional processes. In this context, it is vital to identify the most relevant scales of variation for any reef fish variables of interest (*e.g.* abundance, number of species and diversity), in order to optimize prospective monitoring programmes. This is particularly pertinent in subtidal environments where sampling is logistically challenging, expensive and time limited (*e.g.* due to restrictions associated with scuba diving).
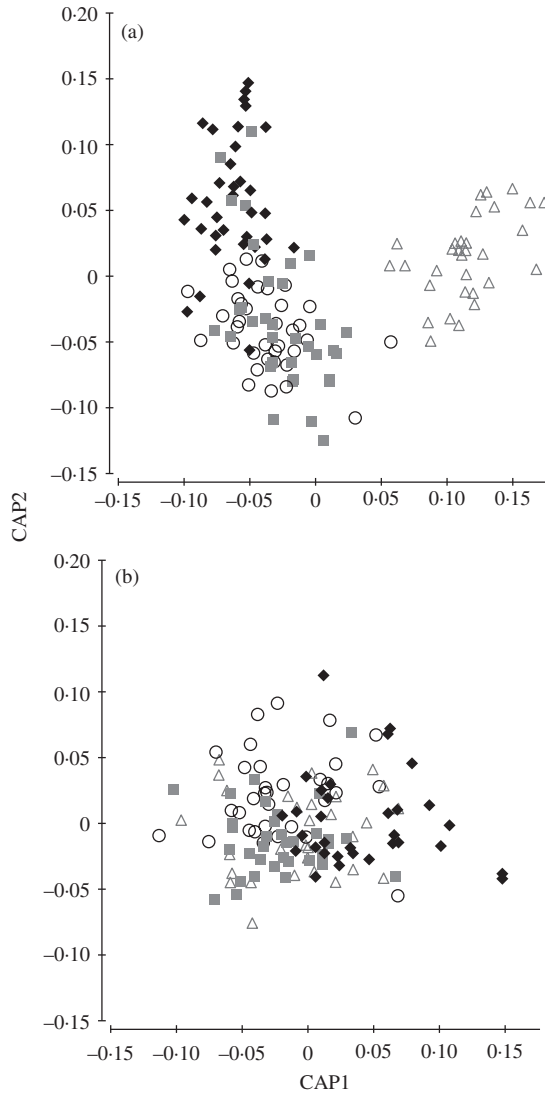
FIG. 6. Ordination (CAP) of reef fish assemblages constrained by (a) region, pooling all sampling times and (b) sampling time, pooling all regions (◆, Hamelin Bay; ○, Marmion; ■, Jurien Bay; △, Kalbarri).

PATTERNS OVER SPACE

Significant variation at a range of spatial scales is common for the abundance and diversity of reef fishes (Newman & Williams, 1996; Connell & Kingsford, 1998; García-Charton & Pérez-Ruzafa, 1998; Anderson & Millar, 2004; García-Charton *et al*., 2004; Tuya *et al*., 2004; Malcolm *et al*., 2007). In this study, variation was by far larger among replicated transects, a few metres apart, than at any other spatial scale, for all fish variables. This is not surprising because fishes move over short periods and over short distances. This leads to a large residual variation, typically of stochastic nature, that has been routinely identified for numerous fish variables

TABLE II. Results of multiple regression models testing the relationship between environmental drivers and the total abundance, species density, species diversity and assemblage structure of reef fishes across south-western Australia. To retain variables with explanatory power, the Akaike information criterion procedure was chosen as model selection criterion [sequential tests, Anderson (2001)]. The contribution of each independent variable is described by means of the amount (%) of explained variation, and P-values provide significance diagnoses (only environmental variables with P-values ≤ 0.1 were included)

| Total abundance			Species density			Species diversity			Assemblage structure		
Variable	% Explained variation	P	Variable	% Explained variation	P	Variable	% Explained variation	P	Variable	% Explained variation	P
X_1 = SWT	0·185	0·108	X_1 = red algae cover	0.425	0·028	X_1 = red algae cover	0.4823	0·003	X_1 = SWT	0.3389	0.0002
			X_2 = large topographic elements	0.267	0·022	X_2 = SWT	0.1540	0·034	X_2 = red algae cover	0.1431	0·0216
			X_3 = SWT	0.172	0·024	X_3 = large topographic elements	0.1156	0·036	X_3 = large topographic elements	0.1070	0·0584

SWT, mean seawater temperature.
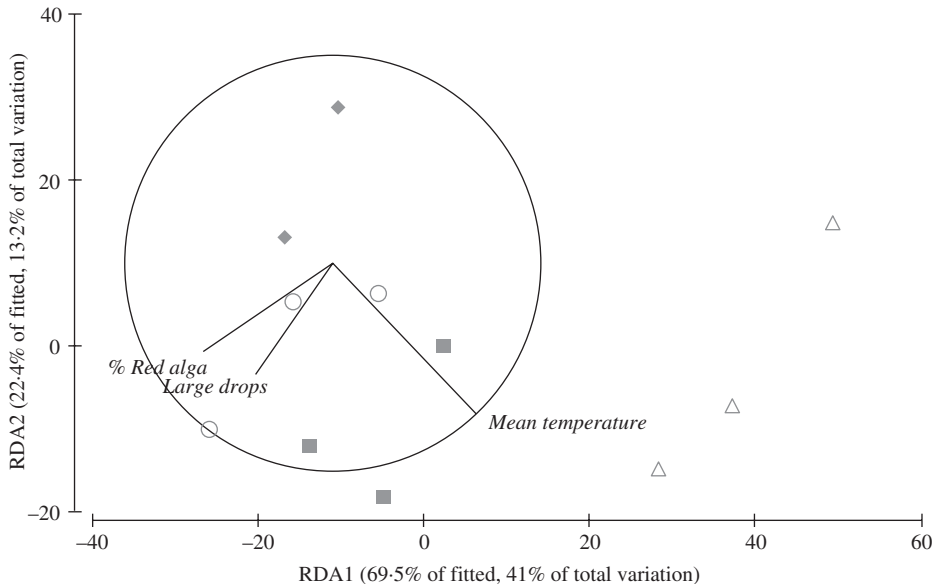
FIG. 7. Distance-based redundancy analysis (db-RDA) biplots of first and second axes relating environmental drivers over the reef fish assemblage structure. Sampling times were pooled for each reef within each region (◆, Hamelin Bay; ○, Marmion; ■, Jurien Bay; △, Kalbarri).

(Connell & Kingsford, 1998; García-Charton & Pérez-Ruzafa, 1998; Jones & Syms, 1998; Anderson & Millar, 2004; García-Charton *et al.*, 2004; Tuya *et al.*, 2004; Ordines *et al.*, 2005; Willis *et al.*, 2006; Malcolm *et al.*, 2007). This small-scale spatial 'noise', however, did not prevent the identification of other relevant spatial scales of variation for fish variables at either the species or assemblage level. Patterns in the number of reef fish species and diversity were largely driven by variation at the regional scale. Variation in the multivariate structure of reef fishes was also mostly influenced by variation at the scale of regions (20·5% of total variability), though variation at the scale of sites also accounted for a relevant amount of variation (13·7%). This result fits previous observations for other temperate reef fish assemblages (Anderson & Millar, 2004), where variation at the scale of locations, >100 km apart, accounted for the large amount of variation (7·8%), followed by variation at the scale of sites within locations (5·4%). Despite responses at the species level that were mostly dominated by variation at the within-transect variation level, a total of 12 (of 20) species showed differences in abundance among regions across the latitudinal gradient. These results highlight the relevance of quantifying variability at the scale of regions.

Spatial variation of reef fishes at scales from tens to thousands of metres (*e.g.* variation among sites within regions) may relate to combinations of variation in habitat structure (Connell & Jones, 1991; Willis & Anderson, 2003; García-Charton *et al.*, 2004), recruitment (Connell & Jones, 1991; Tolimieri, 1995) and local hydrodynamics such as exposure to waves (Friedlander & Parrish, 1998; Depczynski & Bellwood, 2005), among other processes. The present results suggest that both a structural (the number of large topographic elements) and a biological (the coverage of red algae)

attribute of reefs contributed significantly to explain variation in reef fish assemblage structure at this spatial scale. The presence of large topographic elements can increase the number of microhabitats per area, and so affect the composition and abundance of reef fishes (García-Charton & Pérez-Ruzafa, 1998). Macroalgae provide food and shelter for temperate reef fishes (Anderson & Millar, 2004). Patches of small red algae interspersed within forests of laminarian and fucalean macroalgae are encountered across the entire Australian temperate coast (Connell & Irving, 2008). The presence of small red algal patches within larger patches of brown macroalgae might facilitate access to invertebrate prey (Levin, 1994), and thus affect patterns of abundance of temperate reef fishes (Wellenreuther & Connell, 2002). The results have shown that the heterogeneity within these algal habitats affect the multivariate structure of reef fishes at the scale of reefs and reinforce and extend previous observations from the study area that identified small red algal patches as a local driver of the abundance of several species of labrids (Tuya *et al.*, 2009).

Although variation at the scale of sites can account for a substantial amount of variation over reef fishes (García-Charton *et al.*, 2004; Malcolm *et al.*, 2007), the abundances of species frequently vary across biogeographic gradients, *e.g.* due to local selection pressures, limited environmental tolerances and variability in recruitment and larval dispersal (Taylor & Hellberg, 2003; Kinlan *et al.*, 2005). At large spatial scales (>100s of km), traditional biogeographic studies have provided a different perception of the processes influencing entire assemblages (Brown, 1995). Spatial variation in the abundance and composition of reef fishes at large scales may reflect biogeographical and latitudinal affinities (Tuya *et al.*, 2004; Bouchon-Navaro *et al.*, 2005) that potentially is related to oceanographic drivers, *e.g.* temperature and productivity (Leathwick *et al.*, 2006). There are no obvious biogeographical barriers across the latitudinal gradient in south-western Australia, and so a gradual species turnover in assemblage structure was observed between adjacent regions across the latitudinal gradient. This latitudinal effect was clearly evidenced in the RDA ordination space, because seawater temperature was selected as the best driver of reef fish assemblage structure across the latitudinal gradient. Seawater temperature is linearly correlated with latitude across the study area, with an average mean annual difference of *c*. 1° C between adjacent regions (Smale & Wernberg, 2009; Wernberg *et al.*, 2010). This result provides clear evidence of the key role that latitude plays, presumably through changes in seawater temperature, explaining patterns in the assemblage structure of reef fishes across south-western Australia. Similar findings have been reported across this latitudinal gradient for macroalgae (Wernberg *et al.*, 2003).

Kalbarri, the most northern study region, was characterized by a low species density and diversity of reef fishes. This is surprising because Kalbarri, at the cusp of the transition zone between tropical and temperate waters, is a recognized distributional range edge for numerous tropical and temperate species (Edgar, 2008). One possible explanation could be that the very gradual climate transition restricts both temperate and tropical fish species, which are performing sub-optimally there. Coastal landscape structure could also contribute to the patterns of low species density and diversity of reef fishes in Kalbarri. The coast around Jurien Bay, Marmion and Hamelin Bay is characterized by sandy beaches and sections of reef with adjacent seagrass meadows (principally *Posidonia* spp. and *Amphibolis* spp.) (Tuya *et al.*, 2010). In contrast, Kalbarri is characterized by steep cliffs and more extensive reef platforms which potentially could limit the recruitment of reef fishes that use seagrasses as nursery

habitats in south-western Australia (Ayvazian & Hyndes, 1995). Also, while the overall algal habitat composition does not vary, the heterogeneity of algal patches is lower in Kalbarri than the other regions (Wernberg *et al.*, 2011), which could affect the available number of niches for different assemblages of reef fishes.

PATTERNS OVER TIME

Spatial patterns of marine assemblages often vary in time, and temporal sampling is therefore important to test whether observed spatial patterns are stable and general (Fraschetti *et al.*, 2005). The present results support previous observations that temporal variation (on monthly time scales) over assemblages of adult and sub-adult reef fishes is negligible (Willis *et al.*, 2006). In addition, the results build on previous studies that have shown a lack of consistent effects of short-term temporal variability (days to weeks) over assemblages of temperate and coral reef fishes, as long as crepuscular periods are avoided (Thompson & Mapstone, 1997; Willis *et al.*, 2006). Temporal changes in fish abundances, however, can be dramatic, for example, following recruitment pulses (Tolimieri, 1995). The results support the notion that variability in space (from metres to >100 km) is more important than variability in time (weeks to months), particularly when responses are considered at the assemblage level. For example, it is worth noting that the amount of multivariate variability explained by 'times' was 0%; a result similar to that obtained by Anderson & Millar (2004), who observed that variability at the scale of years did not contribute to explaining any multivariate variability. In this sense, spatial patterns of reef fishes, *e.g.* differences in the composition and abundance of reef fishes between neighbouring habitats, are generally consistent through time (Newman & Williams, 1996; Connell & Kingsford, 1998), and even between years (Anderson & Millar, 2004; Malcolm *et al.*, 2007).

IMPLICATIONS FOR CONSERVATION OF REEF FISHES

Spatial variability was high among replicated transects and regions, but comparatively small among sites, and these effects were consistent over months. At the assemblage level, small-scale variation was mainly correlated with the cover of red algae and the presence of large topographic elements, while variation at regional scales was driven by seawater temperature. As a result, conservation efforts on reef fishes need to incorporate large-scale processes operating at regional scales in conjunction with knowledge of processes that shape local reef fish assemblages at small scales. The resurgence of 'macroecology', that unifies biogeography and ecology, provides a sound conceptual framework to connect the effects of different scales on ecological patterns as a way to optimize the sustainable management of coastal fisheries and marine park planning.

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