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Habitat structure affect abundances of labrid fishes across temperate reefs in south-western Australia

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Abstract We tested the effect of reef complexity (number of small vs. large topographic elements, <1 m and >1 m, respectively), and composition of macroalgae (cover of the kelp *Ecklonia radiata*, fucalean and red algae) on the abundance patterns of labrid fishes across ~800 km of coastline in south-western Australia. Fishes and habitat attributes were visually counted at 12 reefs visited at four times over 1 year. Five labrids (*Austrolabrus maculatus*, *Coris auricularis*, *Notolabrus parilus*, *Ophthalmolepis lineolata* and *Pseudolabrus biseralis*) were frequently observed (>20% of counts), while three species (*Bodianus axillaris*, *Choerodon rubescens* and *Thalassoma lutescens*) were rarely censused (< 6%). Patterns of abundance were generally affected by two descriptors of the habitat structure: the number of small topographic elements (100 m^{-2}), and the percentage of red algal cover. Most species showed a tendency for an increase in their abundances with an increase in the number of small topographic elements and cover of red algae. The patterns likely reflect an underlying correlation between habitat structure and prey accessibility and lowered predation risk.

Keywords Habitat structure · Fish · Abundance · Spatial distribution · Temperate reefs · Western Australia

Introduction

Reef-associated fish assemblages respond to changes in environmental conditions with fluctuations in abundance at different spatial and temporal scales (Anderson and Millar 2004). Understanding the processes underlying such variability is a central aim of fish ecologists, and requires identifying the patterns of distribution and abundance of species over the spatial scales of interest. The physical structure of a reef is a key feature that determines

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the organisation of reef fish communities (see reviews by Jones and Syms 1998; Kingsford and Battershill 1998). Studies examining the distribution and abundance of fishes in relation to the habitat structure are particularly common from tropical coral reefs (e.g. Luckhurst and Luckhurst 1978; Letourneur 1996; Friedlander and Parrish 1998; Kuffner et al. 2007), while studies from temperate reefs are comparatively scarce (but see for example Choat and Ayling 1987; García-Charton and Pérez-Ruzafa 1998; Willis and Anderson 2003).

At temperate latitudes, there are two main attributes to the habitat structure of reefs: the presence of topographic elements and the predominance of various types of vegetation cover. The former, often called reef complexity or topography, incorporates elements such as boulders, crevices, cracks, whereas the latter, sometimes called heterogeneity, includes the array of discrete habitat patches (García-Charton and Pérez-Ruzafa 1998, 2001). Variation in both of these attributes alters biotic and abiotic processes, and hence influences patterns of distribution and abundance of temperate reef fishes (Ebeling and Hixon 1991; Levin 1994).

Temperate reefs are often covered by macroalgal canopies, which are punctuated by gaps of varying sizes, typically caused by physical disturbances, e.g. waves, grazing, etc. On temperate Australasian reefs, the main habitat is provided by laminarian (kelps) and fucalean canopy-forming algae, while smaller foliose red algae are interspersed in the gaps (Connell and Irving 2008). Changes in the physical structure of subtidal canopies alter environmental conditions (Wernberg et al. 2005) and biological processes, such as predation pressure (Roberts and Poore 2005), and so affect associated reef communities including fishes (Ebeling and Laur 1985; Anderson 1994; Willis and Anderson 2003). The establishment of a predictive relationship between macroalgal cover and the distribution and abundance of reef fishes remains, however, largely unexplored from many temperate coastal regions, south-western Australia in particular.

Labrids (family Labridae) are a common family of fishes inhabiting both tropical and temperate reefs (Helfman et al. 1997). Species of this family have been used as model organisms to determine the effect of different environmental processes on the ecology of reef fishes (Denny 2005). Labrids typically show little response to the presence of underwater observers, so visual counts are considered a reliable tool to assess their distribution and abundance patterns (Samoilys and Carlos 2000). In this study, we aimed to test, by means of underwater visual surveys, the effect of habitat structure at the scale of reefs (i.e. reef topography and algal cover) on the abundance patterns of labrid fishes across ~800 km of coastline in south-western Australia.

Methods

Sampling design and study locations

This study was conducted on wave-exposed rocky limestone reefs, between 8 to 12 m depth, at four evenly spaced locations encompassing a latitudinal gradient across south-western Australia (Fig. 1). Three reefs, all separated by at least 1 km, were randomly selected within each location, and visited on 4 occasions over 1 year: October 2006, March 2007, May–June 2007 and October 2007. All reefs were outside areas under any protection status (i.e. no-take areas), and were predominantly covered by macroalgae, primarily the small (< 1.5 m), canopy-forming, kelp *Ecklonia radiata*, and frondose fucalean algae (mostly the genera *Sargassum* and *Scytothalia*). Patches of small (generally < 25 cm) foliose red algae were interspersed between the larger stands of canopy-forming algae (see Wernberg et al. 2003 for a detailed description of floral assemblages). Although there is some variation in algal assemblage structure among these locations, the dominant (by size) components do not vary; for example, kelp density and biomass is similar among locations (Wernberg et al. 2009); this was confirmed by measurements in this study (see results).

Fish surveys

Labrids were sampled by visual censuses. Only adult and sub-adult fishes were censused to optimize the *in situ* identification of fishes. On each reef, 3 replicate 25 m transects were haphazardly surveyed during daylight hours. For each sampling period, transects were haphazardly placed on reefs. The abundance of fishes within 2 m of either side of each (100 m^2) transect was recorded on waterproof paper by a SCUBA diver. Concurrently, the diver counted

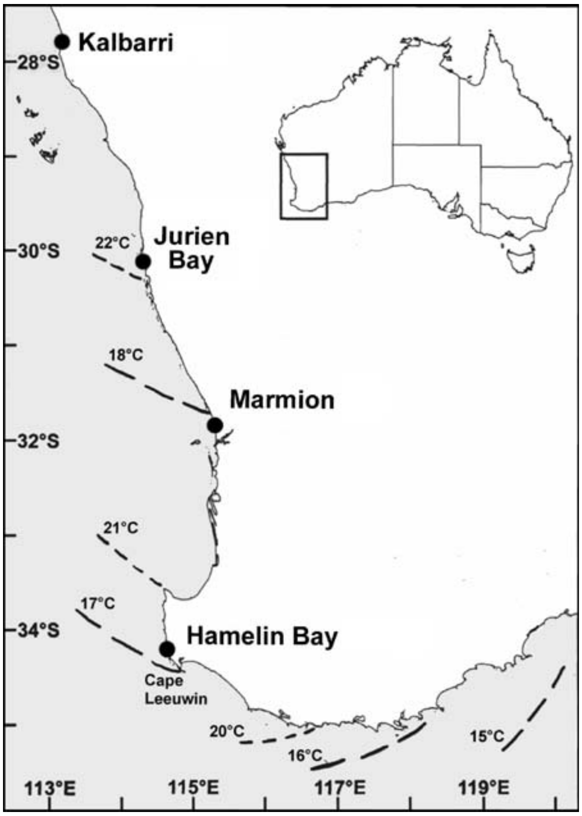


Fig. 1 Map of the study region showing sampling locations across south-western Australia

the number of large (>1 m) and small (<1 m) topographic elements of the rocky substrate (i.e. cracks, crevices, caves, holes per 100 m^{-2}), and visually estimated the percentage cover of kelp, fucalean algae, and red algae, following standardized procedures for the study region (Connell and Irving 2008).

Data analysis

We tested whether differences among locations in the structural elements of the habitat were consistent through sampling times with a 3-way ANOVA. The model incorporated the factors: (1) 'Locations' (fixed factor with four levels), (2) 'Times' (random factor with four levels, and orthogonal to 'Locations'), and (3) 'Reefs' (random factor nested within 'Locations'). Before analysis, Cochran's test was used to check for homogeneity of variances. No transformations were necessary as Cochran's test was non-significant ($P>0.01$) in all cases.

Multiple linear regressions tested whether the number of small and large topographic elements (100 m^{-2}), kelp cover, fucalean cover, or red algal cover affected abundances of each fish species across the study region. To retain variables with good explanatory power, the AIC routine was used as a selection criterion for each species (the smaller the value the better the model, Anderson and Legendre 1999), and the contribution of each independent variable to each model was described with partial r^2 values. Colinearity diagnoses among independent variables were carried out through Spearman-rank-correlations. All analyses were based on a 'forward' selection procedure. The number of small topographic elements (100 m^{-2}) and the percentage cover of red algae showed, in most cases, the largest contribution to variability in fish abundances (see results). Therefore, we plotted the mean abundance of each species per reef against each of these two variables to visualize patterns, and a correlation analysis (Pearson product-moment) tested the significance of these relationships. For each reef, data was pooled through times (see results). Species with<6% observed frequency of occurrence were omitted from the analysis.

Results

Differences in habitat structure among locations were consistent through time (Fig 2; Table 1, 'Loc x Times', $P>0.05$), and all locations had similar habitat structure (Fig. 2; Table 1, 'Locations', $P>0.05$), despite differences among reefs within locations were important (Table 1, 'Reefs (Loc)', $P<0.05$). Consequently, any biogeographical preference along the study region was not correlated with differences in habitat structure among locations to confound the interpretations of our results.

Six labrids (*Austrolabrus maculatus*, *Coris auricularis*, *Notolabrus parilus*, *Ophthalmolepis lineolata*, *Pictilabrus laticlavius* and *Pseudolabrus biseralis*) were observed regularly across the study region (> 20% of counts, Fig. 3a), while three species (*Bodianus axillaris*, *Choerodon rubescens* and *Thalassoma lutescens*) were only rarely censused (< 6%, Fig. 3a). These patterns of occurrence largely matched patterns of mean abundance of labrids across the study region (Fig. 3b).

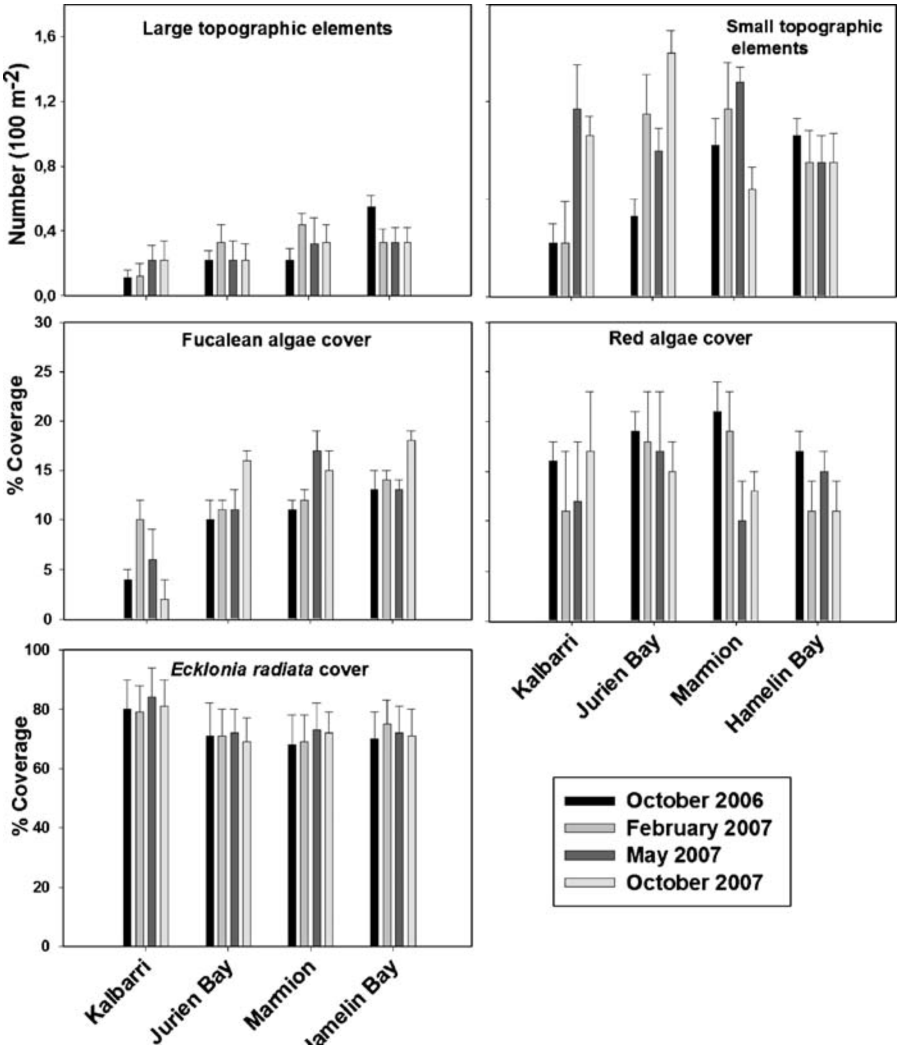


Fig. 2 Mean (+ SE) values of habitat attributes across the study region

Table 1 Results of ANOVA testing the effects of 'Locations' (fixed factor), (2) 'Times' (random factor orthogonal to 'Locations'), and (3) 'Reefs' (random factor nested within 'Locations') on the presence of structural elements of the habitat. Significant values are in bold ($P<0.05$)

Source	DF	Large topographic elements			Small topographic elements			Kelp cover			Fucalean cover			Red algal cover		
		MS	F	P	MS	F	P	MS	F	P	MS	F	P	MS	F	P
Locations=Loc	3	0.54	1.4	0.31	2.63	2.6	0.12	3659.89	5.25	0.06	3438.88	2.5	0.13	1424.24	4.18	0.08
Times=Ti	3	0.04	0.25	0.86	1.69	2.16	0.11	61.2847	1.9	0.1558	6.0185	0.48	0.69	43.6921	1.9	0.15
Reefs (Loc)	8	0.38	1.44	0.19	1.01	2.01	**0.05**	695.83	17.35	**0.0001**	1373.61	87.91	**0.0001**	340.1	15.43	**0.0001**
Loc x Ti	9	0.13	0.78	0.63	0.93	1.19	0.34	20.389	0.63	0.75	8.179	0.65	0.74	28.1057	1.22	0.32
Ti x Reefs (Loc)	24	0.17	0.65	0.88	0.78	1.54	0.07	32.175	0.8	0.72	12.5	0.8	0.72	22.9745	1.04	0.42
Residual	96	0.27			0.51			40.1			15.625			22.0486		

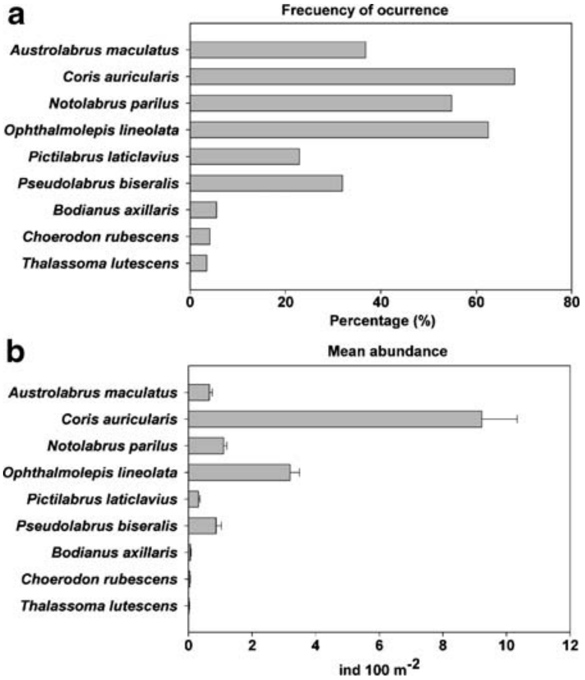


Fig. 3 **a** Frequency of occurrence and **b** mean abundance (+SE) of labrid fish species across south-western Australia

The cover of red algae and kelp were negatively correlated across the study region ($r_s = -0.43$, $P < 0.0001$), demonstrating colinearity between these two habitat features. For the majority of labrid species, the best model provided by the AIC routine included both the number of small topographic elements (100 m^{-2}) and the percentage of red algae cover (Table 2), i.e. patterns of abundance of labrids were, in most cases, affected by these two descriptors of the habitat. *Pseudolabrus biseralis* was the only species affected by the number of large topographic elements (100 m^{-2}) (Table 2).

Four species (*Coris auricularis*, Fig. 4b, *Notolabrus parilus*, Fig. 4c, *Ophthalmolepis lineolata*, Fig. 4d, and *Pseudolabrus biseralis*, Fig. 4f) showed a significant ($P<0.05$) increase in abundance with increasing number of small topographic elements (100 m^{-2}), i.e. all correlations were positive. All labrids, except *Austrolabrus maculatus*, increased significantly ($P<0.05$) in abundance with increasing cover of red algae (Fig. 5, all correlations were positive).

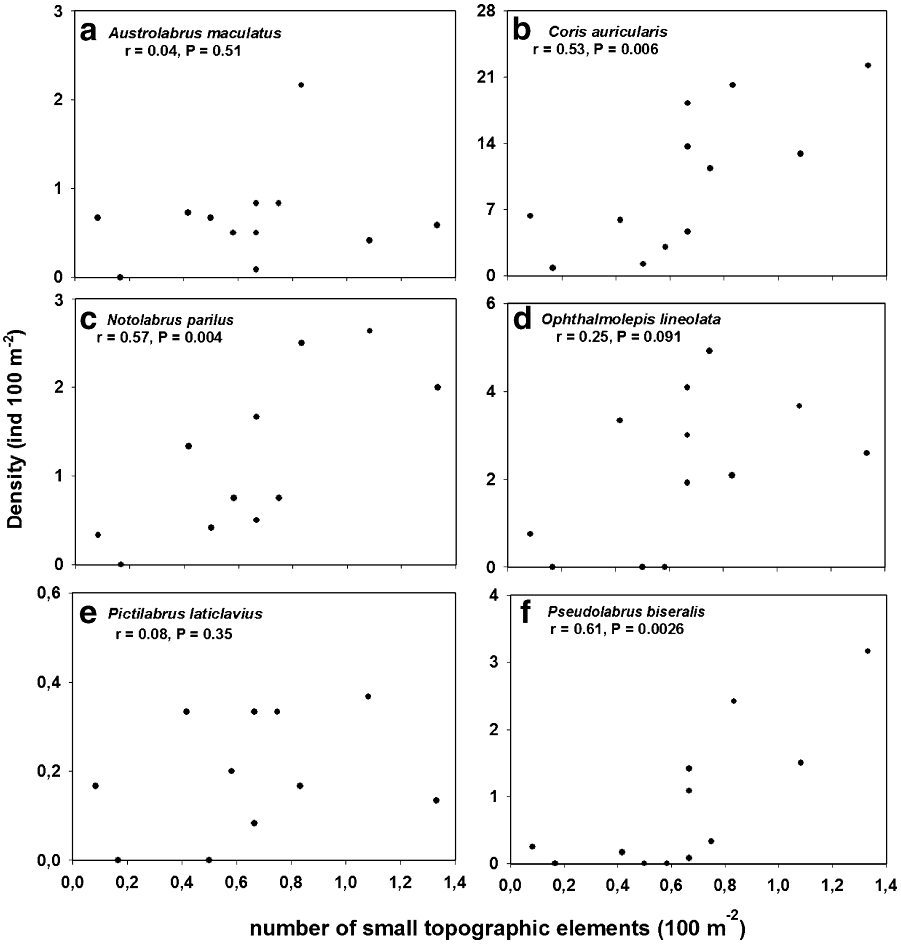
Discussion

This study has documented the importance of habitat structure to the spatial patterns of abundance of adult and sub-adult labrid fishes inhabiting rocky reefs in south-western Australia. We found consistent effects of habitat features on most labrid species across locations separated by hundreds of kilometres.

Table 2 Results of multiple linear regression analyses testing the relationship between the abundance of each labrid species and structural elements of the habitat. The AIC routine was used to retain variables with good explanatory power for each species. The contribution of each independent variable is described by means of partial r^2 values, and p-values provide significance diagnoses. For each species, the linear regression equation is provided, indicating standard regression coefficients for each independent variable

Austrolabrus maculatus		*Coris auricularis*		*Notalabrus parilus*		*Ophthalmolepis lineolata*		*Pictilabrus laticlavius*		*Pseudolabrus biseralis*	
X_1=Small topo. elements (p=0.013)	1.53e-02	X_1=Red algae cover (p=0.002)	3.22e-02	X_1=Red algae cover (p=0.001)	4.85e-02	X_1=Red algae cover (p=0.001)	1.36e-01	X_1=Red algae cover (p=0.001)	2.95e-01	X_1=Red algae cover (p=0.001)	4.42e-02
		X_2=Small topo. elements (p=0.014)	4.47e-02	X_2=Small topo. elements (p=0.004)	6.06e-02					X_2=Large topo. elements (p=0.02)	6.05e-02
										X_3=Small topo. elements (p=0.001)	7.69e-02
$Y=0.45+0.33*X_1$		$Y=2.65+0.29*X1+ 3.08* X_2$		$Y=0.22+0.048*X1+ 0.21* X_2$		$Y=2.22+0.06*X_1$		$Y=-0.04+ 0.023*X_1$		$Y=-0.46+0.058*X_1+ 0.59*X_2+0.34*X_3$	

Fig. 4 Relationship between the number of small topographic elements (100 m^{-2}) and the abundance of the 6 most abundant labrid species (data for each reef were averaged based on 4 sampling times and 3 transect replicates)



Temperate-reef labrids are usually generalists that forage on a wide array of resources, enabling different species to co-exist with little antagonism (Denny 2005). In the study region, most labrids feed on small epiphytal invertebrates (MacArthur and Hyndes 2007; R. K. Howard, unpublished data; E. Lek, unpublished data), while similar labrids inhabiting other Australasian temperate reefs tend to prey on benthic invertebrates as well (Denny and Schiel 2001).

Variation in habitat structure has been highlighted as a key factor influencing the spatial variability of reef fish assemblages (i.e. Luckhurst and Luckhurst 1978; Friedlander and Parrish 1998; García-Charton and Pérez-Ruzafa 2001). We found a general increase in the abundance of labrid species with an increase in the presence of small topographic elements, e.g. cracks, caves, holes <1 m. Similar results have been reported for the richness, abundance and biomass of reef fish assemblages from other temperate latitudes (García-Charton and Pérez-Ruzafa 1998, 2001). For example, in the Mediterranean, those locations where the number of small boulders (diameter <1 m) was large had larger abundances of some labrids (e.g. *Labrus merula*, *Labrus viridis* and *Symphodus tinca*) relative to rocky bottoms without boulders (Ordines et al. 2005). Such increases in the diversity, abundance and biomass of fish assemblages have been suggested to rely upon different mechanisms; for instance, by enhancing shelter opportunities and hence protection against predators (Hixon and Beets 1993), and an increase in the number of microhabitats per area (García-Charton and Pérez-Ruzafa 1998), which may facilitate the access to feeding resources.

In our study, two main mechanisms can explain why labrid species tend to concentrate in and around these structural elements. First, small topographic elements (i.e. small cracks, crevices, holes, etc.) may provide protection against large-sized predators, such as *Glaucosoma hebraicum, Ephinephelides armatus*, *Othos dentex, Orectolobus maculatus*, which are

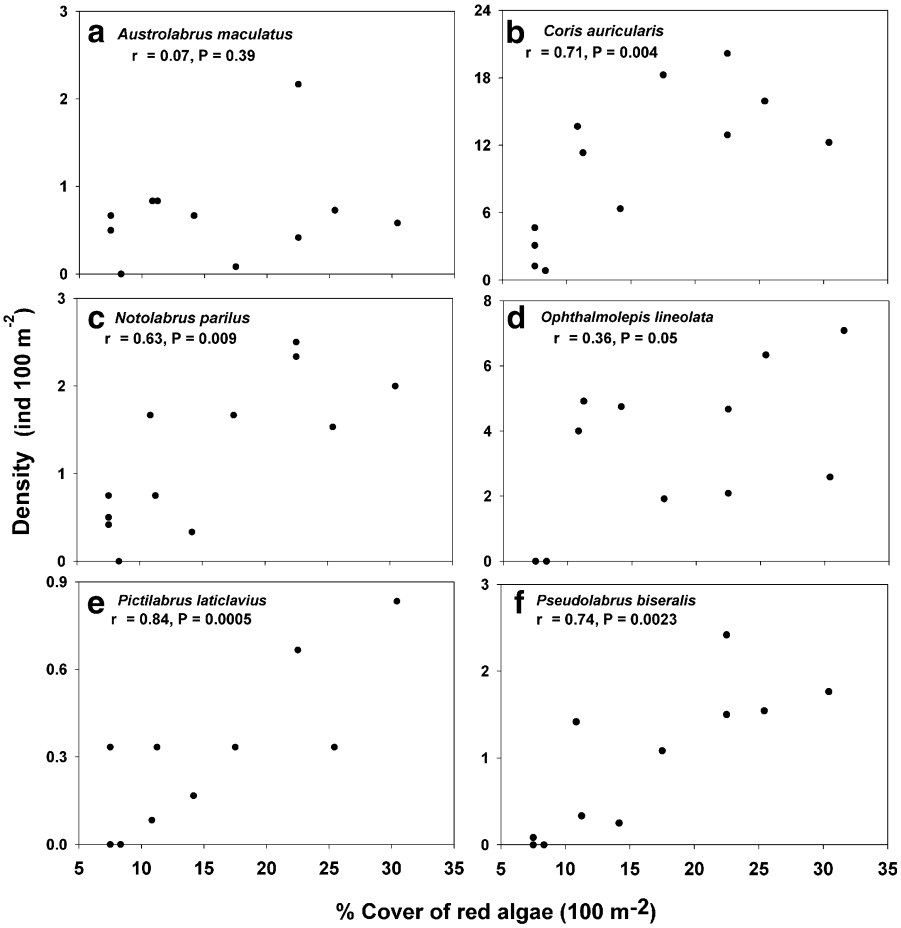


Fig. 5 Relationship between the percentage cover of red algae and the abundance of the 6 most abundant labrid species (data for each reef were averaged based on 4 sampling times and 3 transect replicates)

typically found on reefs across the study area (Kendrick 1999; Kleczkowski et al. 2008). Second, these topographic elements provide a range of microhabitats for potential prey items of labrids such as decapod crustaceans (Edgar 2000) and echinoderms (Vanderklift and Kendrick 2004). Those two species that did not show a significant increase in their abundances with increasing number of small topographic elements (*Austrolabrus maculatus* and *Pictilabrus laticlavius*) were the least abundant species across the study region (of the six test-species). Hence, it is likely that low test power could be responsible for the lack of correlation. Interestingly, the abundance of labrids was, however, not related to the presence of large topographic elements (excepting *Pseudolabrus biseralis*). These large topographic elements tend to concentrate large predatory fishes in the study region (e.g. *Glaucosoma hebraicum*, *Ephinephelides armatus*, *Othos dentex*, *Orectolobus maculatus*, personal observation), and so a potential increase in predation, and/or predation risk, could explain the lack of correlation with these structural elements.

Food and shelter provided by macroalgae are important resources for temperate reef fishes (Anderson and Millar 2004), although disentangling the relative importance of food versus shelter may be difficult. In our study, heterogeneity within macroalgal habitats generally promoted labrid abundances; reefs with medium-to-high cover of red algal patches (15–20%) had larger abundances of labrids than reefs dominated exclusively by kelps (i.e. those where the cover of red algae was <10%). Patches of small foliose algae interspersed within kelp patches might facilitate access to invertebrate prey (Levin 1994), and thus affect patterns of abundance of temperate reef fishes (Wellenreuther and Connell 2002). For example, larger numbers of potential prey, such as prosobranch gastropods, are associated with red algal stands relative to both kelp and fucalean canopies in the study region (Tuya et al. 2008).

In summary, at the scale of reefs, patterns of abundance of adult, and sub-adult, labrid fishes were consistently affected by the structure of the habitat across south-western Australian limestone reefs. A trade-off between prey accessibility and predation risk is a likely ecological mechanism behind the observed patterns.

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