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Testing the 'abundant centre' hypothesis on endemic reef fishes in south-western Australia

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ABSTRACT: The abundance of a species is generally expected to peak at the centre of its distribution range and decline towards the range limits. Empirical evidence for such 'abundant centre' patterns is, however, limited, particularly for subtidal species. We tested the 'abundant centre' hypothesis for 8 fish species endemic to the shallow rocky reefs of south-western Australia. Fish abundances were quantified at 6 locations (18 reefs) across ca. 1700 km of coastline, and patterns of distribution were determined by testing the goodness of fit of 3 biogeographical models: (1) 'normal' (i.e. 'abundant centre' distributions), (2) 'ramped' (increase in abundance towards one of the distributional limits), and (3) 'skewed normal' (skewed 'abundant centre' distributions). Two species had their maximum abundances at the centre of their ranges ('normal' patterns), while one species had its highest abundance near its south-eastern range limit ('skewed normal' pattern). Two species increased progressively in abundances towards their south-eastern range limits ('ramped' patterns), and 3 species showed no apparent patterns across their distribution ranges. Consequently, the expectation that species are most abundant at the centre of their ranges was not supported as a general model by the present study.

KEY WORDS: 'Abundant centre' patterns · Macroecology · Biogeography · Species ranges · Reef fishes · Western Australia

INTRODUCTION

Ecological and evolutionary models, such as the spread of a species from its point of origin or optimal fitness associated with favorable environmental conditions, lead to the expectation that the abundance of a species peaks at its centre of distribution and declines towards its range limits (Brown 1984, 1995). This pattern was first quantified by Whittaker (1956) in his classic studies of the distribution of plants on mountains and is now known as the 'abundant centre' hypothesis (Sagarin et al. 2006, Samis & Eckert 2007). The hypothesis has general implications for several relevant issues in ecology, such as whether the spatial variation in abundance reflects the extent to which local sites satisfy the niche requirements of a species (Brown et al. 1995) and how global warming will affect the geographical distribution of species (Root et al. 2003).

Empirical evidence for abundant centre patterns is, however, limited: Sagarin & Gaines (2002a) found that only 39% of individual tests supported the hypothesis, presumably because abrupt changes in one or more limiting niche variables (either biotic or abiotic conditions) can cause rapid shifts in abundances and so preclude abundant centre patterns (Brown 1984).

Most tests of abundant centre patterns have focused on terrestrial species (Sagarin & Gaines 2002a); in marine systems, studies have largely been limited to

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intertidal invertebrates, mostly gastropods (Sagarin & Gaines 2002b, Defeo & Cardoso 2004, Sorte & Hofmann 2004, Gilman 2005, 2006), with a clear lack of tests of the abundant centre hypothesis for subtidal species. To rigorously test for abundant centre patterns, the complete distribution range of a species must be quantified (Sagarin & Gaines 2002a). Intertidal invertebrates with ca. 1-dimensional geographic distributions are ideal candidates to test for abundant centre patterns: they inhabit a strip of the coast, and their ranges are determined by 2 geographical limits (Sagarin & Gaines 2002b). In contrast, most subtidal animals (e.g. reef fishes) have broad 3-dimensional distributions. However, subtidal species with well-defined, restricted distribution ranges, mostly endemic to a particular land mass, can also be suitable organisms to test for abundant centre patterns, especially those limited to a narrow depth range.

Western Australia is one of 18 major centres of endemism of the world's reefs (Roberts et al. 2002). The south-west region, from Shark Bay to The Reserche Archipelago (Fig. 1), is a transition zone between the Damperian (tropical) and Flindersian (temperate) biogeographical provinces. The high species diversity and endemism of the region (e.g. seagrasses, Kirkman & Walker 1989; macroalgae, Phillips 2001; and demersal fishes, Williams et al. 2001) are largely attributed to a long period of isolation from other continents (ca. 80 million yr), the moderating influence of the warm Leeuwin Current over the past ca. 50 million yr, and the lack of mass extinctions associated with unfavorable conditions, such as glaciations, over the recent geological past (Phillips 2001). In the present study, we tested the abundant centre hypothesis for shallow-water reef fishes endemic to south-western Australia by describing patterns in abundance across this region.

MATERIALS AND METHODS

Sampling. We focused on demersal fish species endemic to the coastal shallow rocky reefs of south-western Australia. Based on previous observations, 8 species (Table 1) were found to be censused efficiently by means of underwater visual counts (e.g. cryptic species or those showing diver-avoiding behaviours were excluded). The abundance of the selected species was studied at 6 locations (4 in the Indian Ocean and 2 in the Southern Ocean) across ca. 1700 km of coastline (Fig. 1). The 2 most distant locations, Kalbarri to the north and Esperance to the south-east, were selected as close as possible to the region edges. Large cliffs extend from Kalbarri to Shark Bay; subtidal sampling is extremely difficult, and this has resulted in a 'gap' in the exact northernmost limit for some species (Table 1). We randomly selected 3 reefs, all separated by >1 km, within each location. All reefs had a similar vertical relief in order to minimize the effect of habitat structure on the distribution and abundances of fishes. This was confirmed by subsequent measurements which did not find differences among locations using 2 common descriptors of rocky reef topography: the number of large (>1 m) and small (<1 m) topographic elements per 100 m^{-2} ($F_{5,12}$ = 1.43, p = 0.28 and $F_{5,12}$ = 0.69, p = 0.63, respectively). Depths varied between 6 and 12 m. Reefs were predominantly covered by macroalgae (primarily the kelp *Ecklonia radiata* and fucalean algae) and were outside areas under fishing restrictions. Sampling was carried out during austral spring to early summer 2007 by the same experienced observer. During daylight hours, a SCUBA diver recorded the abundance of adult and sub-adult fishes within 2 m of either side of each 25 m transect (n = 3 transects per reef).

Data analysis. The relative mean abundance of each species at each location was calculated by dividing

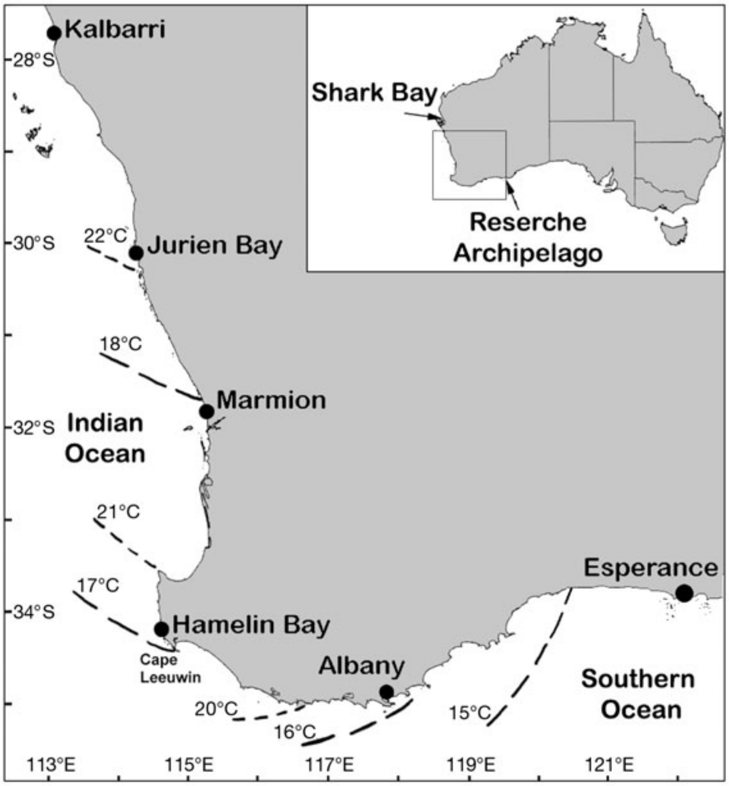

Fig. 1. Study locations across south-western Australia. Summer (short dash) and winter (long dash) surface isotherms are indicated (adapted from Pearce 1991)

Table 1. List of selected endemic reef fishes in shallow waters of south-western Australia. Information on distributional ranges and models describing patterns of distribution in their relative mean abundances (see also Fig. 2) are indicated for each species. Total and mean abundances are also indicated for the overall study. Species' ranges were obtained from the Food and Agriculture Organization (FAO) species catalogues, Edgar (2000) and Kuiter (1996); Reserche Archipelago was the south-eastern range limit for all species. Goodness of fit tests provided p-values to examine the appropriateness of each distributional model. Selected models are in bold

Species	Common name	Family	Northern range limit	Total ind.	Mean ± SE 100 m^{-2}	Model of distribution	R^2 (p-value)
Aplodactylus westralis	Western seacarp	Aplodactylidae	Marmion	8	0.14 ± 0.07	Normal	0.65 (0.99)
						Skewed normal	0.63 (0.99)
						Ramped	0.23 (0.5150)
Chromis klunzingeri	Black-head puller	Pomacentridae	Between Shark Bay and Kalbarri	372	6.88 ± 3.21	Normal	0.96 (0.0076)
						Skewed normal	**0.98 (0.0058)**
						Ramped	0.0587
Ephinephelides armatus	Breacksea cod	Serranidae	Between Shark Bay and Kalbarri	18	0.33 ± 0.09	Normal	**0.99 (0.0009)**
						Skewed normal	0.98 (0.0014)
						Ramped	0.30 (0.2530)
Girella tephraeops	Western rock blackfish	Girellidae	Between Shark Bay and Kalbarri	12	0.22 ± 0.16	Normal	0.61 (0.76)
						Skewed normal	0.00 (1.00)
						Ramped	**0.71 (0.0333)**
Glaucosoma hebraicum	West Australian dhufish	Glaucosomatidae	Between Shark Bay and Kalbarri	6	0.11 ± 0.08	Normal	0.54 (0.3047)
						Skewed normal	0.54 (0.5953)
						Ramped	0.045 (0.8990)
Hypoplectrodes cardinalis	Red sea perch	Serranidae	Jurien Bay	9	0.16 ± 0.11	Normal	0.33 (0.9273)
						Skewed normal	0.32 (0.9139)
						Ramped	0.10 (0.5922)
Parma mccullochi	McCulloch's scalyfin	Pomacentridae	Between Shark Bay and Kalbarri	118	2.18 ± 0.29	Normal	**0.82 (0.0735)**
						Skewed normal	0.77 (0.095)
						Ramped	0.005 (0.8876)
Pseudolabrus biseralis	Red-band wrasse	Labridae	Between Shark Bay and Kalbarri	61	1.12 ± 0.16	Normal	0.54 (0.3108)
						Skewed normal	0.00 (1.00)
						Ramped	**0.57 (0.0823)**

mean abundances per location (n = 9) by the maximum abundance recorded at any reef throughout the region. Locations were converted to Range Indices (RI) to standardize their positions within the region:

$$RI = 2(L - S)/R$$

where L is the position (i.e. the distance in km) of a location relative to the northern range limit (e.g. Kalbarri for 6 species), S is the midpoint (in km) of the geographical range, and R is the extent of the geographical range (km). This index ranges from –1 to 1; values near 0 indicate that the sample was near the centre of the range, and values near +1 or –1 indicate that the sample was near the northern or south-eastern limit of its range, respectively.

Patterns of distribution in abundance of reef fishes across their distributional ranges were determined by testing the goodness of fit of 2 biogeographical models (e.g. Sagarin & Gaines 2002b): 'normal' (e.g. abundant centre distributions) and 'ramped' (increase in abundance towards either the northern or south-eastern limit). Species abundances can, however, peak away from the distributional range centre (Brown 1995) and decrease (sometimes sharply) towards their range limits. This is particularly likely in subtidal organisms, such as reef fishes, as a result of irregular dispersion of pelagic larvae over long distances (Kinlan et al. 2005). Therefore, we additionally considered a skewed normal model (i.e. skewed abundant centre distributions); this model is not functionally different from a normal model and represents a practical extension of abundant centre patterns.

Regression models were fitted following a Gaussian (normal), a Weibull (skewed normal), and a linear (ramped) approach. Goodness of fit tests provided p-values to examine the appropriateness of each model for each species, and R^2 values were used to select the most appropriate model.

RESULTS

Relative mean abundances varied among locations for all 8 fish species (Fig. 2). Two species had maximum

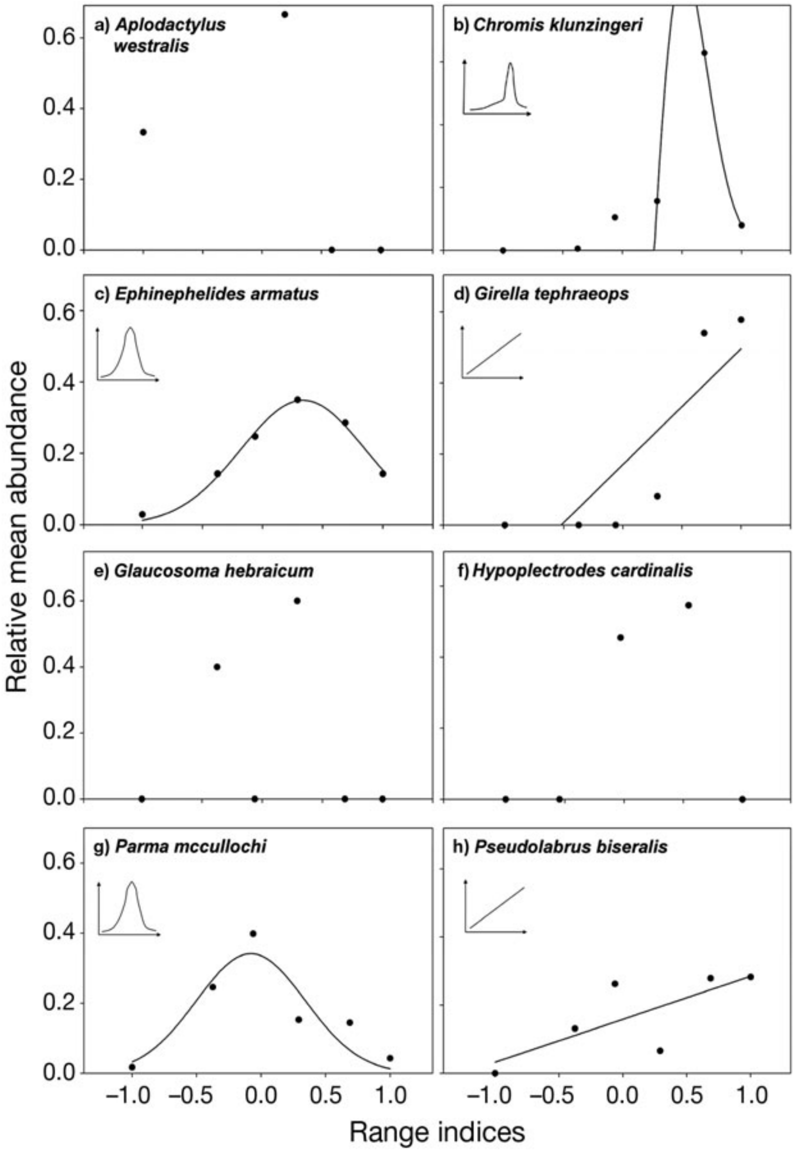

Fig. 2. Mean abundance of 8 species of reef fish endemic to south-western Australia. The inset representing 1 of the 3 distributional models (in b, c, d, g, and h) indicates a significant fit to the depicted model (see Table 1 for p-values associated to goodness of fit tests). Geographic position (*x*-axis) and abundances (*y*-axis) are relativized (see 'Materials and methods'). Geographic position is expressed on a scale from −1 (south-eastern limit) to +1 (northern limit)

mean abundances at the centre of their ranges (normal distribution; Fig. 2c,g, Table 1), and 1 species had higher abundance near its south-eastern range limit (skewed normal distribution; Fig. 2b, Table 1); 2 species increased their mean abundances progressively towards their south-eastern range limits (ramped distributions; Fig. 2d,h, Table 1); and 3 species showed no pattern consistent with the biogeographical models tested across their distributional ranges (Fig. 2a,e,f, Table 1).

DISCUSSION

Endemic reef fishes from south-western Australia displayed variable patterns of abundance across their distribution ranges, a pattern largely consistent with observations from terrestrial animals (Brown et al. 1996). Consequently, the abundant centre hypothesis was not supported as a general model for this group of organisms by the present study. Similar results have been found for many plants and animals in different ecosystems elsewhere in the world (reviewed by Sagarin & Gaines 2002a, Sagarin et al. 2006). In fact, most of these studies support some alternative pattern of distribution of abundance to the abundant centre hypothesis. For example, abundances of some species have been shown to decline consistently from one limit of their range to the other, i.e. ramped distributions (Ferguson & McLoughlin 2000, Sagarin & Gaines 2002b, *Girella tephraeops* and *Pseudolabrus biseralis* in the present study).

Ranges are typically species-specific and determined by multiple factors (Brown et al. 1995, Samis & Eckert 2007); the size, shape and internal structure of ranges reflect the interacting influences of limiting environmental factors (niche variables) and dispersal/ extinction dynamics (Brown et al. 1996). For example, evolutionary history, including dispersal from centers of endemism and environmental gradients, may explain some biogeographic patterns (Brown 1995). Clines in climate, resource availability, and biotic factors (e.g. predation, competition, facilitation, recruitment success) often explain patterns where abundances are lower at one range limit compared to the centre or the other limit (Gilman 2005, 2006, Samis & Eckert 2007). In our case, seawater temperature could explain some of the observed macroecological patterns. There is a gradual temperature gradient of 4 to 5°C from Kalbarri in the Indian Ocean to Esperance in the Southern Ocean (Pearce 1991, Fig. 1), and depending on the physiological tolerances of an individual species, this could increase (or limit) the ecological performance of a species (Gilman 2006). However, other environmental and biotic factors also change along this transition. For example, limestone reefs are progressively replaced by granite reefs from Hamelin Bay to Esperance (Sanderson et al. 2000), and there is a shift in the major algal habitats, with a decline in the dominance of the mono-specific kelp *Ecklonia radiata* beds and a matching increase in the dominance of fucalean algae (Wernberg et al. 2003). A local-scale study from Hamelin Bay showed that reef fish assemblages differed between kelp-dominated limestone reefs and fucalean-dominated granite reefs (Harman et al. 2003). Obviously, the peculiarities of each species also play a key role in their response to these (and maybe other) factors; each species has a unique ecological niche, a set of environmental variables that affect abundance and distribution (Brown et al. 1996). For example, the 2 south-east ramped species identified in the present study (*Girella tephraeops* and *Pseudolabrus biseralis*) belong to fish genera exclusively found in the temperate waters of Australasia and seem particularly adapted to the environmental conditions of the Southern Ocean.

Human perturbations may also interrupt species' distributions and abundances (Channell & Lomolino 2000). For example, the West Australian dhufish *Glaucosoma hebraicum* is a highly priced reef fish in Western Australia that is extensively targeted by recreational fishermen (Kleczkowski et al. 2008). The lack of individuals of this species in Marmion (i.e. the centre of its distributional range) is likely a consequence of the proximity to Perth, the only major metropolitan area on the Australian west coast, where there is a massive fishing effort for this species year-round relative to the other locations (Western Australia Department of Fisheries 2008). Large differences in the abundance of this species between sanctuary and non- sanctuary areas have been observed in south-western Australia in contrast to other fish species such as *Ephinephelides armatus* and *Pseudolabrus biseralis* (Kleczkowski et al. 2008), and this supports the idea that fishing pressure may mask the existence of an abundant centre pattern for this species.

No model described patterns for *Aplodactylus westralis* and *Hypoplectrodes cardinalis*. The northern limit of these 2 species is located south of Kalbarri, where the other 6 species have their northernmost range limit. This resulted in a lower number of locations sampled (4 and 5, respectively) and thus in a decrease in the power to detect significant patterns. It is possible that increasing the number of locations within these 2 species' ranges could have resulted in the detection of significant patterns. It is also plausible that the rarity of these 2 species (<10 individuals were observed across the study region) could have obscured, even more, the detection of significant patterns, and so prevented any inference to be drawn about the hypothesis. We therefore recommend increasing the level of within-reef replication (i.e. sample sizes) in future studies as a way to minimize this limitation.

For all studied species, we cannot rule out the possibility that species ranges are larger than currently known, and so patterns of species abundances could change if 1 or 2 additional locations were sampled outside the study area. In this sense, we recommend the addition of extra points outside the known species ranges as a way to increase the reliability of similar analyses in future studies.

In summary, endemic reef fishes of south-western Australia showed various geographical patterns in the distribution of their abundances, and abundant centre patterns were not more prominent than alternative patterns. Inconsistent results among different species and systems provide only weak support for the abundant centre model as a universal rule.

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