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Australia's marine biogeography revisited: Back to the future?

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Abstract The recognition of broad biogeographic provinces provides an important framework for ecological and conservation biological research. Marine biologists have long recognized distinct biogeographic provinces in southern Australia, primarily on the basis of qualitative differences in intertidal species assemblages. Here we provide an *a priori* test for these traditional eastern (Peronian), western (Flindersian) and south-eastern (Maugean) provinces. Specifically, we analyse distributional data for approximately 1500 algal species using the newly available Australian Virtual Herbarium, an online database of herbarium specimens. Our quantitative algal analyses across southern Australia identify three distinct biogeographic assemblages, consistent with traditional qualitative provinces. We argue that these broad provinces provide a highly effective framework for understanding and managing Australia's marine biodiversity. In particular, biogeographic provinces provide a regional framework for integrating the ongoing discovery of biological variation at finer scales. More broadly therefore we recommend that biologists undertake quantitative analyses to test provincial biogeographic boundaries around the globe.

Key words: Australia, bioregion, macroalgae, marine biogeography, phylogeography, province, seaweed, subtidal.

INTRODUCTION

The recognition of broad geographic trends in biodiversity can provide valuable frameworks for biological research across a range of ecological and evolutionary disciplines (e.g. Wallace 1876; Udvardy 1975; Olson *et al*. 2001). For instance, description of biogeographic provinces can provide a basis for establishing representative reserve systems for conservation (Olson *et al*. 2001; Spalding *et al*. 2007). In terms of marine biodiversity, however, recognition of distinct provinces has typically relied on qualitative rather than quantitative analyses of regional biogeographic pattern (e.g. Briggs 1995; Spalding *et al*. 2007).

Australia's expansive (approx. 6000 km) southern coastline exhibits substantial biogeographic differentiation, as recognized by a host of marine biological studies over the last 75 years (e.g. Whitley 1932; Bennett & Pope 1953, 1960; Womersley & Edmonds 1958; Knox 1963, 1980; Dartnall 1974; Rowe & Vail 1982; Wilson & Allen 1987; Lyne & Last 1996). Many of these traditional marine biological studies recognize broad biogeographic provinces: Peronian (east), Flindersian (west) and Maugean (south-east) (*sensu* Bennett & Pope 1953) (Fig. 1). However, initial recognition of these provinces rested on qualitative analyses of a small number of taxa, with a strong emphasis on easily recognizable macroalgae and intertidal molluscs.

Recent quantitative biogeographic (Sanderson 1997; O'Hara & Poore 2000), phylogeographic (Waters & Roy 2003; Waters *et al.* 2004; Waters 2008; Ayre *et al.* 2009; Fraser *et al.* 2009) and ecological (Irving *et al.* 2004; Connell & Irving 2008) studies have supported the existence of broad east–west differentiation across southern Australia. Although the biogeographic analyses of O'Hara and Poore (2000)

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incorporated a large number of crustacean and echinoderm taxa, they did not explicitly test for the existence of traditionally recognized provinces. Additionally, many recent genetic studies have assessed small numbers of lineages (Waters & Roy 2003; Waters *et al.* 2004; Waters 2008; Ayre *et al.* 2009; Fraser *et al.* 2009), and thus may have limited biogeographic generality.

Southern Australia is characterized by exceptionally diverse benthic macroalgal communities (Phillips 2001; Kerswell 2006) with approximately 1500 species recognized from its temperate waters (Wernberg *et al.* in prep.). Estimated levels of regional endemicity per phylum range from 40% (Chlorophyta) to 77% (Rhodophyta) (Phillips 2001). The recent development of the Australian Virtual Herbarium (AVH) provides online access to all plant specimens deposited in Australia's seven major public herbaria (as of June 2008, over 75 000 marine macroalgal records). This database presents an ideal tool for studying broad marine biogeographic patterns across southern Australia. In the present study we use this macroalgal database to provide a quantitative test of classical provinces described for southern Australia. Specifically, we provide an *a priori* test for the existence of Bennett and Pope's (1953, 1960) Maugean, Flindersian and Peronian biogeographic provinces.

METHODS

A custom-built data matrix was created based on all marine temperate macroalgal species (Chlorophyta, Phaeophyta and Rhodophyta) currently recorded in the AVH (http://www.sapac.edu.au/avh/). Presence and absence values (1 or 0, respectively) were assigned to 21 distinct 'bioregions': geographical regions defined by the National Marine Bioregionalisation of Australia (Commonwealth of Australia 2005; Appendix I). These mesoscale bioregions are also known as Integrated Marine and Coastal Biogeographic Regionalisation of Australia (IMCRA) bioregions, originally designed as marine management units based on geomorphology, oceanography and fish assemblages. For our study, the 25 IMCRA bioregions were reduced to 21 by pooling three South Australian Gulf bioregions into a single bioregion and, similarly, by pooling three Bass Strait bioregions into a single bioregion (Appendix I). Marine temperate Australia was defined as the area extending south from 27°30′S, 114°30′E on the west coast (northern end of the Central West Coast IMCRA bioregion) to 30°30′S, 153°E on the east coast (northern end of the Manning Shelf IMCRA bioregion) (Fig. 1). Within this region there are approximately 76 800 macroalgal records in the AVH. These records correspond to all Australian macroalgal vouchers deposited in major Australian herbaria (Adelaide, Brisbane, Canberra, Hobart, Melbourne, Darwin, Perth) as of 20 June 2008. The New South Wales (NSW) algal collection and the Melbourne crustose coralline red algae collection were not included in the AVH at the time of this analysis. These exclusions are unlikely to have influenced our interpretations because collections of these taxa are held in the included herbaria, and their inclusion would predominantly add rare species with an east coast affinity, which would further strengthen the potential distinctiveness of eastern flora.

After careful taxonomical revision the final data matrix was composed of 1487 species and 21 IMCRA bioregions (Appendix I). The final number of taxa corresponds to the estimated total number of macroalgal species known from the temperate Australian coast. Bray-Curtis dissimilarities were calculated from presence–absence data of macroalgal species within each bioregion. Constrained ordination by canonical analysis of principal coordinates (CAP) was used to visualize dissimilarity patterns among regions. Multivariate analysis of variance by permutation (PERMANOVA), followed by pairwise comparisons, tested if algal assemblages grouped IMCRA bioregions according to the three classical biogeographic provinces of temperate Australia (Fig. 1). The degree of multivariate dispersion within the biogeographical

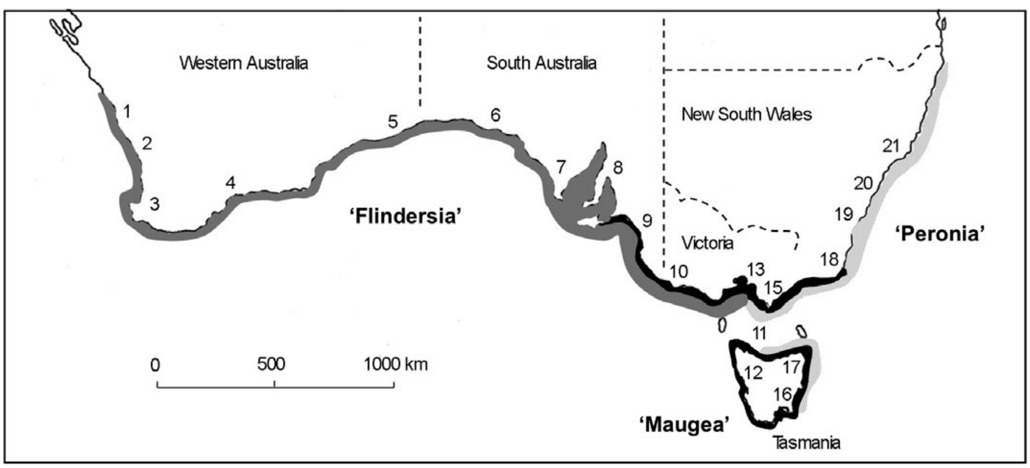

Fig. 1. Map of temperate Australia showing classical Flindersian (dark grey), Maugean (black) and Peronian (light grey) biogeographic provinces of Bennett and Pope (1953). Numbers 1–21 represent Integrated Marine and Coastal Biogeographic Regionalisation of Australia bioregions based on the Commonwealth of Australia (2005) (see Appendix I).

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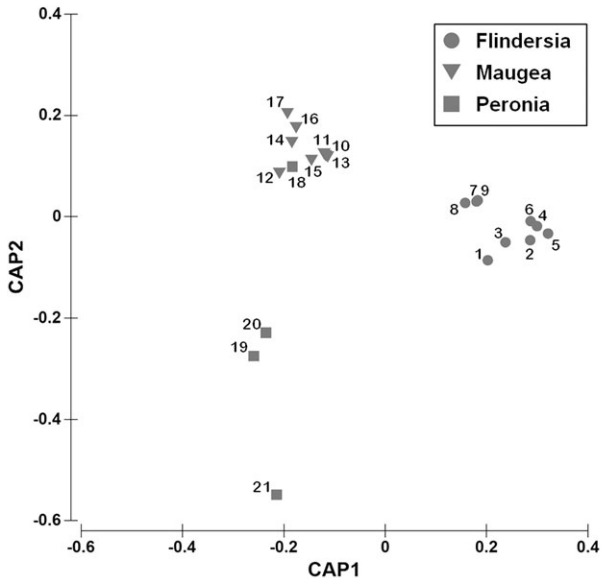

Fig. 2. Constrained ordination by canonical analysis of principal coordinates (CAP) of macroalgal assemblages along the temperate coastline of Australia. Numbers 1–21 represent Integrated Marine and Coastal Biogeographic Regionalisation of Australia bioregions based on the Commonwealth of Australia (2005) (see Appendix I).

provinces was tested with PERMDISP to test for potential differences in assemblage variability between regions. Technical details on the multivariate methods can be found in Anderson *et al.* (2008).

RESULTS

Algal assemblages grouped the 21 Australian IMCRA bioregions into clusters consistent with the classical biogeographic provinces (Fig. 2, PERMANOVA, *pseudo*-$F_{2,18} = 4.97$, $P = 0.001$). The Flindersian, Maugean and Peronian provinces all had distinct algal floras (pairwise comparisons, $P < 0.008$), but the Flindersian province differed more from the Maugean province ($t = 2.52$) and the Peronian province ($t = 2.35$) than these provinces differed from one another ($t = 1.70$). Lack of differences in dispersion of assemblage centroids (PERMDISP, $F_{2,18} = 1.44$, $P = 0.437$) showed that the distinctiveness of the three provinces represented differences in the identities of species among provinces, rather than the degree of spatial variation within provinces.

Although our data support the traditional provinces, they also suggest that the Maugean province extends north to southern NSW (IMCRA bioregion 18; Figs 1,2). In addition, our results indicate that the Maugean–Flindersian provincial boundary lies in western Victoria (between IMCRA bioregions 9 and 10; Fig. 1). These findings represent minor refinements of Bennett and Pope's (1953, 1960) province boundaries.

DISCUSSION

Our detailed biogeographic analyses of 1487 macroalgal taxa provide clear support for the three traditionally recognized broad marine biogeographic provinces in southern Australia. Specifically, our analyses validate Bennett and Pope's (1953, 1960) classic descriptions of Peronian (east), Flindersian (west) and Maugean (south-east) provinces (see also Womersley & Edmonds 1958), qualitative patterns identified on the basis of a relatively small number of coastal taxa. Consequently, even though Bennett and Pope's studies incorporated only a small fraction of Australia's algal diversity, they nevertheless yielded important general patterns. Their cool-water Maugean province, for instance, was characterized by high abundances of *Durvillaea potatorum*, *Lithophyllum hyperellum* and *Cystophora torulosa*, species absent from warmer waters of the Peronian and Flindersian regions. Additional 'Maugean' taxa include *Xiphophora gladiata*, *Lessonia corrugata* and *Macrocystis.* Most of these cool-temperate macroalgal taxa also occur in New Zealand.

As the qualitative intertidal provinces originally described by Bennett and Pope apparently have broad biogeographic relevance – and explanatory power – it may be timely to reconsider the status of the numerous apparently distinct southern IMCRA bioregions more recently proposed by the Commonwealth of Australia (2005) (see also Lyne & Last 1996). These studies partitioned Australia's temperate waters into 25 distinct mesoscale bioregions, defined on the basis of both biotic (e.g. demersal fish distributions) and abiotic (geomorphic features, bathymetry, geostrophic currents, sea surface height) features. However, there is an increasing awareness that broad biogeographic provinces based on large numbers of taxa 'reflect the distributions of species and communities more accurately than do units based on . . . models derived from gross biophysical features' (Spalding *et al.* 2007). As a result, the broad biological relevance of these IMCRA bioregions remains unclear. Indeed, given the congruent findings of Bennett and Pope (1953) and the present study, a question remains concerning the relative effectiveness of the IMCRA studies for defining regional biodiversity and shaping conservation policy (see Phillips 1998). Specifically, it could be argued that these more recent studies are less able to inform our biological understanding of Australia's marine ecosystems. Moreover, we suggest that the incorporation of a hierarchical regional approach (i.e. not all IMCRA regions are 'equal') would aid in the recognition and conservation of Australia's marine biodiversity.

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In addition to the broad differentiation observed in macroalgal species composition, recent studies have documented congruent ecological variation across southern Australia (reviewed by Connell & Irving 2009). Flindersian coasts, for example, have higher kelp forest cover – and higher kelp forest heterogeneity – relative to Peronian coasts (Connell & Irving 2008). Indeed, the *Centrostephanus* (urchin)-mediated barrens that characterize Peronian coasts are not recorded from the Flindersian province. These major regional differences are also consistent with the east–west biogeographic split delineated by the historic bassian isthmus (a palaeogeographic barrier) and maintained by contemporary oceanographic currents (Waters 2008; Wernberg *et al*. in prep.). Along with biotic differences, Flindersian and Peronian coasts also differ substantially in their concentration of (and response to) nutrients (Russell *et al.* 2005; Connell & Irving 2009), and in their broad degree of wave exposure (Hemer 2006). On the other hand, temperature regimes, which are often invoked to explain biogeographic differentiation in macroalgal assemblages (e.g. Schils & Wilson 2006), differ little between Flindersian and Peronian coasts (Wernberg *et al*. in prep.). Temperature gradients may, however, drive mesoscale structure among bioregions within provinces (e.g. Wernberg *et al.* 2003; Smale & Wernberg 2009)

Australia's marine biogeographic provinces provide a clear framework for reconciling apparently conflicting ecological phenomena across different regions (Connell 2007). A failure to accommodate this broad biogeographic differentiation will likely confound attempts to manage natural resources (Connell & Irving 2009). Therefore, it is essential that marine biologists integrate the ongoing discovery of small-scale ecological variability into a broad biogeographic context to help resolve wider problems (e.g. marine protected area planning, water quality guidelines). Although every biogeographic province contains patchiness and variability as a consequence of increasing biological complexity towards finer scales (Anderson *et al.* 2005), well-informed biogeography provides an important framework for integrating and interpreting variation across fine through broad scales.

In conclusion, our analyses provide quantitative support for classical qualitative biogeographic models in southern Australia. These findings indicate that traditional biogeographic provinces continue to provide a highly effective framework for informing marine biological research. Indeed, well-informed biogeographic provinces represent useful models for both applied (e.g. coastal management) and fundamental marine science (e.g. the development of scale-dependent perspectives). Broadly therefore we recommend that marine biologists undertake similar quantitative analyses to test the generality of biogeographic provinces that have, until now, been defined largely on the basis of qualitative pattern alone (e.g. Briggs 1995; Spalding *et al.* 2007).

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APPENDIX I

Temperate regionalization used in this study (based on Integrated Marine and Coastal Biogeographic Regionalisation of Australia bioregions; Commonwealth of Australia 2005): 1 = Abrolhos Islands; 2 = Central West Coast; 3 = Leeuwin-Naturaliste; 4 = WA South coast; 5 = Eucla; 6 = Murat; 7 = Eyre; 8 = Spencer Gulf + North Spencer Gulf + St Vincent Gulf; 9 = Coorong; 10 = Otway; 11 = Central Victoria + Central Bass Strait + Boags; 12 = Franklin; 13 = Victorian Embayments; 14 = Davey; 15 = Flinders; 16 = Bruny; 17 = Freycinet; 18 = Twofold Shelf; 19 = Batemans Shelf; 20 = Hawkesbury Shelf; 21 = Manning Shelf.

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