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Marine macroalgal biodiversity hotspots: why is there high species richness and endemism in southern Australian marine benthic flora?

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Abstract. The southern Australian marine macroalgal flora has the highest levels of species richness and endemism of any regional macroalgal flora in the world. Analyses of species composition and distributions for the southern Australian flora have identified four different floristic elements, namely the southern Australian endemic element, the widely distributed temperate element, the tropical element and a cold water element. Within the southern Australian endemic element, four species distribution patterns are apparent, thought to largely result from the Jurassic to Oligocene fragmentation of East Gondwana, the subsequent migration of Tethyan ancestors from the west Australian coast and the later invasion of high latitude Pacific species. Climatic deterioration from the late Eocene to the present is thought responsible for the replacement of the previous tropical south coast flora by an endemic temperate flora which has subsequently diversified in response to fluctuating environmental conditions, abundant rocky substrata and substantial habitat heterogeneity. High levels of endemism are attributed to Australia's long isolation and maintained, as is the high species richness, by the lack of recent mass extinction events. The warm water Leeuwin Current has had profound influence in the region since the Eocene, flowing to disperse macroalgal species onto the south coast as well as ameliorating the local environment. It is now evident that the high species richness and endemism we now observe in the southern Australian marine macroalgal flora can be attributed to a complex interaction of biogeographical, ecological and phylogenetic processes over the last 160 million years.

Key words: Australia, biodiversity, biogeography, endemism, marine macroalgae, species richness

Introduction

Biologists, long intrigued by the patterns of species diversity on Earth, have proposed many theories in an attempt to explain why some regions, now referred to as biodiversity 'hotspots', feature exceptional concentrations of species with high levels of endemism. Early this century, greatest species richness was thought to occur in historically stable environments in which species numbers gradually increased over long periods of geological time (Willis 1922; Fischer 1960). This theory, however, was superseded with the rise of community ecology in the 1960s, with ecologists then proposing that species diversity was generated by competition and disturbance acting within small areas and habitats. Marine ecologists, in particular, enthusiastically embraced 'the intermediate disturbance model' (Connell 1978), which attributed the high species richness of tropical rain forests and coral reefs to the amount, type and frequency of the disturbance. During the last three decades, the many research programs undertaken on these local ecological processes have demonstrated that single factor explanations are far too simplistic to account for extant regional diversity patterns. Rather, these patterns are now thought to be the result of a complex interaction of historical events, biogeographical circumstances, ecological and phylogenetic processes (Brown 1988; Solbrig 1991; Silva 1992; Schluter and Ricklefs 1993; Hallam 1994).

In his account on global macroalgal diversity patterns, Bolton (1994) divided regional floras into four categories, varying from 'species poor floras' comprising less than 200 species to 'species rich floras' with more than 900 species. He concluded that the macroalgal floras of southern Australia (1150 species), the Mediterranean Sea (1000 species), Japan (900 species) and the Philippines (900 species) are species rich, although other phycologists have included in this category floras from the Pacific coast of North America (Silva 1992), the Atlantic European coast and the Caribbean (Norton et al. 1996). Species rich macroalgal floras are reported from temperate seas, thus providing no convincing evidence for a latitudinal gradient in macroalgal species richness, unlike that reported for several marine animal phyla (Clarke 1992).

Straddling 35–40° south latitude, the south coast of mainland Australia trends west-east for approximately 5500 km from Cape Naturaliste (33°32′ S, 115°01′ E), Western Australia across the Great Australian Bight, the South Australian gulfs, and along the Victorian coast to the Victorian/New South Wales border (37°34′ S, 149°45′ E). The island of Tasmania is located to the south of Victoria, between 40 and 43° S latitude. The southern Australian coast which lies a few degrees north of the Subtropical Convergence, the northern limit of subantarctic waters, has a mean annual surface seawater temperature (SST) variation of 8–20 °C (Womersley 1990). Large sections of this coastline are composed of rocky substrata which provide suitable habitats for macroalgal attachment. The marine benthic flora of the region is relatively well known, reflecting the phycological investigations of the last 150 years, which have produced the five volumes of '*Phycologia Australica*' (Harvey 1858, 1859, 1860, 1862, 1863), the '*Seaweeds of South Australia*' (Lucas 1936; Lucas and Perrin 1947), and the '*Marine Benthic Flora of Southern Australia*' (Womersley 1984, 1987, 1994, 1996, 1998).

Studies of biodiversity rely heavily on detailed knowledge of historical events, systematics, phylogeny, ecology and biogeography. Data on these research areas for Australian algae are incomplete, contributing to the difficulties associated with documenting and understanding the patterns of macroalgal biodiversity for the continent. Knowledge of the impact of past events on macroalgal species will always be constrained by a meagre fossil record, based largely on the relatively small proportion of calcareous species which have good preservation potential (Wray 1977; Elliott 1984; Hillis-Colinvaux 1986). Consequently, the effects of changes in palaeoclimate and of past speciation and extinction events on macroalgae will have to be largely inferred from the extant macroalgal flora. In other cases, further research will gain the essential knowledge required, particularly in the areas of systematics and phylogeny. Studies of evolution which plays an essential role in generating biodiversity should always be included in analyses of biodiversity patterns. However, for the southern Australian macroalgal flora still in the 'description' phase, it will be many years before phylogenetic studies on a large proportion of the flora can be completed.

The high species richness and endemism of the southern Australian benthic flora have long been recognised (Womersley 1959, 1972, 1981, 1990; Hommersand 1986; Lüning 1990; Silva 1992; Bolton 1994), being generally attributed to temperature barriers (Womersley 1990), a favourable climate (Hoek 1984; Womersley 1990), abundant rocky substrata (Lüning 1990; Womersley 1990), the lack of Pleistocene extinctions (Lüning 1990) and to the long isolation of the Australian continent (Hoek 1984; Lüning 1990; Womersley 1990). In view of recent major advances in our understanding of theory of plate tectonics and continental drift and of changes in palaeoclimate and ocean circulation patterns in the Australian region, as well as greater knowledge of systematics, ecology and biogeography of this marine flora, it is time to explore in detail the role that historical, geographical, ecological and evolutionary processes may have played in generating the high species richness and endemism we now observe in the southern Australian benthic flora.

Methods

The geographical range for each species recorded for the Australian south coast was determined for both within and outside the region by extracting species distributional data from the southern Australian (Womersley 1984, 1987, 1994, 1996, 1998) and New Zealand floras (Adams 1994), and from checklists for New South Wales (Millar and Kraft 1993, 1994a, b), Rottnest Island (Huisman and Walker 1990) and Houtman Abrolhos, Western Australia (Huisman 1997). In this paper, species distributional ranges are only referenced when the range differs from that published in the above floras. Orders of the Chlorophyta, Phaeophyceae and Rhodophyta were treated separately in the analyses. Flora treatments for the Delesseriaceae and Rhodomelaceae (Ceramiales) are not yet available and the omission of these families by the present study accounts for the lower number of red algal species used in the analyses. Species included in the southern Australian floras but only recorded from the Australian west coast and distributional data considered unreliable were excluded from the analyses. The unreliability of data based only on drift specimens is well illustrated by records of large brown algae (*Macrocystis angustifolia*, *Cystophora platylobium*, *Scaberia agardhii*), collected as drift only after storms early this century in the Sydney region on the east Australian coast. Attached plants of these species have never been recorded on the east Australian coast and it is probable that these conspicuous algae, which are not easily overlooked, had drifted from the cool temperate Victorian coast.

Results

The extant southern Australian marine flora is composed of four different floristic elements, comprising the southern Australian endemic element, the widely distributed temperate element, a tropical element and a polar element (Table 1). The relative proportions of each element vary among the Chlorophyta, Phaeophyceae and Rhodophyta with the southern Australian endemic element and the widely distributed temperate element accounting for the majority of species in the flora. The widely distributed temperate element is greatest in the Chlorophyta. There are more southern Australian endemic species in the Phaeophyceae and the Rhodophyta than widely distributed temperate species. The southern Australian endemic element is greatest in the Rhodophyta. The tropical element comprises only a small proportion of the flora, and the relatively minor cold water (polar) element is composed largely of species restricted geographically to cooler coasts of southeast and southern Tasmania.

The tropical element comprises widely distributed tropical species which range onto the Australian south coast, often tending to have a sporadic occurrence in the region. Many of these tropical species range from the west coast onto the western end of the south coast, with species such as *Halimeda cuneata* and *Galaxaura obtusata* extending to the Archipelago of the Recherche and Albany, respectively. *Dictyopteris australis* which also ranges to Albany has isolated populations in the Gulfs region of South Australia (Phillips 2000). Other widely distributed tropical species have disjunct distributions on the Australian south coast with isolated populations of *Microdictyon umbilicatum*, *Sargassum decurrens* and *Asparagopsis taxiformis* recorded from the South Australian gulfs and *Chaetomorpha indica* and *Polyphysa peniculus* recorded from some shallow bays along the coast.

Within the southern Australian endemic element, there are many species including *Caulerpa remotifolia*, *Callipsygma wilsonii*, *Chlorodesmis bacifera*, *Dasycladus densus*, *Spatoglossum australasicum*, *Sargassum paradoxum* and *Cryptonemia wilsonii* which belong to typically tropical taxa, particularly the orders Caulerpales, Dictyotales and genus *Sargassum*. These endemic species of tropical affinity are generally found as isolated populations, often in shallow sheltered bays, in the Gulfs region of South Australia and other habitats with suitable microclimates.

Table 1. Percentage composition of the floristic elements in the southern Australian marine macroalgal flora.

	Southern Australian endemic element	Widely distributed temperate element	Tropical element	Polar element
Chlorophyta	40.3	45.2	9.7	4.8
Phaeophyceae	59.3	31.1	4.5	5.1
Rhodophyta	77	16.7	4.8	1.5

Temperate endemic species of the Chlorophyta, Phaeophyceae and Rhodophyta exhibit four different distribution patterns in southern Australia (Figure 1). The first group of species ranges from the west Australian coast onto the south coast, with different species having an eastern distributional limit most frequently in the Port Phillip Bay–Walkerville region of Victoria, or less frequently in the gulfs region of South Australia or rarely in the Great Australian Bight. The second group is restricted to the south coast, with species ranging either along the whole coast, or on the western or eastern sections of the coast. The third group occurs in south eastern Australia, with species having a western distributional limit either in the South Australian gulfs region, or less commonly further west in the Great Australian Bight. The fourth group is composed of widely distributed species which range from the west coast along the south coast and onto the east coast.

Not all orders of the Chlorophyta, Phaeophyceae and Rhodophyta are well represented in southern Australia (Tables 2–4). Among the speciose orders, the Ulvales, Cladophorales, Ectocarpales and Acrochaetiales have a high proportion of species which are also widely distributed outside the region, while the Caulerpales, Fucales, Dictyotales, Chordariales, Gigartinales, Rhodymeniales and Ceramiales

Figure 1. Map of Australia showing the distribution patterns of species comprising the southern Australian endemic element. (I) Species ranging from the west Australian coast onto the south coast, most frequently with an eastern distribution limit in the Port Phillip Bay/Walkerville region. (II) Species occurring only on the south coast. (III) Species extending from the east Australian coast onto the south coast, most frequently with a western distribution limit in the Gulfs region of South Australia. (IV) Species which range from the Australian west coast along the south coast and onto the east coast.

Table 2. Geographical distribution patterns of species of the Chlorophyta occurring in southern Australia. SW species range from the Australian west coast onto the south coast; South coast species are endemic to the Australian south coast; SE species range from the Australian east coast onto the south coast; W, S and E coast species range from the west Australian coast, along the south coast and onto the east Australian coast.

Order	Number of species						
			Southern Australian endemic species				
	Tropical species	Widely distributed temperate species	SW species	South coast species	SE species	W, S and E coast species	Polar species
Tetrasporales	–	–	–	1	–	–	–
Ulotrichales	–	1	1	–	–	–	–
Chaetophorales	–	2	–	–	–	–	–
Ulvales	–	16	–	1	–	–	–
Prasiolales	–	–	–	–	–	–	3
Cladophorales	7	20	2	6	–	1	1
Acrosiphoniales	–	–	–	–	–	–	1
Siphonocladales	–	–	1	–	–	–	–
Codiales	1	7	5	2	–	1	1
Caulerpales	3	6	9	11	–	1	–
Derbesiales	–	4	3	2	1	0	–
Dasycladales	1	–	–	1	–	1	–
Total: 124	12	56	21	24	1	4	6

contain many endemic southern Australian species. The Corallinales have similar numbers of widely distributed and endemic species.

The greatest number of southern Australian endemic species in most orders of the Chlorophyta, Phaeophyceae and Rhodophyta are distributed either only on the south coast, or from the south west coast onto the south coast (Tables 2–4). The Sphacelariales is the only speciose order which has more species ranging from the east coast onto the south coast than occur on either the south coast or southwest coasts. In most orders, relatively few species range from the south east coast onto the south coast and even fewer species range from the west coast along the south coast and onto the east coast.

Differing levels of genus and species endemism are apparent among the southern Australian representatives of the Chlorophyta, Phaeophyceae and Rhodophyta. Only *Palmoclathrus* (Tetrasporales) and *Callipsygma* (Caulerpales) or 5% of green algal genera are endemic to the region, a low level of generic endemism compared to the Phaeophyceae in which 20 genera (19% of genera) occurring in southern Australia are endemic. Greatest levels of generic endemism are evident in the Rhodophyta, with the Gigartinales and Ceramiaceae recording 35% and 40% of genera endemic to the region. Species endemism in the southern Australian macroalgae is greater than generic endemism and shows the same pattern of variation, being the lowest in the Chlorophyta, greater in the Phaeophyceae and greatest in the Rhodophyta (Table 1).

Table 3. Geographical distribution patterns of species of the Phaeophyceae occurring in southern Australia. SW species range from the Australian west coast onto the south coast; South coast species are endemic to the Australian south coast; SE species range from the Australian east coast onto the south coast; W, S and E coast species range from the west Australian coast, along the south coast and onto the east Australian coast.

Order	Number of species						
			Southern Australian endemic species				
	Tropical species	Widely distributed temperate species	SW species	South coast species	SE species	W, S and E coast species	Polar species
Ectocarpales	1	14	–	2	1	–	2
Chordariales	–	16	–	16	2	3	2
Scytothamnales	–	–	–	–	–	–	3
Sphacelariales	1	10	3	4	4	1	2
Dictyotales	5	4	15	7	6	2	–
Cutleriales	–	1	–	–	–	–	–
Desmarestiales	–	1	–	–	–	–	–
Sporochnales	–	3	1	3	1	3	–
Scytosiphonales	–	6	–	–	–	–	–
Dictyosiphonales	–	6	1	1	–	–	–
Laminariales	–	–	–	1	–	1	2
Durvillaeales	–	–	–	–	1	–	–
Fucales	3	7	20	20	4	7	–
Total: 219	10	68	40	54	19	17	11

Caulerpa is the only genus of the Caulerpales to have diversified in southern Australia, recording a total of 19 species in the region, more species than is recorded for tropical Australia or probably for any other tropical region. With the exception of the pantropical *C. racemosa* and *C. scalpelliformis*, 10 species of *Caulerpa* occur on south and southwest coasts with two species also extending to New Zealand, four species are restricted to the Australian south coast and three species range from the west coast along the south coast to the east coast with two also recorded from New Zealand. No species of *Caulerpa* is geographically limited to south eastern Australia. The seven other genera of the Caulerpales recorded for southern Australia have either one or two species (e.g. *Rhipiliopsis*).

The Dictyotales are well represented in southern Australia with 16 of the 19 genera and 38 species recorded for the region. Within the region, dictyotalean genera typically contain one or two species, although *Dictyota* records seven species and *Padina* and *Dictyopteris* four species each for the region. The Chordariales are represented by 25 genera and 40 species in southern Australia, most genera containing one or two species. Of the 14 genera of the Fucales reported for southern Australia, three also occur on tropical coasts, eight are endemic to the region and *Hormosira*, *Xiphophora* and *Cystophora* have an Australasian distribution pattern. Only two fucalean genera have speciated in the region. The majority of the 23 southern Australian

Table 4. Geographical distribution patterns of species of the Rhodophyta occurring in southern Australia. SW species range from the Australian west coast onto the south coast; South coast species are endemic to the Australian south coast; SE species range from the Australian east coast onto the south coast; W, S and E coast species range from the west Australian coast, along the south coast and onto the east Australian coast.

Order	Number of species						
			Temperate Australian endemic Species				
	Tropical species	Widely distributed temperate species	SW and S coast species	South coast species	SE species	W, S and E coast species	Polar species
Bangiophyceae							
Porphyridales	–	4	–	–	–	–	–
Compsopogonales	–	3	–	1	1	1	–
Bangiales	–	1	1	–	–	–	2
Floridophyceae							
Acrochaetiales	–	18	–	2	2	–	–
Nemaliales	5	4	2	5	3	2	1
Gelidiales	1	4	1	3	1	1	–
Hildenbrandiales	–	2	–	1	–	–	1
Gigartinales	11	12	44	69	14	8	–
Gracilariales	–	1	5	1	4	–	1
Rhodymeniales	1	7	12	15	4	2	–
Corallinales	5	22	7	16	2	3	1
Bonnemaisoniales	1	2	1	5	1	0	1
Ceramiaceae*	3	14	42	96	10	15	1
Dasyaceae*	–	–	13	17	2	–	–
Total: 565	27	94	128	231	44	32	9

* Flora treatments for the Delesseriaceae and Rhodomelaceae (Ceramiales) are not yet complete.

species of *Cystophora* are recorded from the south coast (13 species) and south west and south coasts (five species), a similar distribution pattern to the tropical genus *Sargassum* which has five and six species of the 14 endemic species distributed on the south coast and south west and south coasts, respectively. With the exception of *Cystophora*, *Sargassum* and *Myriodesma* which records five species, all other southern Australian endemic fucalean genera contain only one or two species.

In the Rhodophyta, high species richness is derived from a large number of genera, many of which are endemic to southern Australia and contain only one or two species. In the Gigartinales, 25 (35%) of the 72 genera recorded for southern Australia are endemic to the region, 42 genera are monospecific and only 11 genera contain more than three species. The most speciose genera are *Mychodea* (11 species), *Plocamium* (eight species) and *Gigartina* (seven species). The Ceramiaceae has 26 (40%) endemic genera of a total of the 65 genera recorded for the region, 32 genera are monospecific and only 16 genera contain more than three species. *Ceramium* with 15 species, *Antithamnion* with 11 species, *Griffithsia* and *Callithamnion* with 10 species each are the most speciose genera. There are no endemic southern Australian genera in the Dasyaceae, but 31 of the 33 southern Australian species in the family are endemic to the region, including all 21 species of *Dasya*.

Discussion

Species of tropical affinity

The presence of macroalgal species generally associated with tropical seas on the temperate southern Australian coast has long been recognised (Womersley 1959, 1972, 1981, 1990; Silva 1962; Ducker 1967). Temperature is widely accepted as a major determinant of macroalgal distribution patterns (for review see Breeman 1988) and it is probable that warm currents, habitats subjected to localised warming and warm palaeoclimates may have contributed to ameliorating the environment on the temperate Australian south coast in order to ensure the survival of tropical species.

Present day migrations of tropical species into temperate Australia may be facilitated by currents which flow south from the tropics. The warm water East Australia Current does not penetrate onto the south coast of mainland Australia (Jeffrey et al. 1990), unlike the Leeuwin Current which exerts a major oceanographic influence in the region. The Leeuwin Current transports tropical waters from near North West Cape (21°47′ S, 114°10′ E) southward along the west Australian coast, around Cape Leeuwin, and then eastward into the Great Australian Bight, where current waters mix with Bight waters to form the East Bight Current which then flows further east towards the South Australian gulfs region (Pearce and Cresswell 1985; Rochford 1986; Cresswell 1991). The Leeuwin Current flows most strongly during autumn and winter months, warming the waters of the Great Australian Bight and contributing to a warm west to cooler east winter SST gradient on the Australian south coast. Winter SSTs range from 17 to 19 °C in Great Australian Bight to 11–12 °C along the Victorian coast (King 1970).

The role of the Leeuwin Current in extending the distributional limits of tropical macroalgal species onto the temperate south Australian coast has not previously been proposed, even though the current is considered responsible for the sporadic occurrence of tropical macroalgae on Rottnest Island on the west Australian coast (Huisman and Walker 1990; Walker 1991), and for the transport of tropical invertebrates and pelagic tuna into the Great Australian Bight (Maxwell and Cresswell 1981; Lenanton et al. 1991; Caputi et al. 1996). Drift macroalgae could be transported into suitable habitats on the south coast when the offshore Leeuwin Current impinges on coastal waters in the Geographe Bay/Cape Naturaliste/Cape Leeuwin area and along the south coast from D’Entrecasteaux Point to Albany (Pearce 1985; Lenanton et al. 1991; Morgan and Wells 1991). In addition, local environmental conditions generated by storms, wind and water circulation patterns could sweep current waters and drift algae across the continental shelf into coastal waters, although the mechanisms driving these processes are not yet understood (A. Pearce, pers. comm.).

The Leeuwin Current clearly accounts for the range extension of tropical macroalgal species onto the western end of the south coast, the region on the south coast where the current has greatest influence. However, the current which shows great interannual variability in flow strength (Pearce 1991; Phillips et al. 1991) may also account for isolated populations of tropical macroalgal species further east on the south coast, possibly establishing these populations in years of strong current flow in microclimatically favourable habitats, such as intertidal rockpools and shallow bays which warm quickly in summer and in the South Australian gulfs which have a south to north SST gradient of 20–22 °C (Rochford 1975). These habitats have summer SSTs more typical of subtropical coasts, considerably warmer than the SSTs of the Southern Ocean.

Southern Australian endemic species of tropical affinity probably originated in the region during past warm periods, persisting as relict populations of an older more extensive tropical flora in refuges with suitable microclimates, as has previously been suggested to account for the presence of isolated populations of endemic *D. densus* and *Avrainvillea clavatiramea* on the Australian south coast (Womersley 1972, 1990). Similarly, luxuriant growths of the many endemic species of the tropical Caulerpales in the intertidal rockpools at Port Phillip Heads, Victoria have been attributed to high seawater temperatures to 30 °C, resulting from localised warming in these rockpools during the summertime daylight low tides (Ducker 1967). Presumably, these species would be dependent for growth and reproduction on these higher SSTs which are much higher than those normally experienced on the Australian south coast.

These endemic species or their lineages may have persisted as relicts of a more extensive tropical flora for 55 million years, since the end of the last global warm period in the mid-early Eocene (Truswell 1993; Zanchos et al. 1994), when surface and bottom waters in the Southern Ocean were relatively warm (Shackleton and Kennett 1975; Barron 1983; Feary et al. 1991; Frakes et al. 1992). The proposal that some algal lineages can exist for long periods of geological time is substantiated by the fossil record. *Halimeda* is a good example of an old tropical genus which has been common since the late Cretaceous (Flügel 1988), the Mesozoic occurrence of the genus supported by data from molecular studies (Hillis et al. 1998). Alternatively, these endemics may have originated more recently than the Eocene, during the short warming reversals which were superimposed on the current major cooling cycle such as in the earliest Miocene when SSTs were 5–7 °C warmer than today and during the interglacial periods of the Quaternary. During these warm periods, tropical macroalgal species could have migrated onto the Australian south coast by range extension through local dispersal or in the west via the Leeuwin Current, which has flowed periodically since the middle Eocene (McGowran et al. 1997a). As the climate once again cooled, these populations would have been isolated in favourable microhabitats on the south coast following the extinction or range contraction of other populations of the species. Evidence for macroalgal range extensions during these warm periods is not available as macroalgae rarely fossilise. However, the presence of tropical foraminifera in the South Australian gulfs (Cann and Clarke 1993; Li et al. 1999) and of the coral genus *Acropora* in the Great Australian Bight, 500 km south of the modern range of the genus (Kendrick et al. 1991) during the last interglacial warm period of the Pleistocene indicate that SSTs on the south coast during warming reversals were warm enough to support tropical species, including macroalgal species.

The southern Australian element

The four different distribution patterns exhibited by southern Australian endemic species of the Chlorophyta, Phaeophyceae and Rhodophyta can be largely explained using current interpretations of the sequence of geologic events during the fragmentation of east Gondwana. The element is thought to be derived from two biotas which have developed independently from different ancestral stocks. Species currently distributed from the southern section of the west coast onto the south coast probably originated from Tethyan stock which had dispersed into the region, this south-west stock subsequently giving rise to the majority of south coast species which have probably originated on the south coast. Species which range from the east coast onto the south coast probably originated on the Australian east coast and later migrated onto the south coast. Species distributed on the west, south and east coasts may be good dispersers and could have originated on any coast or they may have originated on the south and west coasts before migrating to the east coast or vice versa, although species using the last route would have to contend with the predominant west to east shelf circulation patterns generated by the Leeuwin Current and West Wind Drift.

Continental drift and sea floor spreading are thought to have created the south west and south Australian coasts. During the late Jurassic (160 Ma), Neo Tethys bathed the shores of north west Australia, the Indian subcontinent lay along the south west section of the Australian plate and the southern margin of Australia abutted Antarctica (Veevers 1991; Wilford and Brown 1994). Rifting and drifting north of India by 118 Ma led to the formation of the Indian Ocean and to the southern migration of Tethyan organisms onto the newly formed south west Australian coast. During the late Cretaceous (96 Ma), sea floor spreading was slowly separating Australia from Antarctica in the west, thus enabling the eastward spreading arm of the Indian Ocean to gradually extend almost to Tasmania. By the Eocene, fully marine conditions were established for the first time along the southern continental margin (BMR Palaeogeographic Group 1990; Truswell 1993), but the Southern and South Pacific Oceans did not interconnect until the strait between Australia and Antarctica opened in the late Oligocene (30 Ma). The novel shallow embayment formed on the southern Australian continental margin by these tectonic processes would have been colonised by macroalgae from the west Australian coast, whose ancestors in turn had arisen from Tethyan ancestors, as has previously been proposed for some southern Australian macroalgal

(Hommersand 1986) and invertebrate species (Knox 1980; Wilson and Allen 1987). The many extant macroalgal species recorded only from the south coast are thought to have originated in the region.

During the early Tertiary, another flora derived from different ancestral stock and separated by a land barrier from the south coast flora, was evolving on the east Australian coast (Knox 1980; Hommersand 1986). Many present day species which are largely restricted to south east Australian coasts would probably have arisen from this Pacific palaeoaustral flora.

Submergence of the land barrier between the Australian plate and Antarctica in the late Oligocene would have permitted the Australian south coast flora to mix with the east coast flora, a scenario which has been previously proposed for marine invertebrates occurring in the region (Knox 1980; Darragh 1985; Wilson and Allen 1987). This mixing apparently has been limited, evident from the relatively small number of endemic macroalgal species currently widely distributed on west, south and east or on south and east Australian coasts. Other barriers formed by ocean circulation patterns or abrupt changes in temperature may have prevented species migrations. The predominant west to east water movement on the south coast driven by the West Wind Drift and Leeuwin Current would have restricted the westward migration of east coast species. Eastward migrations of species from the west section of the south coast may be prevented by the generally cooler temperatures on the Victorian coast and also by the cold water Flinders Current which flows during the summer from western Tasmania along the west Victorian coast to Kangaroo Island, South Australia (Lewis 1981; Wilson and Allen 1987; Jeffrey et al. 1990), where the current induces an upwelling further reducing SSTs by 3–5 °C (Schahinger 1987).

The observation that relatively small numbers of macroalgal species have extended their geographical ranges to colonise the other side of the former land barrier is also consistent with the prevailing theories on biotic interchange, a phenomenon which occurs after a barrier between two biotas with separate histories breaks down (Vermeij 1991). Studies on biotic interchanges of both marine and terrestrial biotas which have occurred over the last 25 million years have shown that invading species comprise a small proportion of the donor biota and that the contribution of the invaders to the recipient biota is usually small. Invasions are thought to be more successful in biotas which have experienced recent high levels of extinction, an event which apparently has not occurred in the species rich southern Australian flora.

Diversification of the southern Australian flora

Womersley (1990) reported that the southern Australian coastline has the greatest diversity of Rhodophyta for any coastline in the world. It is the Rhodophyta, with more than 800 species, that contributes greatly to the high species richness of this flora, a fact which may be related to the great diversity of the Rhodophyta which records 4000–6000 species worldwide, compared to the 900–1500 species attributed to the

Phaeophyceae and to the 1040 species of marine green macroalgae (Womersley 1990; Groombridge 1992; Norton et al. 1996). It is not known why Caulerpales, Chordariales, Dictyotales, Fucales, Gigartinales, Rhodymeniales, Corallinales and Ceramiales which record many southern Australian endemic species have speciated in the region while other macroalgal orders have not. However, whatever the cause, high levels of speciation apparently have occurred on the southwest and south Australian coasts, if the extant geographical ranges for species are similar to those of the past. For the Chordariales, Gigartinales, Corallinales and Ceramiales which record twice as many endemic south coast species as south west to south coast species, it would appear that higher rates of speciation have occurred in these orders on the south coast than on the adjacent southwest/south coast.

Little is known of the processes which have generated the high levels of speciation in macroalgal floras, but these processes must be linked to high species richness which has been variously attributed to the effects of latitudinal temperature variation experienced by the Japanese macroalgal flora (Bolton 1994), to the compartmentalisation of the Mediterranean flora into many relatively isolated subregions, each harbouring endemic species (Silva 1992), or to the repeated drying of the Mediterranean Sea between 5 and 6 million years ago (Lüning 1990; Bolton 1994). These hypotheses are consistent with current evolutionary theory which proposes that rapid speciation occurs in regions, referred to as adaptive zones, in which geologically disruptive processes as plate tectonics and sea level fluctuations and/or fluctuating environmental conditions provide new ecological opportunities (Simpson 1953; Newell 1967; Stanley 1979; Knox 1980; Myers and Giller 1988; Brookes et al. 1992). These processes are thought to increase the rate of evolutionary divergence in response to the mixing and then isolation of gene pools caused by the repeated shifting and fragmentation of species ranges, particularly in transitional habitats with patchy mosaics of vegetation or in refugia which shelter diverse taxa (Jablonski 1986; Myers and Giller 1988; Myers 1996; Brown and Lomolino 1998).

During the globally warm Late Cretaceous to Early Cainozoic, the newly forming south west and south Australian coastlines would have represented new adaptive zones, with many unoccupied habitats and niches available for colonisation by tropical macroalgal species. Global climate deterioration which commenced in the mid-early Eocene, and continued with the abrupt cooling episodes of the Eocene/Oligocene boundary (38 Ma), Middle Miocene (13–15 Ma) and the latest Miocene (5–6 Ma) (Shackleton and Kennett 1975; Barron 1983; Feary et al. 1991; Frakes et al. 1992) would have been responsible for the extinction of much of the older southern Australian tropical flora, thus providing the ecological opportunity for the diversification of the temperate flora. This proposal is consistent with reports from the fossil record which documents high diversification rates for certain plant and animal lineages following the mass extinction of a previous biota (Simpson 1953; Stanley 1979; Van Valen 1985) and with divergence of other temperate macroalgal lineages in response to the current global cooling. Divergence estimates for northern hemisphere laminarian kelps based on present day distribution patterns, palaeoclimate data, age of the fossil kelp *Julescrania*, and the chloroplast-DNA molecular clock, indicate that divergence commenced 16–30 Ma to establish the extant members of the order (Estes and Steinberg 1988; Lüning and tom Dieck 1990; Saunders and Druehl 1992), earlier than the cold water red algal Palmariaceae in which divergence is thought to have occurred between 6.9 and 17.3 Ma (Lindstrom et al. 1996).

Great variability in marine conditions around Australia resulting from fluctuations in SSTs, marine transgressions/regressions, upwellings and the intensity of currents from the Eocene to modern times (Truswell 1993; Quilty 1994; McGowran et al. 1997a) may have contributed to high speciation rates in the southern macroalgal flora. Brief warming reversals in the earliest Miocene, middle Miocene and early Pliocene (Quilty 1994) and the interglacial warm periods of the Quaternary punctuated the general cooling trend and increased the variability in SSTs (McGowran et al. 1997a), probably resulting in range expansion for warm water algal species. Upwellings have occurred on the east Victorian coast since the latest Oligocene (Li and McGowran 1994) to the present (Jeffrey et al. 1990), causing localised decreases in SSTs, similar to the 3–5 °C decline evident in present day upwellings on south east coast of South Australia (Lewis 1981; Schahinger 1987). The Leeuwin Current has greatly affected SSTs on the Australian south coast, by switching on and off in the Great Australian Bight in concert with global warm and cool periods (McGowran et al. 1997a). During cool periods, the Subtropical Convergence Zone moved northwards, permitting interactions through time between cooler southern waters and warmer tropical waters normally transported from the north by the current.

Marine transgressions and regressions resulting from rising and falling sea levels, sometimes in the order of 100–200 m in magnitude and coinciding with global warm and cool periods have greatly affected the Australian continent from the late Eocene to the Pleistocene (Williams 1984; McGowran 1989; Veevers 1991; McGowran et al. 1997a,b). During times of low sea levels, the Australian land mass included Tasmania and New Guinea and a wide continental shelf (White 1990). With regressions, species are largely eliminated over most of their geographical range, being restricted to refugia, from which recolonisation can occur during the next transgression (Newell 1967; Van Valen 1985; Valentine and Jablonski 1991; Hallam 1992).

Recent reports of transitional habitats and refuges for macroalgal species implies that they may have also existed in historical time. Warm currents are responsible for transitional habitats having mixtures of temperate (kelps) and tropical macroalgal species on Houtman Abrolhos (28–29° S) on the Australian west coast and on the Solitary Islands (29–30° S) on the Australian east coast (Clayton 1989; Huisman 1997). A refuge, surrounded by ocean depths of 90–140 m and supporting an isolated population of the kelp *Ecklonia radiata*, was recently found on the uppermost rocky outcrops at depths of 30 m on the Chatham Rise, New Zealand (Nelson 1994). Presumably, the species could become more widespread in the region with a fall in sea level which would provide more substrate at suitable depths for algal colonisation.

Similarly, Silva (1992) reported the gametophyte of the kelp, *Nereocystis luetkeana*, on a seamount with the shallowest depth of 35 m, and noted that a fall in sea level would be required before the sporophyte which only grows at depths of less than 22 m could develop on the seamount to complete the life history.

Endemism

On current estimates, the southern Australian marine flora has the highest level of species endemism of any regional macroalgal flora, recording a total of 62% species endemism, greater than the highly endemic macroalgal floras of Jamaica and the Antarctica and sub-Antarctic Islands which record 46.8% and 45% of species endemism, respectively (Norton et al. 1996). In the southern Australian flora, the high levels of endemism are correlated to high species richness, unlike the species rich Mediterranean flora which has only 20% species endemism (Lüning 1990) and the species poor Antarctic flora which has 45% species endemism (Norton et al. 1996). Generally, endemism of regional floras requires critical reassessment as many numerical values for species endemism, including those cited by Norton et al. (1996), are based on studies published decades ago. Establishing the level of endemicity for a flora depends on accurate species recognition, as emphasised by Parsons (1985) who conceded that 38% species endemism for New Zealand green algal flora, less than the 47% cited by Norton et al. (1996), was still an overestimate, attributed to the excessive number of species recognised.

The high level of genus and species endemism of the southern Australian flora can probably be attributed to the long isolation of the Australian continent which restricted gene flow from other geographical regions. With the exception of Antarctica, now largely covered by an ice sheet, Australia has been separated from all other land masses for last 80 million years (Veevers 1991). Generally, regional biotas with high genus and species endemism are thought to have evolved in a region which has experienced a stable environment over a long time period (Myers and Giller 1988; Myers 1996), similar to the environment that southern Australian macroalgae would have experienced since the Eocene.

Womersley (1990) estimated that 30% of genera and 75% of species of southern Australian Rhodophyta are endemic to the region, percentages greater and much greater than those for the Phaeophyceae and Chlorophyta, respectively. These varying levels of endemism may result from several factors, including the differing dispersal potential of the algae. Species of the highly endemic Rhodophyta and of the brown algal Dictyotales and Fucales produce large, non-flagellate reproductive cells that sink to the substrate quickly rather than being widely dispersed. Even motile cells (gametes and/or zooids) produced by many algal species are not good dispersers, settling onto substrates within hours or days, rather than drifting in the water column for months like the planktonic larval stages of invertebrate species. Except for the weedy species of Ulvales and Ectocarpales which are common in fouling communities, long distance dispersal by drifting or rafting macroalgal thalli tends to be an uncommon opportunistic method of dispersal (Hoek 1987), which is often unsuccessful as drift fertile thalli are seldom transported to suitable habitat, evident from the failure of drift specimens of *Durvillaea antarctica* from the Kergulen Islands, 4800 km to the west, to establish in Tasmania (Moore and Cribb 1952). Macroalgae are generally considered to be poor dispersers across ocean basins (Hoek 1987), lacking high levels of dispersal which would have reduced the high levels of endemism apparent in the southern Australian macroalgal flora.

Area and habitat heterogeneity relationships

The high species richness of the southern Australian marine flora is partially related to the extensive rocky substrata which form large sections of the south coast. Macroalgae require a firm substrate for attachment, evident from the greater number of species found on rocky substrates compared to mud or sand substrates. It is now widely accepted that within a geographical region, species number increases with an increase in area which is due largely to the greater number of habitats, each with its compliment of characteristic species (MacArthur and Wilson 1967; Connor and McCoy 1979; Boecklen and Simberloff 1986; Brown 1988).

The southern Australian continental shelf, which is one of the largest in the world (P.G. Quilty, pers. comm., cited from *Australia's Biodiversity*, 1993), is well provided with an abundance of rocky headlands, intertidal and subtidal rock platforms exposed to wave action, offshore islands and large sheltered embayments, each containing many different habitats. Weathering of the many intertidal sedimentary rock platforms in the region produces an enormous range of habitats including horizontal rock surfaces, rockpools of varying size and depths, vertical rock faces of subtidal fringe and the undersurfaces of ledges, each habitat supporting characteristic macroalgal assemblages. These much-pitted gently sloping intertidal platforms retain seawater during low tide, thus reducing the effects of aerial exposure on the algae which in turn helps to sustain a diverse intertidal flora, which is absent from other Australian coasts. Subtidal rocky substrates support luxuriant algal communities, including kelp forests in which the canopy species provide habitat for many understorey algal species.

Lack of recent mass extinction events

The maintenance of high species richness in the southern Australian benthic flora is partly due to the lack of mass extinction events caused by adverse environmental conditions. Southern Australia has experienced favourable SSTs and an equitable climate, little affected by ice sheets, glaciation and cold currents throughout the Cainozoic. Although the south coast lay at 50–60° south latitude in the Eocene, the Earth's oceans were relatively warm and the pole to equator gradient in SST was low (Shackleton and Kennett 1975; Barron 1983; Feary et al. 1991; Frakes et al. 1992).

The northward drift of the Australian continent through 30° of latitude (White 1990; Markgraf et al. 1995) coincided with the change from the tropical conditions of the early Eocene to the cooler conditions of today, generated by the global high-latitude cooling trend of the Earth's oceans. By the mid-Miocene, southern Australia had entered the warm temperate zone, further removed from cooler climatic zones which were subjected to more frequent and severe climate oscillations during the glacial/interglacial periods of the Quaternary. Consequently, Australia was little affected by glaciation, unlike New Zealand where glaciation was widespread and severe (White 1990).

The Leeuwin Current is unique in the southern hemisphere as an eastern boundary current as it transports tropical waters south, unlike the Benguela Current of southwest Africa and the Humboldt Current of Pacific South America which flow north transporting cold water along their respective coastlines (Morgan and Wells 1991; Pearce 1991). Cold water macroalgal floras are usually depauperate (Bolton 1994) and had a cold current flowed along the Australian west coast since the Eocene, macroalgal species richness in southern Australia would be much lower than it is today. Furthermore, the warm water Leeuwin Current has probably contributed to maintaining favourable SSTs in southern Australia since the Eocene, as well as being responsible for localised warming which ameliorated the environment in southern Australia during the last interglacial period of the Pleistocene (Cann and Clarke 1993; McGowran et al. 1997a).

Conclusions

The high species richness and endemism of the southern Australian macroalgal flora appears to be the result of complex interactions of past geological events which have provided new marine environments along the southern continental margin, favourable palaeoclimates and present day climates, gene pools derived from Tethyan and high latitude south Pacific ancestors, high speciation rates presumably caused by fluctuating environmental conditions, abundant suitable rocky substrata and habitat heterogeneity, the influence of the warm water Leeuwin Current and the long isolation of the Australian continent. The maintenance of this high species richness and endemism is attributed to the lack of mass extinction events caused by environmental harshness.

The southern Australian benthic flora is largely derived from Tethyan stock which migrated onto the south west Australian coast and then onto the south coast after the fragmentation of East Gondwana in the late Mesozoic/Early Cainozoic led to the formation of new marine environment in the region. Initially, tropical Tethyan species colonised these new environments, but these species were later replaced by temperate endemic species following the climatic deterioration which commenced in the mid-early Eocene and has continued to establish the cool glacial climates of today. Ecological opportunity, thought to promote high levels of speciation, would have been provided by the extinction of the older tropical flora together with fluctuating environmental conditions caused by variability in SSTs, sea level, current flow and upwellings events. The submergence of the land barrier between Australia and Antarctica in the late Oligocene permitted the invasion of species from the Australian east coast on to the south coast, further increasing species richness in the region.

Abundant rocky substrata which form large sections of the extensive southern Australian continental shelf provide many different habitats, each supporting a characteristic macroalgal assemblage, further contributing to the high species richness of the region.

The warm Leeuwin Current has been the dominant oceanographic feature on the Australian south west and south coasts since the Eocene, dispersing macroalgal species onto the south coast and contributing to the maintenance of favourable environment in the region. Since most of the south coast macroalgal flora is largely derived from west coast species, a cold current flowing north along the west Australian coast since the Eocene, as is the case in southwest Africa and Pacific South America, could reasonably be expected to substantially reduce species richness on the Australian south coast.

The high level of endemism in the southern Australian macroalgal flora is related to the long isolation of the Australian continent coupled with low rates of macroalgal dispersal across ocean basins. The high levels of generic endemism is interpreted as indicative of a long evolutionary history, with divergence occurring *in situ*.

The lack of mass extinction events caused by adverse environmental conditions has maintained the high species richness of this southern flora. The east west trending coastline has experienced an equitable climate since the Eocene drifting north into warmer regions, free from the ice sheets, glaciation and cold currents which would have caused biological impoverishment.

Future research

There is enormous scope for further studies on the biodiversity of Australian macroalgae. Studies of biodiversity rely heavily on detailed knowledge of systematics, biogeography, phylogeny, ecology and past events and there is great need to collect more data in these areas for Australian marine macroalgae. Although the southern Australian benthic flora is the best documented algal flora in Australia, there are still many new species to be described, endemic species to be identified, phylogenetic relationships of taxa to be established and patterns of speciation to be determined. Local areas of high species richness and endemism also need to be identified.

Comprehensive ecological surveys are urgently required to accurately document species distribution patterns and abundances along the entire coastline. Existing collections are the result of sporadic sampling effort which often tends to record widely distributed and/or abundant species but not seasonal or narrowly distributed species. Although the geographical ranges of species are broadly known, existing data permit only generalised distribution patterns to be described. More distributional data is required before fine scale resolution can establish species distributions with greater accuracy, particularly when establishing the distributional limits of species. Locality data from drift specimens should not be used in determining geographical ranges as macroalgal thalli are known to be transported long distances in some circumstances. Furthermore, the patchiness of the distributional data is apparent when significant range extensions can be reported. The brown algae *D. gracilis* (Huisman et al. 1999; Phillips 2000) and *Scoresbyella profunda* (Huisman and Walker 1990; J. Phillips, pers. obs.), previously recorded only from the South Australia gulfs region (Womersley 1987), have recently been collected on Rottnest Island and in the Geraldton region on the west Australian coast, extending the geographical ranges of the species by approximately 3000 km.

We should now be directing research programs toward collecting the essential data necessary for detailed studies of macroalgal biodiversity patterns. Although broad scale regional (gamma) diversity patterns for southern Australia have been described, these patterns need to be described at much greater resolution, as do the regional macroalgal biodiversity patterns for other Australian coasts which remain little known. Furthermore, there is little data available on the number of species per unit area of seafloor (alpha diversity) or the turnover of species between adjacent small areas (beta diversity) and whether species rich floras have higher levels of alpha diversity and/or beta diversity than less species rich floras. These data need to be urgently collected so that considerations of macroalgal biodiversity and conservation can be included in Australian Government marine conservation and management initiatives, particularly in the development of regional marine plans.

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