Influence of the Leeuwin Current on the Marine Flora of the Houtman Abrolhos

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Abstract

The influence of the Leeuwin Current on the marine flora of the Houtman Abrolhos is examined. The marine plants (seaweeds and seagrasses) are assessed by comparisons of the Houtman Abrolhos species diversity and composition relative to a nearby coastal region (Jurien Bay), using the tropical and temperate floras of Western Australia as benchmarks. Our results demonstrate that, in terms of assemblage structure and taxonomic distinctness, the marine flora of the Houtman Abrolhos clearly represent a transitional zone between tropical and temperate regions, with the strong tropical influence a direct result of the Leeuwin Current. In contrast, the nearby inshore flora of the Jurien Bay region exhibits a much lower, almost negligible tropical influence.

Introduction

The Houtman Abrolhos is an archipelago of 122 mainly coral islands lying some 65–90 km offshore from Geraldton, Western Australia, at a latitude of 28 to 29°S. They include the southernmost examples of major coral reefs in the eastern Indian Ocean and are one of the highest latitude reef systems in the world (Wells 1997). The islands sit near the northern limit of what is known as the 'western overlap zone', a broad region extending from Cape Leeuwin in the south to North West Cape in the north. The flora and fauna of this region shows, to varying degrees, the southern temperate influence as well as the northern tropical.

It is well documented that the marine biota of the Houtman Abrolhos includes a high proportion of tropical species that would generally not be found at such high latitudes. These species would appear to owe their presence to the influence of the Leeuwin current, which brings warm waters from the tropics along the coast of Western Australia (Maxwell & Cresswell 1981; Morgan & Wells 1991; Huisman 1997; Pearce 1997; Wells 1997). This hypothesis, however, has never been tested in any meaningful or statistically robust way and doing so is the motivation behind the present contribution.

The influence of the Leeuwin Current can be sporadic, and this juxtaposition of warm tropical water with the colder water more typical of these latitudes encourages unusual associations and contributes to a wide diversity of organisms (Hatcher 1991; Huisman 1997). It is one of the few places where temperate kelps such as *Ecklonia*

radiata (C.Agardh) J.Agardh can be seen growing intermixed with tropical corals. It is thought that the warmer and nutrient-poor waters of the current promote coral growth at the expense of macroalgae, but periodic upwelling of nutrient-rich water promotes extensive algal growth (Hatcher 1991). Hatcher (1991) drew parallels between the Houtman Abrolhos and the Galapagos, another archipelago where 'coral and macroalgal communities vie for dominance' the outcome dependent on local oceanography.

Marine Plants

Until relatively recently, the marine flora of the islands was poorly known. Only sporadic records appear in the literature (e.g., Lucas 1926; May 1946, 1951; Levring 1953), mostly derived from collections made by the 'Percy Sladen Trust' expeditions of 1913 and 1915 (see Dakin 1918–1922) or collections made by school groups (Sammy 1972) and presently lodged in the Adelaide herbarium. These publications included, at most, only a few species (Huisman 1997). The same description could also be applied to much of the Western Australian coastline, with, until recently, the level of knowledge of the flora severely limited northward of Perth and becoming even more so into the tropics (Huisman et al. 1998). Recently, however, there has been a marked increase in activity. During the early 1990s one of us (JH) visited the Houtman Abrolhos on numerous occasions to collect marine plant specimens. Several new taxa were described as a result (e.g., Huisman & Gordon-Mills 1994; Huisman & Kraft 1992, 1994; Huisman & Millar 1996) all of which were included in a catalogue for the islands by Huisman (1997). The flora of the tropical Dampier Archipelago was documented by Huisman & Borowitzka (2003) and Huisman (2004). Underwater photographs of many

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Western Australian species were included in Huisman (2000) and Huisman et al. (2006). These publications represent only a small section of ongoing floristic and taxonomic studies of the Western Australian marine flora by JH and JP. In addition, collections held on the Western Australian Herbarium (PERTH) have recently been databased and the information made available via the Department of Conservation and Environment's 'FloraBase' website http://florabase.dec.wa.gov.au/). The PERTH collection now includes all marine plant specimens previously held by CSIRO, Murdoch University, and the University of Western Australia and therefore includes the vast majority of important historical and contemporary collections. As well as collection data for each specimen, also included in the PERTH database are precise location coordinates.

In addition, the 'Australian Marine Algal Name Index' is now available through the Commonwealth Department of Environment and Water Resources website (http://www.anbg.gov.au/abrs/online-resources/amani/). This index collates all published records of algal species in Australia and can be searched in a variety of ways, including by State boundaries, broad bioregional provinces (e.g., the tropical Dampierian Province or the temperate Flindersian Province) or, in a few instances, by more precise localities (e.g., the Houtman Abrolhos).

Added to this trove of information are the significant records generated by surveys undertaken by one of us (JP) and jointly identified (JP and JH). These surveys include the Jurien Bay region, allowing us an onshore focus with which comparisons with the Houtman Abrolhos can be drawn.

Thus the level of knowledge since the previous Leeuwin Current Symposium in 1991 has increased manyfold and the scope for analyses of species' distributions and regional biodiversity has been greatly expanded. Given this wealth of new resources, we have undertaken analyses in an attempt to:

- Assess, in a statistically meaningful way, the biogeographical affinities (tropical versus temperate) of the Houtman Abrolhos marine flora, and:
- Compare the flora with that of Jurien Bay region, the nearest onshore locality that we have comparable data for.

The Environment of the Houtman Abrolhos Islands

The Houtman Abrolhos archipelago sits some distance offshore on the edge of the continental shelf and is subjected to a different set of environmental parameters relative to nearshore localities such as Geraldton and Jurien Bay. The most significant difference is the influence of the Leeuwin Current, as the archipelago lies in the direct path of the current and often receives its full force, whereas the nearshore experiences very little direct influence. This was first noted by Saville-Kent (1897), who recorded the waters surrounding the islands to be approximately 2°C warmer than those inshore and suggested that this was due to a southward flowing current sitting offshore. The impact of the Leeuwin

Current on the Houtman Abrolhos environment has subsequently been documented by several authors (see Pearce 1997). While it appears that the Leeuwin Current is the dominating environmental feature, other factors should not be excluded.

Winds

Winds at the Houtman Abrolhos and nearshore were reviewed by Pearce (1997) and Chua (2002), and a detailed analysis of hourly and seasonal Houtman Abrolhos winds for 1995 was included in Sukumaran (1997). Generally there are strong seasonal southerlies (*i.e.*, northward) during late autumn to early spring, whereas the winter winds are much more variable due to gales and also periods of calm (Steedman & Associates 1977). The seasonal wind pattern is similar at both the Houtman Abrolhos and the mainland coast (Pearce 1997), but the wind strength tends to be greater at the Abrolhos (Abrolhos: mean wind speed in winter 6.5 m/s and summer 8.6 m/s; Geraldton airport: 4.4 m/s winter and 6.9 m/s summer) (Pearce 1997).

There is a diurnal seabreeze wind cycle evident both at the Houtman Abrolhos and the coast, although the pattern is somewhat weaker offshore (Pearce 1977). The seabreeze patterns and wind speeds are stronger during summer months than in winter. At Jurien Bay, easterlies (blowing offshore) dominate in the mornings, with the seabreeze coming in at 10 to 15 m/s from the south/southwest/west in the afternoon (Chua 2002). At the Abrolhos, these diurnal patterns were less marked, but there is a southeasterly wind in the morning followed by a southwesterly in the afternoon (Sukumaran 1997).

Currents

The Leeuwin Current is the dominant ocean current off the Western Australian coast, flowing southwards along the edge of continental shelf and therefore directly affecting the Houtman Abrolhos islands (Pearce 1997). Satellite images show a variety of current jets and meandering waters off the archipelago, ranging from southward currents (the Leeuwin Current) brushing the islands to large offshore anticlockwise eddies causing (potentially) northward currents along the shelf break (Pearce 1997). Records from current-measuring moorings for the period September 1986 to August 1987 were reported by Boland et al. (1988). These showed the southward Leeuwin Current flowing at up to 50 cm/s (1 knot) offshore of the Abrolhos, with the strongest and most persistently southward flow in November 1986 and between February and June 1987, and more variable directions (and lower speeds) in January and June/July (see also Pearce 1997). Satellite buoy tracks (e.g., Pearce 1997) also indicated onshore flow through the Islands and into the nearshore waters on occasion.

Currents on the continental shelf were very much weaker and also more variable in direction (with more current reversals) (Pearce 1997; Boland *et al.* 1998). This variability was also observed by Cresswell *et al.* (1989), using earlier current meter data from the mid-1970s. Generally there was a southward flow between March and August 1974 (p.117) and northward at other times of the year. Pulses of onshore/offshore currents with speeds generally <20 cm/s have been recorded (Pearce 1997), but

there is little direct influence of the Leeuwin Current near the coast.

Chua (2002) deployed a current meter in Essex Lagoon (near Jurien) for 2 weeks in August 2002 (*i.e.*, winter) to validate his modelled currents. This recorded a predominantly southward flow at speeds of up to 15 cm/s, highly correlated with the wind although also influenced by other factors (p.60–62).

Water temperature

The only long-term time-series data at the Houtman Abrolhos (Rat Island) and inshore (Dongara, Jurien) are from Fisheries Western Australia temperature loggers recording hourly. Pearce et al. (1999) reported monthly mean temperatures at Rat Island ranging from 19.5°C (August) to 23.3°C (March), Dongara ranging from 17.5°C (July) to 23.9°C (February), and Jurien ranging from 18.3°C (September) to 22.2°C (March), based on data from 1990 to 1994. The temperature data reported by Pearce (1997) and Pearce et al. (1999) clearly shows that the Leeuwin Current maintains warmer temperatures at the Houtman Abrolhos over winter, effectively dampening atmospheric influences and restricting the annual variation to approximately 20-24°C, a range of 4°C. In contrast, the shallow coastal waters of Dongara are more directly influenced by atmospheric conditions, warming to 24°C in February and dropping to less than 18°C in July/August, an annual range of 6°C and in phase with coastal air temperatures.

Salinity

Water samples taken monthly at the same sites as the temperature loggers (Pearce 1997) showed salinity ranges at Rat Is. of 35.37 (July) to 35.74 (January); Dongara 35.40 (July) to 36.34 (February). The higher inshore salinities in summer are due to evaporation, whereas the lower offshore salinities in winter are due to the Leeuwin Current

Tides

Observed tides at the Houtman Abrolhos and inshore are mainly diurnal with a small amplitude of 0.5 to 1 m (Pearce 1997), with a high correlation between the two areas (Pearce 1997). Water movement due to wind and atmospheric pressure changes can have a marked impact, and as a result predictive tide tables can be unreliable. Tidal currents are negligible because of the small tidal range (Chua 2002)

Materials and Methods

Species data

Our marine plant data are derived from species lists generated by several surveys conducted in each region. Houtman Abrolhos data were predominantly collected by JH during qualitative surveys conducted during the 1990s (Huisman 1997). Records for the Jurien Bay region (here defined as the area extending from Wedge Island (30°49'43"S, 115°11'18"E) to Dongara (29°15'17"S, 114°55'05"E) consist largely of the extensive collections made by JP during 2003 to 2006 as part of CSIRO's quantitative ecological surveys of the region (Babcock *et*

al. 2006) and joint CSIRO/Western Australian Museum surveys conducted in March 2006. All marine plants were hand-collected from five randomly placed 0.25 m² quadrats at 45 sites located throughout the region, covering both reef and seagrass habitats at varying depths and levels of wave exposure. All specimens were identified to species level by either JP or JH. Species data from these surveys were supplemented by additional records of lodged specimens from other collectors held in the Western Australian Herbarium (PERTH). Quantitative data were converted to presence-absence data prior to analyses.

Benchmark floras from the Dampierian and Flindersian Provinces were extracted from the 'Australian Marine Algal Name Index' (http://www.anbg.gov.au/abrs/online-resources/amani/), representing tropical and temperate floras of Western Australia, respectively, and were included in analyses. The biogeographic provinces follow the scheme illustrated by Womersley (1981) and later (with slight modifications) by Huisman (2007; p. 544, Fig. 77), who note that the distribution of marine algae appears to agree with most of these provinces. Species data for these provinces were extracted from the database of specimens lodged at the Western Australian Herbarium (PERTH).

Data analyses

Multivariate analyses were performed in PRIMER v6 (Clarke & Gorley 2006) following transformation of all data to presence/absence species lists for each region. A non-metric multi-dimensional ordination (nMDS) was then performed, using a Jaccard similarity measure. Additionally, the average taxonomic distinctness (Δ^+) was calculated, which is an intuitive measure of biodiversity that measures the average degree to which species in each region are related to each other (Clarke & Warwick 1998; Warwick & Clarke 1998; Ellingsen et al. 2005). Taxonomic distinctness analysis was used because it is independent of sampling effort and not influenced by the number of observed species (Clarke & Warwick 1998). Taxonomic distinctness incorporates the number of species present as well as the path length linking each pair of species in a hierarchical classification (see Clarke & Warwick 2001 for full equation).

In this study the taxomonic levels used for marine plants were species, genus, family, order and division, according to the classification described by Guiry & Guiry (2008). Equal path lengths were used between taxonomic levels to calculate Δ^+ , such that the path length for different species in the same genus was 20, while species that were related only at the highest taxonomic level (*i.e.*, belonging to the same division) had a path length of 100. Following computation of Δ^+ , values were tested for the departure of Δ^+ for each region from the overall value of Δ^+ expected for the 'global' species list, from 1000 independent simulations for each subset size (no. of species, m = 200, 250, 300, ... 800) drawn randomly from the 'global' total of 987 algal species.

Results

A total of 295 and 341 species were recorded from the Houtman Abrolhos and Jurien Bay region, respectively.

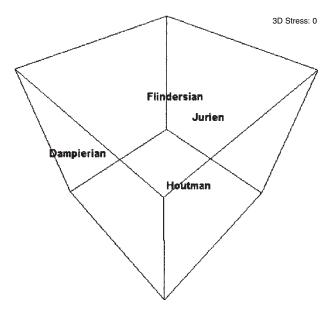


Figure 1. Non-metric 3-dimensional scaling plot of algal regions used in this study, based on presence/absence species data for each region.

Of these, 13.6% of species recorded from the Houtman Abrolhos were endemic to the area (when compared with other areas included in this study), compared with 2.6% for the Jurien Bay region. Furthermore, 9% of Houtman Abrolhos marine plants have a tropical affinity (Table 1) compared with only 0.9% of species from the Jurien Bay region. Using the Dampierian flora as a benchmark for

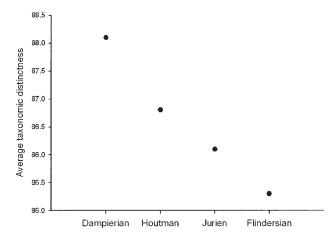


Figure 2. Average taxonomic distinctness for each of the four algal regions, arranged from north to south (L to R). $R^2 = 0.98$.

the tropical flora of Western Australia, it was found that 25% of species were common to the Houtman Abrolhos and tropical Dampierian Province. A similar proportion of species were common to both the Houtman Abrolhos and the temperate Flindersian Province. Markedly different trends were seen in the Jurien Bay region flora; around 17% of species were shared with the Dampierian flora, compared to 39% shared with the Flindersian flora.

The ordination based on the assemblage-level data showed a large separation (*i.e.*, high dissimilarity) between the floras of most regions (Figure 1). The least similarity observed among regions was between the

Table 1

Tropical algal species recorded from the Houtman Abrolhos (information updated from Huisman 1997)

RHODOPHYTA

Amphiroa fragilissima (Linnaeus) Lamouroux

Antithamnion antillanum Børgesen

Botryocladia skottsbergii (Børgesen) Levring

Callophycus serratus (Harvey ex Kützing) Silva

Ceramium macilentum J.Agardh (as C. mazatlanense Dawson)

Ceratodictyon spongiosum Zanardini (Figure 4H)

Chondria dangeardii Dawson

Chrysymenia kaernbachii Grunow

Chrysymenia ornata (J. Agardh) Kylin

Coelothrix irregularis (Harvey) Børgesen

Corallophila huysmansii (Weber-van Bosse) Norris

Dasya iyengarii Børgesen

Dasya pilosa (Weber-van Bosse) Millar

Endosiphonia spinuligera Zanardini

Parviphycus tenuissimus (Feldmann & Hamel) Santelices (as Gelidiella pannosa Feldmann & Hamel)

Gelidiopsis variabilis (J. Agardh) Schmitz

Gloiocladia indica Weber-van Bosse

Gloiocladia rubrispora (Searles) Norris

Gracilaria canaliculata Sonder

Lomentaria corallicola Børgesen

Monosporus indicus Børgesen

Platysiphonia victoriae (Harvey ex J.Agardh) Womersley & Shepley (as Platysiphonia corymbosa (J.Agardh) Womersley & Shepley)

Platysiphonia marginalis Wynne, Kraft & Millar

Polysiphonia gracilis Tseng

Predaea laciniosa Kraft

Predaea weldii Kraft & Abbott

Spirocladia barodensis Børgesen

Titanophora pikeana (Dickie) Feldmann (as T. weberae Børgesen) (Figure 4E)

Trichogloea requienii (Montagne) Kützing (Figure 4B)

Yamadaella caenomyce (Decaisne) Abbott

CHLOROPHYTA

Anadyomene plicata C. Agardh (as A. brownii (Gray) J.Agardh) (Figure 4F)

Boodlea composita (Harvey) Brand

Caulerpa fergusonii Murray

Caulerpa mexicana Sonder ex Kützing

Caulerpa racemosa var. corynephora (Montagne) Weber-van Bosse

Caulerpa racemosa var. lamourouxii (Turner) Weber-van Bosse

Caulerpa racemosa var. peltata (Lamouroux) Eubank

Caulerpa racemosa var. turbinata (J. Agardh) Eubank

Caulerpa serrulata (Forsskål) J. Agardh

Caulerpa webbiana Montagne

Codium geppiorum Schmidt (Figure 4G)

Dictyosphaeria cavernosa (Forsskål) Børgesen (Figure 4C)

PHAEOPHYCEAE

Dictyota ceylanica Kützing

Dictyota mertensii (Martius) Kützing

Padina boryana Thivy (as Padina tenuis Bory de Saint-Vincent)

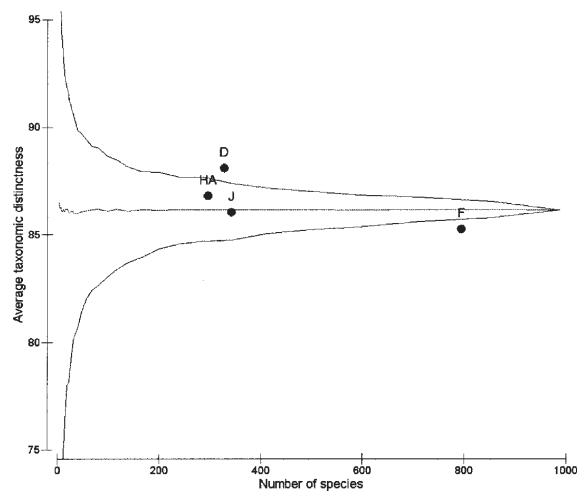


Figure 3. The 95% probability limits (solid upper and lower lines of 'funnel') for the average taxonomic distinctness of algae (Δ^+) from 1000 simulations for a range of species subset sizes. Also shown are the actual values for each algal region plotted against the number of species recorded in each region, and the Δ^+ for the 'global' list of 987 algal species (dashed line). D = Dampierian; F = Flindersian; HA = Houtman Abrolhos; J = Jurien.

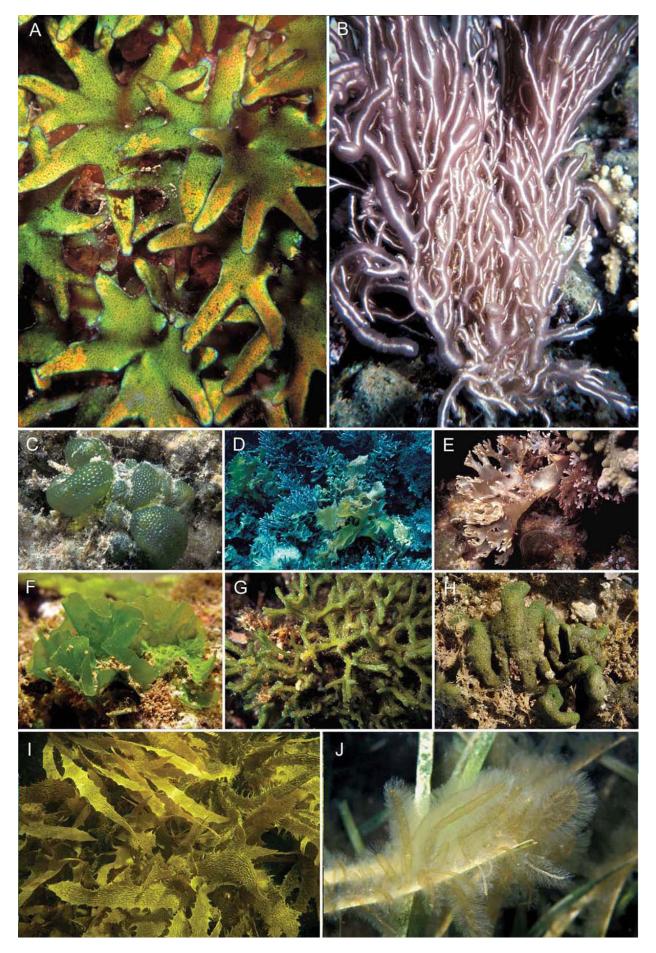
Jurien Bay region and the tropical Dampierian assemblage (Jaccard similarity = 17.6%), while greatest similarity (39.1%) was between the Jurien Bay region and the temperate Flindersian assemblage. When considering the similarity between the Houtman Abrolhos assemblage and those of other regions, it showed a similarity of 25.2% and 32.8%, respectively, to the Dampierian Province and Jurien Bay region.

The average taxonomic distinctness (Δ ⁺) decreased with increasing latitude south (Figure 2), indicating greater taxonomic breadth, or biodiversity, in regions closer to the tropics. The temperate Flindersian flora had the lowest taxonomic biodiversity of all regions considered.

Testing for the departure of calculated values of Δ^+ from expected values based on the 'global' master list revealed that the 'benchmark' temperate Flindersian flora, despite having the greatest number of species recorded (S=794), had significantly lower than expected Δ^+ (p = 0.002; Figure 3). Conversely, the Δ^+ of the 'benchmark' tropical Dampierian flora was significantly greater than expected (p = 0.002). The floras of the Houtman Abrolhos and Jurien Bay regions fell within the expected range (95% CI) of Δ^+ values.

Discussion

The marine flora of the Houtman Abrolhos islands is a diverse assemblage, and as previously noted (Huisman 1997) includes a mixture of species from both tropical and temperate origins. The former category includes typically tropical taxa such as the green algae Boodlea composita (Harvey) Brand, Caulerpa webbiana Montagne, C. cupressoides (West) C. Agardh, C. lentillifera J. Agardh, and the red algae Asteromenia exanimans Saunders, Lane, Schneider & Kraft (Figure 4A), Trichogloea requienii (Montagne) Kützing (Figure 4B), Spirocladia barodensis Børgesen, Predaea weldii Kraft & Abbott, Titanophora pikeana (Dickie) Feldmann (Figure 4E), and Ceratodictyon spongiosum Zanardini (Figure 4H) (see Table 1). Examples of taxa with more temperate affinities are the green algae Caulerpa obscura Sonder, C. simpliciuscula (R. Brown ex Turner) C. Agardh, Codium laminarioides Harvey, the brown algae Myriodesma quercifolium (Bory de Saint-Vincent) J. Agardh, Asperococcus bullosus Lamouroux (Figure 4J), Ecklonia radiata (C.Agardh) J.Agardh (Figure 4D, 4I), and the red algae Carpothamnion gunnianum (Harvey) Kützing and Hennedya crispa Harvey. Many of these species are at the southernmost limit (in the case of tropical species) or northernmost limit (in the case of



temperate species) of their distribution at the Houtman Abrolhos.

Our analyses at the assemblage level gave some insight into the influences of the Leeuwin Current on the marine plant floras of the Houtman Abrolhos and Jurien Bay regions, using the Dampierian and Flindersian Provinces as benchmarks. The flora of the Houtman Abrolhos showed a slightly greater affinity with the tropical (Dampierian) rather than the temperate (Flindersian) region of Western Australia, while the more southerly located Jurien Bay region was clearly strongly affiliated with the temperate flora. This suggests the Leeuwin Current exerts a greater influence on the algal flora of the offshore Houtman Abrolhos compared to the inshore Jurien Bay region, although it must also be recognised that differences in sampling methods, intensity and objective, as well as the number of species recorded in each region, could be confounding our results. Our choice of the Jurien Bay region as a comparison was based on availability of species records, as comparable data are not available for the more northerly mainland immediately adjacent to the Houtman Abrolhos. Thus it could be argued that our findings simply represent a latitudinal gradient and are not illustrative of the Leeuwin Current's influence. While we acknowledge this, we also point out that a search of the WA Herbarium records (undertaken 16 July 2008) of the tropical species recorded for the Houtman Abrolhos (Table 1) vielded no records of these species on the adjacent mainland, and only two further south (a single record of Yamadaella caenomyce at Rottnest Island and several of Chondria dangeardii at Jurien Bay). Conversely, records of temperate species are also scant, but several of the examples given above (including Ecklonia radiata, Hennedya crispa, Caulerpa simplicuiscula and Myriodesma quercifolium) have been found to as far north as Kalbarri (27°42'S). The most northerly mainland record of Ecklonia radiata is a drift specimen at Horrock's Beach (28°22'S), further south but closely comparable to the Houtman Abrolhos record at North Island (28°18'S). These observations would suggest that some temperate species, at least, are found at comparable latitudes to the Houtman Abrolhos on the mainland, but no tropical species. However, the records from the region are sparse and often based on drift specimens, so we refrain from drawing any conclusions regarding species distributions. These observations do suggest, however, that our results would not have changed in any way if a more northerly mainland region was included in the analyses. What is also clear is that the marine flora of many regions of the Western Australian coastline is poorly represented in the WA Herbarium, a situation that can only be remedied by increased collecting.

A more robust method of determining the influence of the Leeuwin Current is to consider the taxonomic

breadth of each algal region. The measure used in this study, average taxonomic distinctness (Δ^+), is independent of sampling effort and techniques and is an intuitive measure of biodiversity (Clarke & Warwick 2001). In this study, Δ^+ was negatively correlated with increasing latitude. Although latitude itself is not considered a major driver of biodiversity, it is welldocumented that the temperature (and therefore influence) of the Leeuwin Current decreases with increasing latitude, due to mixing, radiation and evaporation (Cresswell 1991: Figure 1). The observed decrease in taxonomic breadth moving south along the Western Australian coastline may be, in part, related to the southerly-flowing Leeuwin Current although other environmental factors including habitat diversity (Clarke & Warwick 2001) may play a role. Furthermore, although the Houtman Abrolhos lie within the Flindersian Province with the result that many species are common to both areas, the similarity in Δ^+ values between the Houtman Abrolhos and the Dampierian Province indicate a substantial tropical influence at the former. From this, we conclude that the affinities of the marine algae of the Houtman Abrolhos clearly indicate a transitional zone between tropical and temperate regions, with the strong tropical influence a direct result of the Leeuwin Current. In contrast, the nearby inshore flora at Jurien Bay exhibits a much lower, almost negligible tropical influence. Both Hatcher (1991) and Huisman (1997) recognised the influence of the Leeuwin current on the marine algal assemblages of the Houtman Abrolhos on a broad scale - this is now confirmed by the more detailed analyses undertaken here.

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◀ Figure 4. Marine algae from the Houtman Abrolhos. A. Asteromenia exanimans Saunders et al., found at the Houtman Abrolhos and also at Jurien Bay. B. The red alga Trichogloea requienii, a widespread tropical species found at the Houtman Abrolhos. C. The green alga Dictyosphaeria cavernosa is found in the tropics worldwide and reaches its most southerly distribution in Western Australia at the Houtman Abrolhos. D. The kelp Ecklonia radiata growing amongst the coral Acropora, one of many unusual associations of temperate and tropical species at the Abrolhos. E. H. Tropical species at their southern limits at the Houtman Abrolhos: E. The red alga Titanophora pikeana. F. The green alga Anadyomene plicata. G. Another green alga, Codium geppiorum. H. The red, sponge-associated alga Ceratodictyon spongiosum. I, J. Temperate species at their northern limits at the Houtman Abrolhos: I. The kelp Ecklonia radiata. J. The brown alga Asperococcus bullosus. (Photos: J. Huisman).

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