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## Where is the western limit of the tropical Indian Ocean seaweed flora? An analysis of intertidal seaweed biogeography on the east coast of South Africa

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**Abstract** New, large-scale collections have been made of marine benthic macroalgae (seaweeds) on the east coast of South Africa, and the distributions of shallow-water species were analyzed in detail by multivariate, clustering and  $\beta$ -diversity methods. The two northernmost sites are distinct, with a predominance of tropical species, and it is concluded that the changeover from a tropical Indian Ocean flora to a temperate South African flora occurs most rapidly in the vicinity of St. Lucia, 135 km south of the Mozambique border. It is imperative that all future biogeographical studies on the South African inshore marine biota include detailed collections north of St. Lucia. The remaining 440 km of the South African east coast (southern and central Kwazulu-Natal Province) is populated by a mixture of tropical and temperate elements, with only 2% endemism in this data set. This, thus, represents a true overlap region, with relatively equal numbers of species with affinities in the temperate Agulhas and tropical Indo–West Pacific floras, rather than a distinctive sub-tropical marine province, as the South African east coast is considered to be by most previous authors. The distinction between this overlap region and the south coast (Agulhas) region proper is not as clearly distinct. The change from a temperate to a

tropical flora shows a relative increase in green algae from 15% to 25% of the species present. Criteria for the delineation of marine biogeographical regions are critically discussed, and it is concluded that the monitoring of distributions of all species, including rare species, is necessary. This is particularly relevant with regard to using these data to assess effects of potential changes in seawater temperature, including those which may be caused by global warming. Criteria for the delimitation of biogeographic entities such as “marine provinces” need to be clearly spelt out in all investigations.

### Introduction

Seaweeds are, in many respects, ideal organisms for the study of biogeographic patterns on shallow, marine rocky shores. They are ubiquitous primary producers in these habitats, attached and non-motile, and easy to collect and preserve. In addition, they have relatively similar species numbers in any one large region from temperate to tropical regions (Bolton 1994), and comprise representatives of three major phyla, which, though widely divergent phylogenetically, have a series of convergent functional forms (Littler and Littler 1980). A wealth of information is available documenting experimentally the environmental basis of seaweed geographic distribution (e.g. Breeman 1988; Lüning 1990), much more than is the case for other co-existing groups of organisms. Seaweed data have been used in studies on the effects of marine climate change (Breeman and Packer 1994; Beardall et al. 1998), and a number of studies have been made using temperature and ocean current patterns in geological time to explain modern seaweed phylogeographic patterns (e.g. Hoek 1984; Hommersand 1986; Breeman 1990; Adey and Steneck 2001).

The tropical Indo–West Pacific is the largest coastal biogeographic region on earth (Briggs 1974; Adey and

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Steneck 2001), and also has the most seaweeds recorded for any one region, with 2991 seaweed species and sub-specific taxa for the Indian Ocean alone (Chlorophyta, Phaeophyceae and Rhodophyta; Silva et al. 1996). Silva et al. (1996) used a geographical definition of the Indian Ocean, and placed the western limit of the region at the southernmost point of Africa (Cape Agulhas, Fig. 1). This is not consistent with biogeographical patterns, as it includes the south coast (Agulhas marine province) of South Africa, which is clearly warm temperate, floristically and in temperature regime (Stephenson 1948; Hommersand 1986; Lüning 1990; Bolton and Anderson 1997). Stephenson (1948) carried out a major intertidal survey of the, then, Union of South Africa. Although these studies were primarily zoological, Stephenson also collaborated with a number of seaweed taxonomists, notably G.F. Papenfuss (see Bolton 1999), and produced a significant list of the seaweeds of South Africa (280 “species and major varieties”; Stephenson 1948). South Africa has since been shown to have an extremely rich seaweed flora of well over 800 species; Bolton and Stegenga (2002) gave a figure of 803 species, and there have been numerous additions since this listing was completed (e.g. by Leliaert et al. 2001; Stegenga et al. 2001a, 2001b, 2002a, 2002b; De Clerck et al. 2002a, 2002b, 2002c).

There have been two main criteria for delineating marine provinces. Many have followed Eckman (1953) in using endemism as a primary criterion. This is most clearly described by Briggs (1974), thus: “in this work, an admittedly arbitrary decision has been made: if there is evidence that 10 percent or more of the species are endemic to a given area, it is designated as a separate province”. In contrast, seaweed biologists have tended to follow Hoek and Donze (1967), who regarded an algal phytogeographic province as “a part of the coast characterized by a more or less homoge-

neous flora and separated from other such parts by comparatively small stretches of coast with a rapidly changing flora, i.e. by floristic discontinuities”. Using simple discontinuity to delimit marine provinces has been followed on the South African coast by both botanists and zoologists (e.g. Bolton 1986; Emanuel et al. 1992; Farrell et al. 1994; Proches and Marshall 2002).

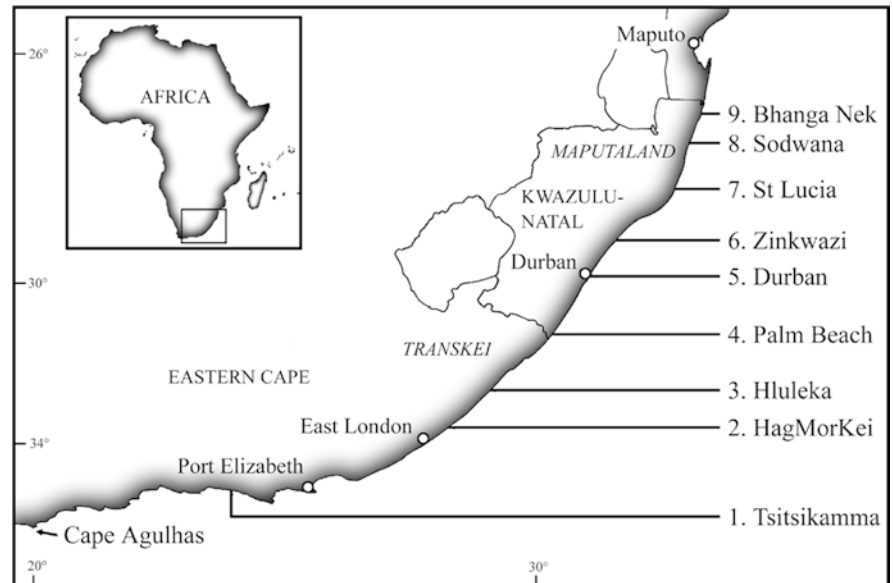
A marine biogeographic region or province could thus be described as a length of coastline that:

1. has a homogenous biota, separated by floristic and/or faunistic discontinuities from adjacent coastlines with different biotas and
2. has a significant proportion of its biota endemic to it, and is thus formed to a significant extent by the geographically limited evolution of new species, rather than predominantly by dispersal from other regions with similar temperature regimes.

The inclusion of item 2 makes it possible to study these criteria in a more scientific manner, by making it feasible to test evolutionary hypotheses using biogeographic data (see Hommersand 1986 for the formulation of such hypotheses using the South African seaweed flora, and Hommersand and Fredericq 2003 for an initial test of these phylogeographic hypotheses using molecular data). It is, however, important to clearly document limits and discontinuities of all species, in order to track biotic change over time, increasingly important with global warming (see Breeman 1990) and with increasing numbers of human introductions (e.g. Ribera and Boudouresque 1995; Maggs and Stegenga 1999).

The east coast of South Africa, comprising the coast of Kwazulu-Natal Province (KZN) formerly known as Natal (Fig. 1), was described as “sub-tropical” by Stephenson (1948). Stephenson carried out extremely

**Fig. 1** Map of the study area, showing sites and regions mentioned in the text



limited sampling in the northern section of the South African east coast, with only one site in the northernmost 311 km (“Umpangazi” near the present day Cape Vidal, 127 km from the Mozambique border). It is clear from Stephenson’s writings that he did not have a clear idea of the nature of the biota along this coastline, as can be seen from the following comments (from Stephenson 1948): “... the fauna of Natal can be put down as a typical subtropical fauna ... and is also characterized by an admixture of temperate species. How strong the endemic element will prove to be ... we cannot tell: and upon this depends whether Natal can be put down as a typical subtropical fauna or as one primarily of a transitional nature.”

Quite a number of the species in Stephenson’s (1948) seaweed list are tropical species, recorded for “Umpangazi” only, and, furthermore, a list of species produced for the “Maputland” region of northern Kwazulu-Natal by Seagrief (1980) includes a number of Indo-Pacific tropical species recorded for the first time in South Africa.

South African inshore marine zoogeographers still generally accept at least most of Stephenson’s biogeographic system, as described in the review of Brown (1999). There are, however, a number of different ideas in the literature on the overlap between tropical and temperate regions along this coastline. More recent zoogeographers have followed Stephenson in documenting the existence of an overlap region between the south and east coasts, as well as a sub-tropical east coast region or marine province, although the proposed boundaries vary considerably (Day 1967; Brown and Jarman 1978; Branch and Branch 1981; Siegfried 1981; Thandar 1989; Emanuel et al. 1992; Farrell et al. 1994; Turpie et al. 2000; Proches and Marshall 2002). Bolton and Anderson (1997), working with seaweed data, differed in not recognizing a sub-tropical east coast region or marine province, instead postulating an extended overlap region. They were of the opinion that “although this matter is not clearly resolved ... at this stage we consider an ‘Eastern Overlap’ between Agulhas and Indo-West Pacific marine provinces comprising the coastline from around East London to the Mozambique border”.

Considerable taxonomic work was carried out on the red seaweeds of Kwazulu-Natal by R.E. Norris (around 40 publications from 1985 to 1995, including a few in collaboration with Y.M. Chamberlain, M.J. Wynne and others; see bibliographies in Norris 1992; Silva et al. 1996). This work has made the production of accurate seaweed diversity and distribution data in the region much more feasible. The current analysis is a result of a recent project on the seaweeds of Kwazulu-Natal, which involved considerable collecting, both intertidally and subtidally, along the entire coastline of the region (see Bolton et al. 2001). This large dataset, comprising a large number of actual in situ records of the seaweeds of Kwazulu-Natal, was analyzed to investigate the following:

1. Is there evidence of a sub-tropical marine province on the east coast of South Africa, bounded by floristic discontinuities, with species endemic to it?
2. Where is the western limit of the tropical Indo-Pacific seaweed flora?

## Materials and methods

The dataset of Kwazulu-Natal seaweeds was based on collections made in 1999 and 2000 along the whole coastline of the province. A total of 3447 seaweed specimens was collected and preserved. These comprised 285 species that had previously been recorded for the region, as well as 45 new records for Kwazulu-Natal. As it was not possible to sample all sites subtidally by SCUBA, the current analysis uses only the shore collections, comprising intertidal, as well as shallow-water collections by snorkeling (a total of 270 species). In addition our dataset included voucher specimens of KZN seaweeds from the Norris Herbarium (NU, Bews Herbarium, Scottsville, South Africa), where they added distributional information.

For the purposes of the analysis, the KZN seaweed data was combined into six coastal sections, focused on major collecting areas [known as “Palm Beach” (site 4), “Durban” (5), “Zinkwazi” (6), “St. Lucia” (7), “Sodwana Bay” (8), “Bangha Neck” (9), see Fig. 1]. For all analyses, data were included from lists of seaweeds of three other coastal regions in the eastern Cape Province of South Africa. These were:

- “Tsitsikamma” (site 1): a list of the seaweeds of Tsitsikamma Coastal National Park (Stegenga, Anderson and Bolton, unpublished data),
- “HagMorKei” (site 2): a list of the seaweeds of the Kei Mouth to Haga Haga region (Stegenga, Bolton, Anderson and De Clerck, unpublished data) and
- “Hluleka” (site 3): published records for Hluleka Nature Reserve (Bolton and Stegenga 1987), plus unpublished records from a collection at Ntlongonyana by Engledow.

It was essential to combine sampling localities into these coastal sections, as individual localities often did not combine all types of seaweed habitat, and are thus not easily comparable.

Only taxa which could be identified to species level were included in the analysis. Distributions were interpolated, filling in gaps between species records along the coastline, a standard procedure in this type of analysis (e.g. Hoek and Donze 1967; Hoek 1975; Emanuel et al. 1992; Awad et al. 2001; Bolton and Stegenga 2002; Proches and Marshall 2002).

$\beta$ -diversity ( $\beta_T$ ) was calculated, as a measure of species turnover between the sites, based on presence/absence data, using the index of Wilson and Shmida (1984):

$$\beta_T = \frac{g(H) + l(H)}{2\alpha} \quad (1)$$

where  $g(H)$  equals the species gained between sites,  $l(H)$  equals the species lost between sites, and  $\alpha$  is the average species richness of the sites.

For ordination, the program CANOCO (Ter Braak 1988) was used. A detrended correspondence analysis (DCA) was used as an indirect ordination method. A two-way indicator species analysis (Hill 1979) was used as a classification method. Cluster analysis was also performed with STATISTICA 5.5 (Statsoft 2000), using Euclidean distances as a distance measure and unweighted pair group average as a linkage rule (UPGMA).

A further analysis was carried out to estimate the numbers of species at each site that also have been recorded in a true temperate south coast site and a true tropical Indo-Pacific region, and their percentage occurrence in the flora of each site. Thus, numbers of species at sites 2–9 that also occurred at site 1

(Tsitsikamma: considered a “south coast” site by all previous authors) and in tropical Tanzania (data from Silva et al. 1996) were calculated.

## Results

At the nine sites, 270 shallow-water species were collected, with an average of 143 species per site (range 118–160). There was no consistent geographical pattern in the species diversity between sites. As these data are only for taxa that could be identified to species, they are, in any event, not entirely accurate as a comparison of between-site diversity. The species total consisted of 68% red algae, 17% green algae and 14% brown algae. There was, however, a clear pattern of relative increase in species of green algae moving northwards, with an increase from 15% to 25% of the flora, and a consequent decrease in red algae from ca. 70% to 59% of the flora. Actual numbers of green algae ranged from 20 at site 1 to 35–40 at sites 8–9, whereas numbers of red algae varied in the range of 85–105 with no clear pattern. Species of brown algae comprised 14–18% of the flora at each site (20–25 species).

Values for  $\beta$ -diversity between sites ranged from 0.03 to 0.24 (Fig. 2). There was a low level turnover of species along most of the coastline studied, with values between most adjacent sites being around  $\beta_T=0.1$ . A slightly more rapid change in species composition occurred between sites 3 (Hluleka) and 4 (Palm Beach),  $\beta_T=0.15$ . This was caused mostly by an increase in species from warmer water, moving northwards. The greatest change in species along this stretch of coastline was between

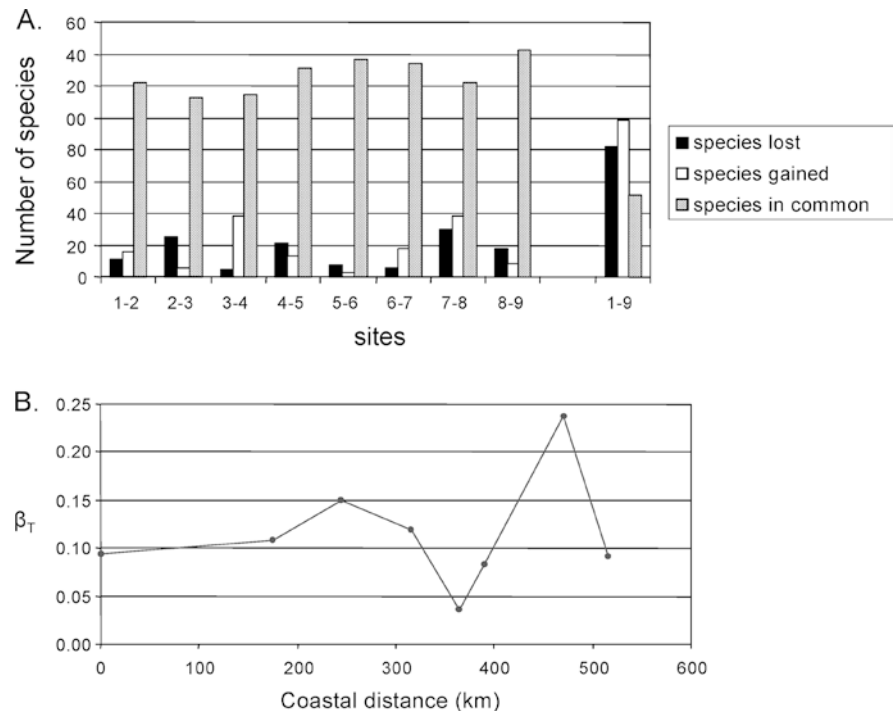
sites 7 (St. Lucia) and 8 (Sodwana),  $\beta_T=0.24$ , with fairly equal numbers of cool-water species lost and warm-water species gained.

The DCA (Fig. 3) shows little clear clustering. Axis 1, which shows most of the variation (eigenvalue 0.40), has the largest separation between sites 7 (St. Lucia) and 8 (Sodwana). The other largest differences on axis 1 are between sites 2 (Hagmorkei), 3 (Hluleka) and 4 (Palm Beach). Axis 2 (with a very low eigenvalue, 0.04) distinguishes the south coast site 1 (Tsitsikamma) from all others.

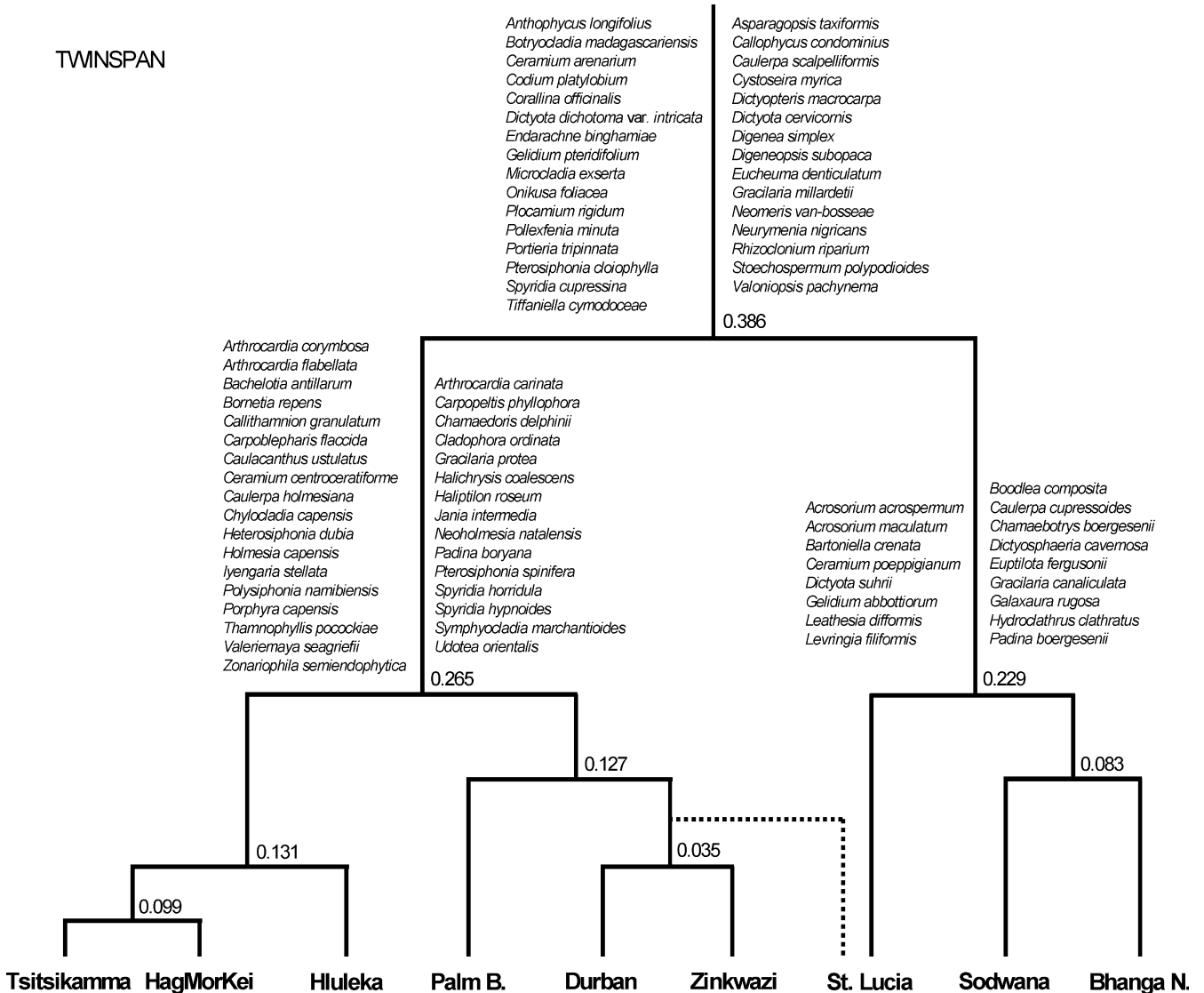
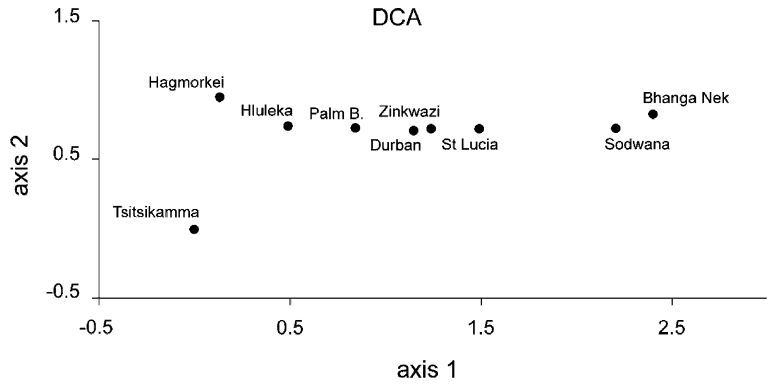
Both the TWINSpan and cluster analysis (Fig. 4) clearly separate the floras from sites 8 (Bhanga Neck) and 9 (Sodwana) from those of sites 1–6 (Zinkwazi southwards). The position of the St. Lucia (site 7) sample varied, with TWINSpan linking it with sites 8 and 9, but the UPGMA linking it with sites 1–6. The initial separation in the TWINSpan analysis shows preferential species that have clearly temperate South African affinities at sites 1–6, with tropical Indo-Pacific preferential species for sites 7–9. Similarly, at the second step the preferential species for St. Lucia are South African temperate, whereas those for sites 8–9 have tropical Indo-Pacific affinities. The other second-step separation shows species that generally occur west of Cape Agulhas (documented in Stegenga et al. 1997) as being preferential for sites 1–3, whereas the preferential species for sites 4–6 are primarily Indo-Pacific species, extending a considerable distance down the KZN coastline.

It can also be seen from Fig. 5 that there is a major changeover in the St. Lucia region. At St. Lucia the flora consists of a fairly equal number of species that occur on

**Fig. 2A, B** Species turnover between sites shown in Fig. 1. **A** Number of species lost and gained between sites moving from west to east, and **B**  $\beta$ -diversity ( $\beta_T$ ) using the index of Wilson and Shmida (1984)



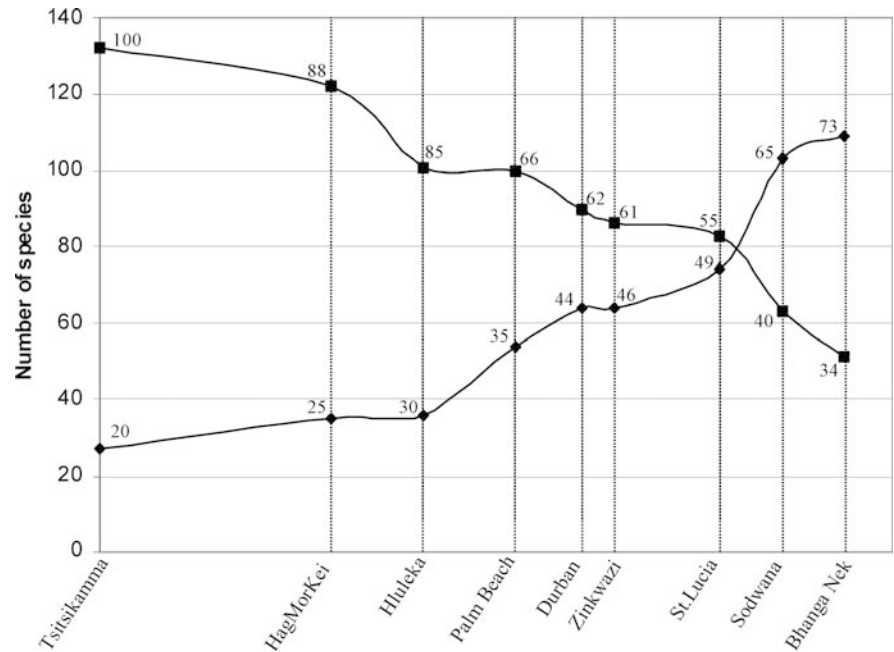
**Fig. 3** Detrended correspondence analysis (DCA) of presence/absence data for shallow-water seaweed species from the sites shown in Fig. 1. Axis 1 has an eigenvalue of 0.40; axis 2 has an eigenvalue of 0.04



**Fig. 4** Two-way indicator species analysis (TWINSPAN) of presence/absence data for shallow-water seaweed from the sites shown in Fig. 1, showing preferential species at each junction. A cluster analysis using Euclidean distances as a distance measure and unweighted pair group average as a linkage rule, showed identical groupings, except for the position of the St. Lucia site (shown by a dotted line)

the south coast (Tsitsikamma) and in a true Indo-Pacific region (Tanzania). At Sodwana, there is a clear dominance of tropical Indo-Pacific species, which make up 65% of the flora at Sodwana and 73% of the flora at Bhanga Neck. In the region from Hluleka southwestward, > 85% of the species grow at Tsitsikamma, and < 30%

**Fig. 5** Numbers of shallow-water seaweed species present at the sites shown in Fig. 1, which occur at a south coast site (Tsitsikamma, squares) and a tropical East African site (Tanzania, diamonds). Numbers represent the percentage of species at each site that are present at the south coast and tropical sites, respectively



grow in Tanzania. At the central sites (4–6), the flora consists of ca. 60% of species growing on the south coast and ca. 40% of species growing in Tanzania.

## Discussion and conclusions

$\beta$ -diversity indices, DCA, TWINSpan and cluster analysis are congruent in that they reveal three coastal regions: sites 8–9, sites 4–6 and sites 1–3, with site 7 having affinities with either sites 4–6 or 8–9 using various analysis methods. As is shown in both  $\beta$ -diversity and DCA analyses, the distinction between sites 1–3 and 4–6 is not a clear one. All analyses thus reveal that the major discontinuity in the seaweed floristic patterns along the coastline studied occurs between sites 6 (Zinkwazi) and 8 (Sodwana). Most analyses (DCA,  $\beta$ -diversity, Euclidean distance clustering) place this discontinuity between sites 7 (St. Lucia) and 8 (Sodwana), whereas the TWINSpan analysis clusters St. Lucia with sites 8–9. This suggests that the St. Lucia region encompasses considerable change and, as is seen from Fig. 5, the St. Lucia flora consists of approximately equal numbers of species occurring at Tsitsikamma on the temperate south coast and in tropical Tanzania. Between St. Lucia and Sodwana there is both a significant decrease in temperate elements and a significant increase in tropical elements (Figs. 2, 5). In the central region of our study area, from the southern KZN (site 4, Palm Beach) to site 6 (Zinkwazi), the seaweed flora changes relatively little (Figs. 2, 3, 5). From our analysis, a “south coast” cluster comprises sites 1–3, although the changeover between sites 3 and 4 is relatively much more gradual than between sites 7 and 8.

How can these various clusters be best described, when compared with previous analyses of biogeo-

graphical patterns on this coastline? The south coast cluster includes sites 2 (HagMorKei) and 3 (Hluleka), both of which would have been included in the “eastern overlap” of Stephenson (1948) and some later authors. A major difficulty with Stephenson’s classic interpretation of biogeographical patterns on this coast lies in his concept of warm-water species, the “eastern warm water component” (Stephenson 1948; Stephenson and Stephenson 1972). This comprised species which occurred on the east coast but not on the west coast, in his collections. There is thus some confusion concerning species occurring only on the South African south and east coasts, and true tropical Indo-Pacific species. From our seaweed data, we conclude that a temperate Cape, south coast flora delineates an Agulhas marine province (sensu Bolton and Anderson 1997). At the eastern limits of this province, the “Transkei” region [exemplified in this dataset by site 3, Hluleka; see Bolton and Stegenga (1987; Fig. 1)] is still dominated by south coast elements, with only 30% of the flora also occurring in tropical Tanzania. Thus, this region should be included in the Agulhas marine province. This is contrary to the findings of Bolton and Stegenga (1987), owing to their use of Stephenson’s misleading concept of a “warm-water species” (see above).

The major floral discontinuity occurs in the vicinity of St. Lucia, with most analyses showing it just north of this site. The two northernmost sites have 65% and 73% true tropical species, and can thus be designated as the southernmost section of the tropical Indo-Pacific floristic region.

In order for a true “sub-tropical” region to exist, there should be a significant proportion of species that are confined to the proposed region, which in the current analysis comprises sites 4–6. We collected a total of 186 shallow-water species at these sites, of which 44% had

tropical East African affinities and 40% had wide distributions from the east to west coasts of South Africa. A further 11% could be considered ubiquitous in a South African context, occurring from tropical East Africa to the South African west coast. Only 12 species remain (6%), which were exclusively recorded in this study at sites 4–6. Of these, only four species were endemic to southern Africa, one of which [*Gracilaria aculeata* (Hering) Papenfuss] does also occur, albeit less frequently, on the South African south coast. Thus, this region has only three seaweed species in our dataset (2%) that are truly endemic to it (*Cryptonemia papenfussii* Chiang, *Plocamium affine* Kützinger, *Osmundaria papenfussii* Norris). The latter two are interesting in that they are only known from the type collections. In the case of *P. affine*, this implies that the species has not been collected again since 1849. According to Engledow (unpublished data), the species bears close resemblance to a taxon known from southern Australia and New Zealand, *P. angustum* (J. Ag.) Hooker & Harvey, and its inclusion in the South African flora could possibly be the result of an historical mislabeling event. Most of the KZN coast flora (Palm Beach to St. Lucia) is thus clearly a mixture of temperate and tropical elements, with slightly more of the former (55–66% in Fig. 5), lacking a significant amount of shallow-water endemic species. This should, therefore, be treated as an overlap region between the tropical Indo-Pacific and the temperate South African south coast (Agulhas) region.

It is imperative, therefore, that biogeographic studies of the South African inshore marine biota include detailed collections from the extreme northeast (Sodwana Bay northwards). The changes apparent in the seaweed species composition in this region, demonstrated in this paper, are not clearly shown in other studies, most of which are analyses of distributions of groups of inshore fauna. The probable reason for this is that the extreme north of South Africa is poorly collected historically, due to logistical difficulties in reaching sampling sites. The recent paper on the biogeography of intertidal mites (Proches and Marshall 2002) has St. Lucia as its northeasternmost site. This initial study of the distributions of these organisms, made up of several terrestrial groups that have colonized the intertidal environment, reveals patterns that closely mirror the available seaweed data. For example, there are three major regions in the South African mite fauna, with the greatest species diversity in the southern province (see Bolton and Anderson 1997; Bolton and Stegenga 2002 for comparable seaweed data). If the pattern is consistent, a changeover to a tropical intertidal mite fauna could be hypothesized to occur in the St. Lucia region.

Cheney (1977) showed that in the North Atlantic there is a clear pattern in the ratio of red and green to brown seaweed species, with higher figures in warmer waters. It has been pointed out (Bolton 1986) that this pattern does not apply in southern Africa, as the cool-water brown algal flora in this region is relatively species poor (Bolton 1995). There is in our data, however, a

change in the ratios of major groups, with a clear increase in the green algal component (from 15% to 25%) moving from our temperate/tropical overlap region to the tropical flora at sites 8–9.

It is necessary to compare our biogeographical patterns with physical data. Recent oceanographic studies provide evidence of a temperature discontinuity between Cape Vidal and the Cape St. Lucia area. North of Cape St. Lucia, the continental shelf is narrow (about 10 km wide) and the shelf break (where the shelf steepens most, on this coast at about 40–50 m depth) is often <3 km from the shore (Schumann 1988). As a result, the coastal environment here is completely dominated by the warm, southward-flowing Agulhas Current. At Cape St. Lucia, the shelf begins to widen and the coast indents, creating the relatively shallow, up to 50 km wide, Natal Bight. Here, the current diverges from the coast and a topographically induced upwelling cell extends 160 km southwards, almost to Durban (Schumann 1988). The northern end of the bight feeds sub-surface water onto the shelf that is 2–3°C cooler than that of the Agulhas Current (Lutjeharms et al. 2000).

There is also a marked discontinuity in water turbidity and sediment load in the Cape St. Lucia region. Northwards, there is little riverine sediment input, and the Agulhas Current water is clear and nutrient poor (Lutjeharms et al. 2000; Flemming and Hay 1988). By contrast, south of St. Lucia, there are major mud deposits from the Umfolozi and Tugela Rivers, and the water in the Natal Bight is usually very turbid (Flemming and Hay 1988).

The in situ temperature data thus far available are not sufficient for a clear comparison. In the northern KZN, detailed data are only available for Sodwana Bay (Celliers and Schleyer 2002). Temperatures at Sodwana are clearly tropical, with monthly means varying from 22.5°C to 27.4°C. Also relevant is that good evidence exists that the mean sea temperature at Sodwana increased at a rate of 0.27°C per year from 1994 to 2000. This underlines the importance of the collection and analysis of baseline species data, as in the present contribution, for future studies on the effects of marine climate change. It is very unfortunate that there are no useable continuous inshore temperature data available for the St. Lucia region, our region of greatest change in the flora, but studies are under way to fill this gap.

In order for species data such as these to be useful in plotting the impacts of changes in temperature regime, for example as a result of global warming, it is necessary to have an understanding of the evolution of temperature tolerance in the organisms concerned. Temperature tolerance has usually been regarded as a conservative trait in seaweeds (see Lüning 1990), although there are a number of studies on ecotypic genetic variation within seaweed species with respect to temperature tolerance (e.g. Bolton 1983; Breeman and Packer 1994). The impact of climate change on seaweeds has been studied with respect to the ENSO phenomenon; for example, Carballo et al. (2002) demonstrated an increase in

abundance of warm-tolerant tropical seaweeds with increased ambient seawater temperatures. Similar methods to those used here need to be carried out on a number of coastlines and rates of change of species needed to be correlated with environmental variables, particularly seawater temperature regime. It is possible to correlate rates of change of environmental factors, such as seawater temperature regime, with the rate of change of species along a coastline, expressed either as  $\beta$ -diversity or a value for an axis on a multivariate analysis such as DCA (see Bolton and Anderson 1990 for an example of the latter). A combination of these different types of study is needed to provide a full picture.

It is also very likely that other components of the biological communities also vary along this gradient, which could affect the seaweed distributions. For example, there is a great increase in fish species diversity moving northwards in Kwazulu-Natal (Turpie et al. 2000), and many of these fish species are grazers or omnivores. Preliminary data also suggest a region of change in the echinoderm fauna in the vicinity of St. Lucia (Bolton et al. 2001). These community changes will undoubtedly affect the nature of the seaweed communities along this stretch of coastline, although it would be very difficult to assess the effects of other members of the community on seaweed presence/absence.

Adey and Steneck (2001) argue against the use of the criteria used in this paper for delimiting biogeographic regions, as, firstly, they involve the use of endemics, which are "generally rare", and, secondly, "to use species geographic limits as a marker for biogeographic boundaries almost certainly deals with rarity at those limits for even the most abundant species". They are of the opinion that this "mostly leaves biogeographers searching for extreme rarity, while inevitably dealing with problems of intensity of investigation and collection, as well as routine climatic fluctuations and human transport". We would challenge these opinions as, in our experience, most species in a seaweed flora, at any one site, are rare and/or low in biomass. This is especially true of seaweed floras in tropical regions. For example, in a community study of subtidal turf algal vegetation at Sodwana, 105 seaweed species were recorded in an area of 1.56 m<sup>2</sup>, and 54% of these taxa always occurred with a fresh biomass of <0.2 g m<sup>-2</sup> (Anderson, McKune, Bolton and De Clerck, unpublished data). Also, when the conservation of seaweed diversity is considered, it is the rare and endemic species that are critical in the investigation. Using community data of abundant organisms, as proposed by Adey and Steneck, is simply a different criterion for delineation of regions, not necessarily a better one. A variety of systems of biogeographic regions needs to be used and tested, with different organisms and different criteria (both presence/absence and abundance), and utilizing both modern and available historical data, to produce a comprehensive picture. It is clear, however, that the criteria for delimitation of the biogeographic entities need to be clearly spelt out in

all studies, which has not always been the case in the past.

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## References

- Adey WH, Steneck RS (2001) Thermogeography over time creates biogeographic regions: a temperature/space/time-integrated model and an abundance-weighted test for benthic marine algae. *J Phycol* 37:677–698
- Awad AA, Griffiths CL, Turpie JK (2001) Distributions and endemism patterns of marine benthic invertebrates in South Africa applied to the selection of priority conservation areas. *Diversity and Distributions* 8:129–145
- Beardall J, Beer S, Raven JA (1998) Biodiversity of marine plants in an era of climate change: some predictions based on physiological performance. *Bot Mar* 41:113–123
- Bolton JJ (1983) Ecoclinal variation in *Ectocarpus siliculosus* (Phaeophyceae) with respect to temperature growth optima and survival limits. *Mar Biol* 73:131–138
- Bolton JJ (1986) Marine phytogeography of the Benguela upwelling system on the west coast of southern Africa. *Bot Mar* 29:251–256
- Bolton JJ (1999) Global seaweed diversity: patterns and anomalies. *Bot Mar* 36:241–246
- Bolton JJ (1995) Patterns of species diversity and endemism in comparable temperate brown algal floras. *Hydrobiologia* 326/327:173–178
- Bolton JJ (1999) Seaweed systematics and diversity in South Africa: an historical account. *J R Soc S Afr* 54:166–177
- Bolton JJ, Anderson RJ (1990) Correlation between intertidal seaweed community composition and sea water temperature patterns on a geographical scale. *Bot Mar* 33:447–457
- Bolton JJ, Anderson RJ (1997) Marine vegetation. In: Cowling RM, Richardson DM, Pierce SM (eds) *Vegetation of southern Africa*. Cambridge University Press, Cambridge, pp 348–375
- Bolton JJ, Stegenga H (1987) The marine algae of Hluleka (Transkei) and the warm temperate/sub-tropical transition on the east coast of southern Africa. *Helgol Meeresunters* 41:165–183
- Bolton JJ, Stegenga H (2002) Seaweed biodiversity in South Africa. *S Afr J Mar Sci* 24:9–18
- Bolton JJ, Coppejans E, Anderson RJ, De Clerck O, Samyn Y, Leliaert F, Thandar AS (2001) Biodiversity of seaweeds and echinoderms in the western Indian Ocean; workshop report. *S Afr J Sci* 97:453–454
- Branch GM, Branch ML (1981) *Living shores of southern Africa*. Struik, Cape Town
- Breeman AM (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgol Meeresunters* 42:199–241
- Breeman AM (1990) Expected effects of changing seawater temperatures on the geographic distribution of seaweed species. In: Beukema JJ, Wolff WJ, Brouns JJWM (eds) *Expected effects of climate change on marine coastal ecosystems*. Kluwer, Dordrecht, pp 69–76
- Breeman AM, Packer H (1994) Temperature ecotypes in seaweeds: adaptive significance and biogeographic implications. *Bot Mar* 36:171–180
- Briggs J (1974) *Marine zoogeography*. McGraw Hill, New York



- Brown AC (1999) Marine invertebrate systematics and zoogeography in southern Africa: an historical overview. *Trans R Soc S Afr* 54:21–30
- Brown AC, Jarman NG (1978) Coastal marine habitats. In: Werger MJA (ed) *Biogeography and ecology of southern Africa*. *Monogr Biol* 31:1239–1277
- Carballo JL, Olabarria C, Osuna TG (2002) Analysis of four macroalgal assemblages along the Pacific Mexican coast during and after the 1997–98 El Niño. *Ecosystems* 5:749–760
- Celliers L, Schleyer MH (2002) Coral bleaching on high latitude marginal reefs at Sodwana Bay, South Africa. *Mar Poll Bull* 44:1380–1387
- Cheney DF (1977) R and C/P, a new and improved ratio for comparing seaweed floras. *J Phycol* 13[Suppl]:12
- Day JH (1967) A monograph of the Polychaeta of southern Africa. 2. Sedentaria. Trustees of the British Museum (Natural History), London
- De Clerck O, Anderson RJ, Bolton JJ, Robertson-Andersson D (2002a) *Schimmelmanna elegans* (Gloiosiphoniaceae, Rhodophyta): South Africa's first introduced seaweed? *Phycologia* 41:184–190
- De Clerck O, Leliaert F, Engledow HR, Bolton JJ, Anderson RJ, Coppejans E (2002b) Report of 20 new records of macroalgae from KwaZulu-Natal, South Africa. *Bot Mar* 45:413–431
- De Clerck O, Wynne MJ, Stegenga H (2002c) *Valeriemaya seagrifii* sp. nov. (Delesseriaceae, Rhodophyta) from South Africa. *S Afr J Bot* 68:199–204
- Eckman S (1953) *Zoogeography of the sea*. Sidgwick and Jackson, London
- Emanuel BP, Bustamante RH, Branch GM, Eekhout S, Odendaal FJ (1992) A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *S Afr J Mar Sci* 12:341–354
- Farrell EG, Critchley AT, Aken ME, Pienaar RN (1994) The biogeographical affinities of the seaweed flora of Natal, South Africa, as typified by Isipingo Beach: a multivariate approach. *Bot Mar* 36:277–285
- Flemming BW, Hay ER (1988) Sediment distribution and dynamics on the Natal continental shelf. In: Schumann EH (ed) *Coastal ocean studies off Natal, South Africa*. Springer, New York Heidelberg Berlin
- Hill MO (1979) TWINSPAN—a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Cornell University, Ithaca
- Hoek C van den (1975) Phytogeographic provinces along the coast of the northern Atlantic Ocean. *Phycologia* 14:317–330
- Hoek C van den (1984) World-wide latitudinal and longitudinal seaweed distribution patterns and their possible causes as illustrated by the distribution of rhodophytan genera. *Helgol Meeresunters* 38:227–257
- Hoek C van den, Donze M (1967) Algal phytogeography of the European Atlantic coasts. *Blumea* 15:63–89
- Hommersand MH (1986) The biogeography of the South African marine red algae: a model. *Bot Mar* 29:257–270
- Hommersand MH, Fredericq S (2003) Biogeography of the marine red algae of the South African west coast: a molecular approach. In: Chapman ARO, Anderson RJ, Vreeland VJ, Davison IR (eds) *Proceedings of the 17th international seaweed symposium*. Oxford University Press, Oxford, pp 325–336
- Leliaert F, De Clerck O, Bolton JJ, Coppejans E (2001) New records of the Chlorophyta from South Africa, with the emphasis on the marine benthic flora of Kwazulu-Natal. *S Afr J Bot* 67:450–459
- Littler MM, Littler D (1980) The evolution of thallus form and survival strategies in benthic marine macroalgae: field and laboratory tests of a functional form model. *Am Nat* 116:25–44
- Lüning K (1990) *Seaweeds: their environment, biogeography and ecophysiology*. Wiley, New York
- Lutjeharms JRE, Valentine HR, Van Ballegooyen RC (2000) The hydrography and water masses of the Natal Bight, South Africa. *Contin Shelf Res* 20:1907–1939
- Maggs CA, Stegenga H (1999) Red algal exotics on North Sea coasts. *Helgol Meeresunters* 52:243–258
- Norris RE (1992) The marine red algae of Natal, South Africa: Order Gelidiales (Rhodophyta). *Mem Bot Surv S Afr* 61:1–43
- Proches S, Marshall DJ (2002) Diversity and biogeography of southern African intertidal *Acari*. *J Biogeogr* 29:1201–1215
- Ribera MA, Boudouresque CF (1995) Introduced marine plants, with special reference to macroalgae: mechanisms and impact. *Prog Phycol Res* 11:187–268
- Schumann EH (1988) Physical oceanography off Natal. In: Schumann EH *Coastal ocean studies off Natal, South Africa*. *Lect Notes Coast Estuar Stud* 26:1–271
- Seagrief SC (1980) Seaweeds of Maputaland. In: Bruton MH, Cooper KH (eds) *Studies on the ecology of Maputaland*. Rhodes University and the Natal Branch of the Wildlife Society of Southern Africa, Durban, pp 18–41
- Siegfried WR (1981) The estuarine avifauna of southern Africa. In: Day JH (ed) *Estuarine ecology with particular reference to southern Africa*. Balkema, Rotterdam, pp 223–250
- Silva PC, Basson PW, Moe RL (1996) Catalogue of the benthic marine algae of the Indian Ocean. *Univ Calif Publ Bot* 79:1–1259
- Statsoft (2000) *STATISTICA for Windows—Computer program manual*. Statsoft, Tulsa, Okla.
- Stegenga H, Bolton JJ, Anderson RJ (1997) Seaweeds of the South African west coast. *Contrib Bolus Herb* 18:1–655
- Stegenga H, Anderson RJ, Bolton JJ (2001a) *Hypoglossum imperfectum* nov. spec. (Rhodophyta, Delesseriaceae), a new species from the South African south coast. *Bot Mar* 44:157–162
- Stegenga H, Engledow H, Bolton JJ, Anderson RJ (2001b) The distribution of the family Erythropeltidaceae (Rhodophyta) along the temperate southern African coast, with the description of *Erythrotrichia platyphylla* nov. spec. *Nova Hedwigia* 73:367–379
- Stegenga H, Bolton JJ, Anderson RJ (2002a) *Elachista endarachnae* sp. nov. (Phaeophyceae, Elachistaceae), a peculiar representative of the genus in South Africa. *Phycologia* 41:432–435
- Stegenga H, Bolton JJ, Anderson RJ (2002b) The genus *Prilothamnion* (Ceramiaceae, Rhodophyta) in South Africa, with the description of *P. goukammae* spec. nov. *Blumea* 47:581–595
- Stephenson TA (1948) The constitution of the intertidal fauna and flora of South Africa, part III. *Ann Natal Mus* 11:207–324
- Stephenson TA, Stephenson A (1972) *Life between tidemarks on rocky shores*. Freeman, San Francisco, pp 1–425
- Ter Braak C (1988) *CANOCO—a FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal component analysis and redundancy analysis (version 2.1)*. Agricultural Mathematics Group, Wageningen
- Thandar AS (1989) Zoogeography of the southern African echinoderm fauna. *S Afr J Zool* 24:311–318
- Turpie JK, Beckley LE, Katua SM (2000) Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biol Conserv* 92:59–72
- Wilson M, Shmida A (1984) Measuring beta diversity with presence-absence data. *J Ecol* 73:1055–1064