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BIODIVERSITY RESEARCH

Using the biogeographical distribution and diversity of seaweed species to test the efficacy of marine protected areas in the warm-temperate Agulhas Marine Province, South Africa

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ABSTRACT

Aim To study the siting of marine protected areas (MPAs) with respect to the biogeographical distribution of seaweeds within the Agulhas Marine Province and to assess the effectiveness of current MPAs in including (conserving) seaweeds of the South African south coast.

Location South Africa – the south coast between Cape Agulhas and the Eastern Cape/Kwazulu-Natal border, and eight MPAs within that area.

Methods We used interpolated seaweed distribution records from all available sources, in 50-km coastal sections. Cluster analysis (Jaccard Average Linkage) of species presence/absence data provided measures of similarity between coastal sections and between MPAs. Complementarity analyses identified the sequence of 'importance' of sections/MPAs for conserving seaweed species.

Results Species presence/absence data indicated two main groups, representing western (cooler water) and eastern (warmer water) biogeographical divisions, as well as several biogeographical subdivisions within each of these groups. Complementarity analysis yielded a sequence of 'importance' of coastal sections (in terms of the highest number of species included) that began with a section just east of central in the Agulhas Marine Province, around Port Alfred, where there is no MPA. This was followed by the easternmost section (warmest water), which contains the Pondoland MPA, and then by the westernmost (coolest water) section, containing the De Hoop MPA. Similar analysis of the actual species collected in MPAs showed a generally similar pattern.

Main conclusions Seven current MPAs and one proposed coastal MPA in the Agulhas Marine Province appear to be well distributed and well sited to include (conserve) the full biogeographical range of seaweeds. However, if further MPAs are to be considered, the Port Alfred area is recommended for improved conservation. This study did not examine estuaries, which may require improved conservation efforts. Seaweed distribution data, which are often relatively complete, offer a good tool for planning the siting of coastal MPAs.

Keywords
Biogeography, marine conservation, marine protected areas, seaweed species distributions.

INTRODUCTION

Systematic conservation planning, which attempts to identify conservation aims, to analyse existing information and protected areas, and to identify priority areas for protection, is a well-established ideal in terrestrial systems (e.g. Margules & Pressey, 2000). However, in marine conservation such systematic approaches lag, largely because of fundamental differences

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between terrestrial and marine systems and a lack of biological information on the latter (Carr *et al.*, 2003; Lourie & Vincent, 2004). Nevertheless, marine protected areas (MPAs) are established and are being planned in many countries, and are acknowledged as an important tool in marine conservation.

Given that establishing an MPA is usually a long and difficult process, it is critical that its location should be based on the most appropriate combination of scientific, social and economic factors (Lundquist & Granek, 2004). These factors are determined by the intended functions of the MPA, which usually include some or all of the following: (1) to conserve marine biodiversity (including genetic diversity and rare, range-restricted or endemic species), (2) to preserve or rebuild fisheries, (3) to provide for research and education, and (4) to create or improve tourism (e.g. Pressey *et al.*, 1993; Agardy, 1994; Attwood *et al.*, 1997a,b; Hockey & Branch, 1997; Roberts *et al.*, 2003). The conservation of marine biodiversity is not only a core aim of most MPAs, but it is also a necessary prerequisite for fulfilling many of the other aims mentioned above. Biodiversity, in turn, can be fully conserved only if a network of MPAs covers the biogeographical range of the organisms in the ecosystem.

Several recent studies have examined the biogeography and conservation of certain groups of southern African marinze fauna. A zoogeographical study of 2000 species of marine invertebrates recognized five provinces, including two on the cool-temperate west coast, and argued for an additional MPA there (Emanuel *et al.*, 1992). A detailed study of the distributions of fishes in 50-km sections of the South African coast fauna (Turpie *et al.*, 2000) identified biogeographical patterns similar to that of previous studies of marine fauna, but used complementarity analysis of fish distributions to evaluate the conservation potential of the sections. Complementarity analysis (Pressey & Nicholls, 1989) is in this context a repetitive method that ranks coastal sections according to species richness but selects a minimum set of sections to include all the species in at least one conservation area.

Given that many MPAs exist (although some may not be ideally placed), it is necessary to consider their effectiveness in conserving the biogeographical ranges of various groups of organisms. Because an explicit aim of many MPAs is to protect marine biodiversity, and because greater habitat diversity should result in greater species diversity, an assessment approach based on species data should provide the best measure of MPA effectiveness. However, detailed species data that allow comparisons between the MPA and the rest of the coast, and that take the biogeography of the organisms into account, are seldom available.

Although biogeographical information is important in conservation planning (Lourie & Vincent, 2004) and in the siting of marine reserves (Roberts *et al.*, 2003), it is often unavailable for many groups of marine organisms (Carr *et al.*, 2003). Seaweeds, although they are seldom directly threatened (however, see Millar, 2003), have several attributes that make them useful biogeographical indicators on coasts where there are rocks for attachment. Seaweeds comprise three distinct phylogenetic and evolutionary groups of autotrophs in that the green, red and brown seaweeds belong to three distinct phyla (respectively the Chlorophyta, Rhodophyta and Ochrophyta). Seaweeds are almost all sessile, and usually comprise communities that include species with a range of life spans, from several weeks to many decades in the case of clonal species. They have a high degree of biogeographical 'faithfulness', with geographical distributions that are not only overwhelmingly controlled by temperature (e.g. Breeman, 1988; Lüning, 1990), but may also be controlled by the interaction of temperature and daylength on certain life-history stages (Maggs & Guiry, 1987). There is also good evidence relating seaweed community composition on a geographical scale to sea temperature (Bolton & Anderson, 1990), and relating the biogeographical distribution of seaweed communities to patterns of species distribution (Shears *et al.*, 2008). Furthermore, seaweeds are often the dominant life-form on intertidal and shallow subtidal hard substrata, and are often better collected than other groups of organisms.

South Africa has almost 3000 km of coast and a rich and biogeographically varied inshore flora and fauna. Stephenson (1948) used the distribution of 318 intertidal species (including 116 seaweeds) to propose three biogeographical provinces: a cold-temperate west coast, a warm-temperate south coast and a subtropical east coast. It is not appropriate to discuss in this work how subsequent studies have refined our ideas of local inshore biogeography (see for example, a generalized scheme in Lombard *et al.*, 2004). However, from the seaweed perspective, our current understanding is that the coast of South Africa spans three distinct seaweed biogeographical regions, with overlap zones between them (Fig. 1). The west coast, which forms part of the Benguela Marine Province, is dominated by cool, upwelled waters with annual mean temperatures of 12–13 °C, and inhabited by a seaweed flora of *c.* 400 species that is cool-temperate (as defined by Bolton, 1986; Stegenga *et al.*, 1997). The Agulhas Marine Province extends from Cape Agulhas to the East London/Transkei region of the Eastern Cape (*c.* 1000 km) and has a warm-temperate seaweed flora of about 500 species including many endemics (Bolton & Anderson, 1997; Bolton & Stegenga, 2002; Bolton *et al.*, 2004), with annual mean temperatures of 17.2–18.2 °C (Bolton, 1986). In northern Kwazulu-Natal (KZN), where annual mean sea temperatures exceed 22 °C, the tropical seaweed flora of the Indo-West Pacific Marine Province reaches its southernmost extent near Cape St Lucia (Bolton *et al.*, 2004; Anderson & Bolton, 2005). Between this and the Agulhas Marine Province lies a long overlap zone that covers the central and southern KZN coasts as well as the former Transkei coast, with a warm-temperate flora intermediate between those of the Agulhas and Indo-West Pacific Marine Provinces (Bolton & Anderson, 1997; Bolton *et al.*, 2004).

With respect to seaweed biogeography, the coast between Cape Agulhas and the southern border of KZN (the south coast of South Africa) thus comprises the entire Agulhas Marine Province as well as a small part of the Agulhas–Tropical overlap region including the former Transkei region of the Eastern Cape. This south coast is unusual in that it contains a series of MPAs

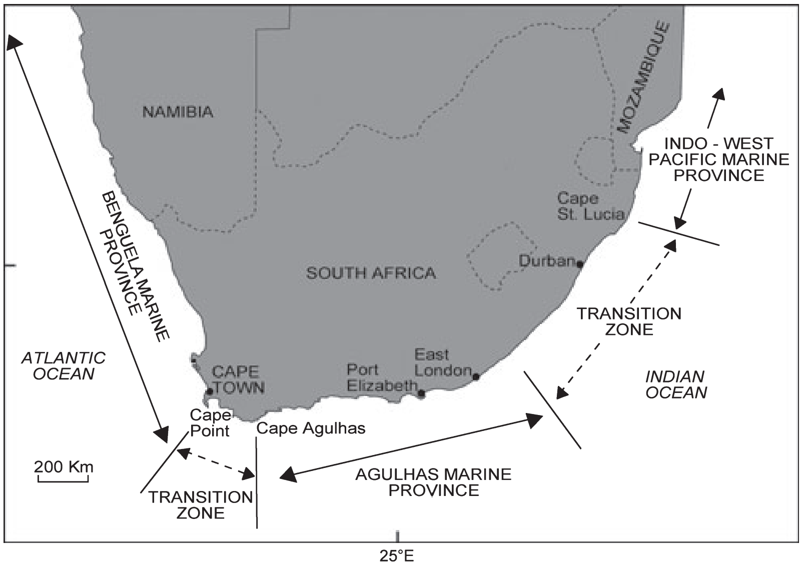

Figure 1 Map of the coast of southern Africa to show seaweed biogeographical Marine Provinces and transition zones, following Bolton & Anderson (1990) and Bolton *et al.* (2004) (Modified Winkel's Projection).

(Fig. 2) that are spread fairly evenly along its extent, from the De Hoop MPA in the west to the Pondoland MPA in the east, and several proposed MPAs (Government Gazette, Republic of South Africa, 2005), including Kei MPA. Nowhere else on the southern African coast is there such a regular series of MPAs covering an entire Marine Province, although only two of these MPAs contain significant estuaries (Pondoland and Stilbaai). Phillips (1998) noted that although there are many MPAs in Australia, their value in conserving macroalgae is unknown. The seaweed flora of South Africa is relatively well collected and we have built up a large database of records over the previous two decades from extensive collections, particularly along the SA south coast (see Methods). The South African south coast is thus an ideal region to test the effectiveness of MPAs in covering the biogeographical range of seaweeds.

The aims of this study were to analyse the biogeographical patterns of seaweed distribution along the SA south coast with respect to the ideal siting of MPAs; to assess the effectiveness of current (and one proposed) MPAs in conserving the biogeographical range of the south coast seaweed flora and to present data to improve our understanding of the MPA coverage necessary to conserve seaweeds across the biogeographical range of a warm-temperate marine province.

METHODS

Sample and data collection

The species lists used in this study were based on those used by Bolton & Stegenga (2002), which were obtained from all available records at the time: herbarium records (especially BOL, GRA, NH), publications and the authors' collections. For their analyses, they divided the whole SA coast into 50-km sections and recorded the occurrence of each seaweed species in each section. The data are interpolated. For example, if a species has been collected in sections 23 and 26, it is assumed to occur in the intervening sections 24–25 as well. In this study, we updated the south coast data of Bolton & Stegenga (2002) with records from all subsequent collections or publications. Although the use of historical records (some dating back to almost a century) may be questioned, we note that Rindi & Guiry (2004) showed that there was essentially no change in the benthic algal flora of Clare Island (NE Atlantic) between 1910 and the present. Furthermore, there is no evidence that humans have caused environmental changes on the South African south coast that would have affected seaweeds, except perhaps in the large harbours in Port Elizabeth and East London.

For our analysis, we used the same 50-km sections used by Bolton & Stegenga (2002) for the south coast, which we define in this study as the area from just east of Cape Agulhas to the Eastern Cape/KZN border. The boundaries of our study therefore include areas 23–47 of Bolton & Stegenga (2002). Because their area 22 extended west of Cape Agulhas and included many species that do not occur east of Cape Agulhas, it was omitted from our analysis. Similarly, their area 48 was omitted from this analysis because it extends from Mzamba (only *c.* 4 km west of the KZN border) to 46 km east of the border and includes eight species that have not been collected from south of the border. Only definite identifications of entities to species level were used in the analyses, although our records contain a number of taxa that have not yet been described.

Seaweed collections were made in seven MPAs and one proposed MPA (Kei) that are distributed fairly evenly along the south coast (Fig. 2), to compare on-site collections with predicted totals from interpolated records. In each of these, four to six people collected for 4–5 days mainly in the intertidal zone and subtidal fringe, and also by wading and snorkelling in the shallow subtidal. Dates of collections were: De Hoop – October 1984 and June 1985 (also smaller collections March, May and September 1984); Stilbaai –

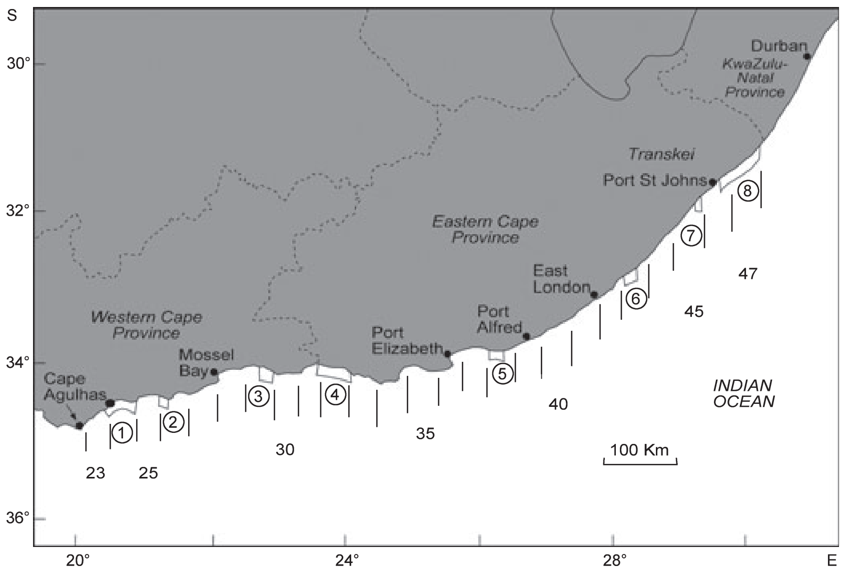

Figure 2 Map of the South African south coast showing boundaries of 50-km coastal sections as used by Bolton & Stegenga (2002) (see Table 1 for details). Marine Protected Areas (and one proposed MPA, Kei, 6) that were included in this study, and their approximate coastline lengths, are: 1 De Hoop (51 km), 2 Stilbaai (13 km), 3 Goukamma (12 km), 4 Tsitsikamma (65 km), 5 Addo (8 km), 6 Kei (24 km), 7 Hluleka (7 km) and 8 Pondoland (90 km).

October 2001; Goukamma – October 2000; Tsitsikamma – April 1997 (short visit), October 1997; Addo – October 2003; Kei – October 1999; Hluleka – June 1983; Pondoland – October 2002. All these collections except Hluleka, therefore, included sampling in spring (October). Limited SCUBA collections (one dive each) were also made at Stilbaai, Goukamma and Tsitsikamma. Data for Addo include SCUBA collections made previously around Bird Island (Anderson & Stegenga, 1989), which lies within this MPA. Records for Hluleka are those of Bolton & Stegenga (1987), excluding the Mtakatye Estuary, which lies outside this MPA. Records for Pondoland include those of Celliers *et al.* (2007). Several smaller MPAs (e.g. Robberg near Plettenberg Bay, Sardinia Bay near Port Elizabeth and Dwesa in Transkei) and proposed MPAs (Gxulu and Gonubie near East London) were not included because we have not collected in them.

Analyses

The interpolated numbers of green (Chlorophyceae), brown (Phaeophyceae) and red (Rhodophyceae) seaweeds were plotted for each coastal section, as well as the numbers actually found in each MPA (Fig. 3).

A cluster analysis of (interpolated) species per coastal section was carried out (Fig. 4) using the Pisces Conservation Community Analysis Programme (Pisces Conservation Ltd, Lymington, UK). The Jaccard coefficient was chosen as it is useful for binary (presence/absence) data and does not use species absence in its calculation of similarity (Legendre & Legendre, 1983).

Complementarity analysis, an iterative analysis that selects the lowest number of sites necessary to contain and thus potentially conserve a set of species (Pressey & Nicholls, 1989; Pressey *et al.*, 1993), was applied to two sets of our data: the interpolated distribution data of all species in the 50-km coastal sections along the south coast (Fig. 5a) and on the actual species collected in the eight MPAs (Fig. 5b). We performed the analyses using first principles. Using a spreadsheet of all recorded species in each coastal sections (or MPA, for the separate MPA analysis), the section (or MPA) with the highest number of species was first selected and then this section (its column of species) was removed from the analysis. The section (or MPA) with the greatest number of species not included in the first section (or MPA) was then selected, and this process was followed sequentially through the dataset, to obtain a series of sections (or MPAs) ranked according to their importance in containing (conserving) the greatest number of species.

Although the lengths of the MPAs differed, there are several reasons why this is likely to have little influence on the results. Firstly, the relationship between coastline length and species number is logarithmic (Santelices *et al.*, in press), so that doubling of coast length has a relatively small effect on species number. The latter study included a global analysis showing a significant correlation between log seaweed species richness of geographical regions and log coastline length. Secondly, the area of habitat (e.g. rock, in the case of most seaweeds) is more important than the length of an MPA, but the area of habitat is usually not known, although all of these MPAs include extensive and varied rocky shores interspersed with sandy bays and beaches. Thirdly, the quality of habitat may be as or more important than a simple measure of habitat area. For example, Goukamma MPA contains one section of sandstone, a long beach and an area of aeolianite. The sandstone is dominated by invertebrates (limpets, urchins, chitons and turbinid snails) and has a lower diversity of seaweeds (we found a total of 71 species), whereas the aeolianite has very few invertebrates and a higher seaweed diversity (118 species recorded). It is seldom possible to measure the quantity and quality of habitat, and we consider our methods of collection and analysis to give a reasonable approximation of species richness.

Table 1 The 50-km long coastal sections used by Bolton & Stegenga (2002) that fall within the south coast, as defined in this study. Numbers, with geographical coordinates, positions of boundaries relative to known places, and well-known sites included in each section, as in Bolton & Stegenga (2002).

No.	*X*-coordinates	*Y*-coordinates	Limits	Including
23	20.47732	−34.49243	Struisbaai–Skipskop	Struisbaai, Arniston
24	20.87056	−34.38810	To just E of Cape Infanta	Koppie Allen, Infanta, Witsand
25	21.35563	−34.42480	To just E of Jongensfontein	Puntjie, Skurwe Bay
26	21.82968	−34.38157	To just W of Gouritzmond	Stilbaai, Bloukrans, Bull Point
27	22.11571	−34.15734	To just E of Mossel Bay	Gouritzmond, Vleesbaai,
28	22.53969	−34.01308	To just W of Victoria Bay	Hartenbos, Grootbrak, Herolds Bay
29	23.01642	−34.07989	To just W of Knysna Heads	Victoria Bay, Wilderness, Walker Bay
30	23.35867	−34.10201	To just W of Plettenberg Bay	The Heads, Neusgate
31	23.78027	−34.00998	To Elandsbos River	Plettenberg Bay, Keurbooms, Blousloep
32	24.26944	−34.08458	To Skuinsklip	Storms River, Voelkrans, Skietgate
33	24.73894	−34.18988	To Thyspunt	Tsitsikamma River, Klipdrif River
34	25.03553	−34.97130	To just W of Gamtoos River	Cape St Francis, Jeffreys Bay
35	25.51952	−34.03581	To just E of Sardinia Bay	Van Stadens River, Claasen Point
36	25.69996	−33.79133	To just E of St Georges Beach	Chelsea pt, Port Elizabeth, Bluewater
37	26.17661	−33.72051	To just W of Woody Cape	St Croix Is., Sundays River
38	26.64813	−33.70001	To just W of Kenton-on-Sea	Bird Is., Cape Padrone, Cannon Rocks, Boknes
39	27.10371	−33.52269	To just E of Kleinemonde	Kasouga, Port Alfred
40	27.51706	−33.26662	To just E of Keiskamma River	Great Fish River, Madagascar Reef
41	27.92591	−33.01227	To just E of East London	Kayser's Beach, Kidd's Beach, Cove Rock
42	28.30072	−32.73128	To Haga-Haga	Gonubie, Cintsa
43	28.68348	−32.43986	To Qora River	Morgan bay, Kei Mouth, Mazeppa Bay
44	29.04811	−32.11370	To just E of Xora River	Dwesa, The Haven
45	29.37234	−31.76221	To Sharks Point	Mncwasa river, Coffee bay, Hluleka
46	29.74337	−31.46446	To Mkozi River	Bolder Bay, Port St Johns, Montshe, Ntsubane
47	30.12123	−31.17581	To Mnyameni River	Cathedral Rock, Lambasi Bay, Wild Coast

The numbers of species that were predicted to occur in each MPA but that were not found there during collecting visits are shown in Fig. 6.

The interpolated ranges of species were used to calculate the number of species predicted to occur in only two to five contiguous coastal sections (i.e. a range of 100–250 km), and the numbers are plotted for each section (Fig. 7). These are referred to as range-restricted species. Species recorded from only one coastal section were omitted because we consider most of these to be very rare and/or under-collected, with some only known from the type collection. Species that are both endemics and range-restricted were also plotted separately. It is important to note that the ranges of species that we used are those found along the whole South African coast. In other words, those found towards our eastern and western limits may have ranges that extend beyond our 'South Coast' – we did not exclude these species if part of their range lay outside the south coast.

RESULTS

The total number of species per coastal section is highest in the sections just north of the central south coast (between about 31 and 43), with slightly lower numbers towards the southern and northern extents of the South Coast (Fig. 3). This pattern is mirrored by the red algae, which make up 70–75% of the species in each section. The numbers of greens per section rise steadily from west to east, whereas browns show no latitudinal trend. Numbers of the three seaweed groups that were collected in the eight MPAs show trends similar to that above, except for Tsitsikamma, which is slightly higher, and Addo, which is slightly lower. In the eight MPAs that we surveyed, we found a total of 377 species of green, brown and red seaweeds, representing 77% of the 489 species recorded from the south coast.

Cluster analysis of the seaweed data (Fig. 4) shows two main groups at the highest level of dissimilarity: a western group including sections 23–39 and an eastern group (sections 40–47), with the area of division just west of Port Alfred. The western group contains five MPAs, from De Hoop to Addo, and the eastern group the Kei (proposed MPA), Hluleka and Pondoland MPAs. Both groups split into two subgroups. Within the western group, the subgroups split between sections 30 and 31 (between Knysna and Plettenberg Bay). The eastern group divides around the Xora River in Transkei. It is notable that even at a fairly low level of dissimilarity (indicated by the line in Fig. 4), when there are two main groups containing seven subgroups, each subgroup contains at least one of the MPAs we surveyed.

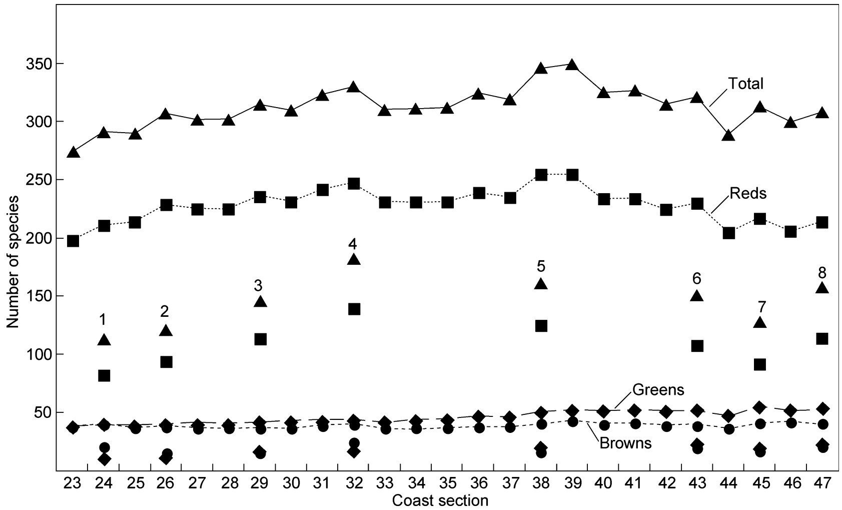

Figure 3 Numbers of green, brown and red seaweeds in 50-km coastal sections (line graphs) and in marine protected areas (MPAs; single points) along the South African south coast. MPAs are: 1 De Hoop, 2 Stilbaai, 3 Goukamma, 4 Tsitsikamma, 5 Addo, 6 Kei Proposed MPA, 7 Hluleka and 8 Pondoland.

Complementarity analysis of the interpolated species in all coastal sections (Fig. 5a) showed that section 39 has most species (384 out of total S coast list of 489). A further 64 species are found in section 47 (which includes the Pondoland MPA), followed by a further 45 species in section 24 (which includes De Hoop MPA). The number of species added by each coastal section then drops sharply: section 32 (including Tsitsikamma MPA) and section 45 (including Hluleka MPA) each add six species, section 38 adds five species and section 36 adds two species. A further group of coastal sections (denoted as Group A: 29, 30, 41, 42, 43 and 46) each add one species. No further species are added by the remaining coastal sections (23, 25, 26, 27, 28, 31, 33, 34, 35, 37 and 40).

Complementarity analysis of the species collected in the eight MPAs (Fig. 5b) gave somewhat different results to the above. Tsitsikamma MPA had the highest number of species (185 species collected, or just under 40% of the total collected in all MPAs). Once these species were excluded, the next most important MPA was Pondoland (an additional 75 species), followed by Addo (42 species), then down through the remainder to Stilbaai MPA, which had only 1% of the species (four species) not found in the other MPAs.

The highest number of species not found in any of the MPAs during surveys (Fig. 6) was recorded in section 39 (Port Alfred area). In general, the sections 36 eastward contained more of the species not collected in any of the MPAs. However, there were also reasonably high numbers of these species in the most westerly sections (23–26).

Almost all of the range-restricted species (species with ranges between 100 and 250 km) are found in the eastern half of the south coast (Fig. 7). Coastal section 47 (containing the Pondoland MPA) has five range-restricted species, including two endemics, *Ptilophora diversifolia* (Suhr) Papenfuss and *Ptilophora spissa* (Suhr) Kützing. Sections 42 and 43 (the latter containing the Kei proposed MPA) contain the endemic range-restricted species *Stilophora flanaganii* Kylin. Sections 38 and 39 contain one range-restricted endemic (*Onychocolax polysiphoniae* M.A. Pocock) and a further range-restricted species [*Aglaothamnion tenuissimum* (Bonnemaison) Feldmann-Mazoyer] that extends into section 40. The endemic range-restricted species *Cystophora fibrosa* Simons occurs only in coastal sections 23 and 24 (the latter including the De Hoop MPA). None of the other coastal sections contain range-restricted species.

DISCUSSION

The somewhat higher number of species in sections 31–43 of the south coast (Fig. 3) is probably a result of their central position in this biogeographical region. Eastwards (where the water becomes warmer), more species drop out than are replaced by warm-water species extending into the south coast. Similarly, more species drop out westwards (where it becomes progressively colder) than are replaced by cool-water species extending their ranges from the Benguela/Agulhas overlap region west of Cape Agulhas.

The changes in species numbers appear mainly in the Rhodophyceae, which are by far the most numerous. The slight increase in the numbers of Chlorophyceae, with the increasing temperatures from west to east, is consistent with patterns in most parts of the world, where diversity in this group is highest towards the tropics (Santelices *et al.*, in press). It also accords with the results of Bolton *et al.* (2004) who found an increase in Chlorophyceae from the South African temperate/tropical overlap region (southern and central KZN) towards the tropical flora in northern KZN. The similar numbers of Phaeophyceae throughout the south coast accord with previous observations on the paucity of this group in the South African seaweed flora in general (Bolton, 1986, 1996; Bolton & Anderson, 1997; Bolton *et al.*, 2004).

That 77% of the species recorded historically on the south coast were collected during relatively brief surveys in the eight MPAs suggests firstly that these surveys were reasonably effective, and secondly that overall MPA coverage (at least for seaweeds) is good.

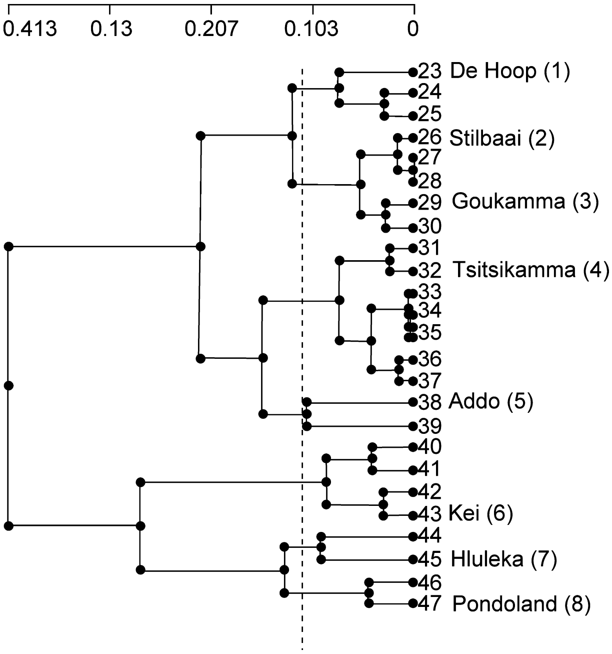

Figure 4 Cluster analysis (Jaccard, average linkage) of seaweed presence/absence for each 50-km section of the South African south coast. Positions of marine protected areas (MPAs) that were surveyed in this study are shown on the right. Vertical line shows dissimilarity level at which each cluster of sections contains at least one MPA. Kei MPA proposed but not yet declared (enacted) at the time of writing.

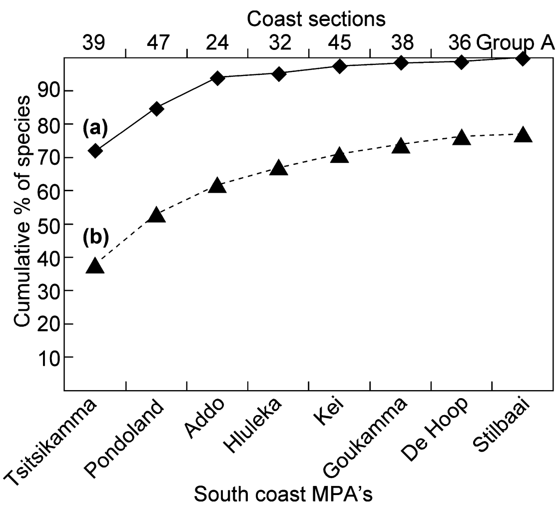

Figure 5 Results of complementarity analyses. Line a shows the percentage of species included as more coastal sections are included (upper axis) and is based on interpolated records for all coastal sections. Line b shows the percentage of species included as more marine protected areas (MPAs) are included (lower axis) and is based on actual records from the MPAs. Kei MPA proposed but not yet enacted at the time of writing.

Although biogeographical comparisons between seaweeds and other groups of organisms are complicated by differences in habitats and biology, some general patterns are noticeable.

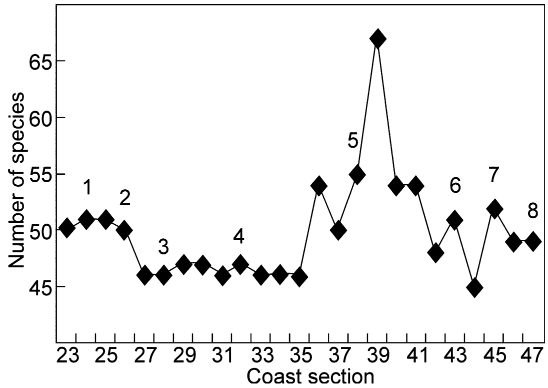

Figure 6 Number of species in each coastal section that were not found in any of the marine protected areas (MPAs) during actual collections. The positions of the MPAs are shown by their numbers (see Fig. 2).

Southern African marine acari (mites) show their highest species richness in 'southern province' (between about Cape Point and central Transkei), but notably, the highest number of species occurred in the Port Alfred region (Proches & Marshall, 2002) where seaweed species richness is also highest.

Turpie *et al.* (2000) found that for coastal fishes, species richness declined from the Mozambique border westwards with decreasing water temperatures. However, species diversity of seaweeds, unlike that of fish, does not peak in the tropics (Bolton, 1994; Santelices *et al.*, in press). Furthermore, Turpie *et al.* (2000) found that richness of endemic species of fish was the highest on the south coast. Their complementarity analysis of core distributions of these fishes in 50-km sections showed that the south coast held three of the six most important (species-rich) sections: the areas around Tsitsikamma, Port Alfred and Port St Johns. Our results also emphasize the importance of those areas.

The primary biogeographical division in our seaweed species data lies between section 39 (which includes Port Alfred) and section 40 (Great Fish River to just east of the Keiskamma

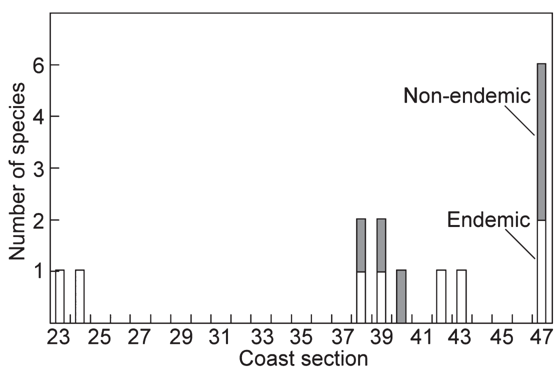

Figure 7 Number of range-restricted seaweed species (occurring only in 100–250 km of coast) per coastal section. Solid bars show non-endemic species, hollow bars show endemic species (see text for details).

River) (Fig. 4). Water temperatures here are somewhat anomalous: Lutjeharms *et al.* (2000) showed that upwelling along the landward side of the Agulhas Current significantly reduces inshore water temperatures on 45% of days, between Cape Padrone (just east of Port Elizabeth) and Port Alfred. While the effects of this upwelling may extend as far as the East London area, or (rarely) as far as Port St Johns in northern Transkei, they are centred in the Port Alfred area, lowering sea temperatures by up to 10 °C and causing large temperature ranges that are not necessarily seasonal (Lutjeharms *et al.*, 2000).

Our biogeographical break in this area may indicate a change from an Agulhas Province seaweed flora (Port Alfred westwards) to the start of a transitional flora that extends northwards through most of KZN up to the Cape St Lucia area, north of which the seaweed flora is overwhelmingly tropical Indo-West Pacific in nature (see Bolton & Anderson, 1997; Bolton *et al.*, 2004). However, the location of the Agulhas Province/transition zone boundary can be more accurately established only by analysing records for the whole region from Cape Agulhas to northern KZN, which we did not carry out in this study.

Although the seaweed flora of the south coast can be split into seven biogegraphical subdivisions at a fairly low level of dissimilarity (Fig. 4) and there is at least one existing MPA (or proposed MPA in the case of Kei) in each, the cluster analysis of coastal sections is based on the full complement of species in each, rather than on an analysis of the species actually recorded in the MPAs. As most MPAs are smaller than the 50-km coastal sections and may not contain all the species or all the habitat types in that section, it is reasonable to ask how effective they are in conserving seaweed species. Figure 3 shows that in each MPA, we generally recorded around 40–50% of the seaweed species predicted to occur in that coastal section, although collecting trips were short. Spring collections (October) were made in all MPAs except Hluleka, thus these comparisons between MPAs are unlikely to have been affected by season. We therefore believe that MPA cover is good, within each section, and that further collecting would greatly increase the numbers of records for each MPA.

Complementarity analysis gives a clearer idea of the biogeographical importance of each coastal section and of each MPA. The sequence of 'priority' of coastal sections revealed (Fig. 5a) can be explained by the biogeographical affinities of the floras of the coastal sections. This iterative process showed that when the section with the most species (39: Kenton-on-Sea to Port Alfred) is removed, 47 (the easternmost section) contains the highest number of additional species, and is therefore the second most important from a conservation perspective. Section 47 (which includes the relatively new Pondoland MPA) contains some warmer-water species that extend a short distance into the south coast from southern KZN and a few species that are restricted to the Pondoland/southern KZN coasts (see later).

Once these warmer-water elements are accounted for in the complementarity analysis, it is not surprising that the next section with the highest number of unaccounted-for species is 23, where water temperatures are the coolest and which contains the De Hoop MPA. The flora here contains few warmer-water species and relatively more cooler-water species that extend eastwards from the Benguela/Agulhas Overlap region that lies between Cape Point and Cape Agulhas. At this stage of the analysis, over 90% of south coast seaweed species are accounted for in three coastal sections: one fairly central, one in the far east (warm) and one in the far west (cool). This result is perhaps predictable, since it represents the greatest spread of temperature regimes along the south coast that is possible with three sections.

Coastal sections 32, 45, 33 and 36 each added some species, and all of these lie from the Tsitsikamma area (section 32) eastwards, indicating the importance of MPAs in this part of the south coast. Sections 29, 30, 41, 42, 43 and 46 (Group A: Fig. 5a) each add one species: their importance is uncertain, as the species are rare or under-collected (see later). The remaining coastal sections that added no further species therefore add no further conservation value (at least from a seaweed perspective). How does this analysis of the floras of the coastal sections correspond to an analysis of the species we found in the eight MPAs? Tsitsikamma MPA contained the highest percentage of south coast species (185 spp), indicating how important this relatively large and long-standing (established in 1964) MPA is on this coast (Fig. 5b). However, some of this effect may be a result of higher collecting effort in this MPA (see Methods). The highest percentage of additional species was found in the Pondoland MPA (75 species) which covers section 47, and was also identified as very important in our analysis of coastal sections. A notable difference between actual MPA collections and coastal sections is that in the former, the De Hoop MPA comes out as the second last in importance, adding only 12 species. However, the MPA collections should not be expected to include all the species in that coastal section, because the collections were of limited extent and duration.

The similar slopes of the two complementarity analyses indicate the importance of a spread of MPAs that includes central, eastern and western elements of the flora. Seven coastal sections are predicted to contain about 98% of the species, and with a relatively large number of MPAs spread along this coast, there is apparently good cover of biogeographical subdivisions.

Considering our results, are there any sections of the coast that appear under-protected? Most of the sections between 36 and 45 have relatively more species that we did not find in any of the MPAs (Fig. 6). Section 39 (Kenton to Port Alfred) is particularly important, because it contains no MPA, but has the highest species diversity (from the complementarity analysis) as well as the largest number of species (67) that we did not record in any of the MPAs. The position of this section is also biogeographically interesting because it lies on a major division between warmer- and cooler-water elements of the south coast flora (Fig 3) and is identified as particularly rich in various faunal groups as well. This area scored fifth out of the 19 sections of the whole SA coast identified for conservation of coastal fishes (Turpie *et al.*, 2000), and was the richest collecting site for southern African marine mites in the study by Proches & Marshall (2002). The Port Alfred area is unremarkable in terms of intertidal and shallow inshore habitats. Its shore of sandy beaches interspersed with sections of rock ledges, shelves and scattered subtidal reefs is typical of much of the Eastern Cape. However, Port Alfred is known to be a centre of upwelling of colder, more nutrient-rich water (Lutjeharms *et al.*, 2000 and see earlier discussion), and large temperature ranges (and perhaps higher productivity) may account for the biogeographical value of this area.

The slightly lower number of species found in Addo MPA, compared with the interpolated totals for section 38, may result from a relatively poor intertidal habitat for seaweeds. The mainland shore comprises low, flat aeolianite banks with little surface relief and evidence of frequent sand burial.

Although sections 23–26 have a fairly high number of species not recorded by us in any MPAs (Fig. 6), there are two MPAs in this region: De Hoop (in 23) and Stilbaai (in 26) and these sections are probably adequately protected. In any case, more collecting effort in these MPAs would almost certainly raise this number. In particular, more sampling is likely to increase records from De Hoop, as our collections there were restricted to several kilometres of easily accessible shore.

The distributions of rare, range-restricted and endemic species are often considered particularly important in the siting of protected areas (Roberts *et al.*, 2003). We consider rare species to be those that are extremely uncommon at any locality, and may be widely or narrowly distributed, but are seldom found. Because of the difficulties of finding often small, cryptic (and sometimes subtidal) seaweeds, we have not attempted to assign species to this category. Our definition of range-restricted species (those limited to between two and five contiguous coastal sections or > 50 to < 250 km of coastline) includes only one species (*Cystophora fibrosa*, which is also an endemic) on the western edge of the south coast (Fig. 7: sections 23 and 24): this is common, and protected, in the De Hoop MPA. The two range-restricted species in sections 38 and 39 (one of which is endemic and not found in section 40) were not found by us in our (limited) survey in Addo MPA, but notably both are found in section 39, which we identified as an important section for conservation. *Stilophora flanaganii*, the endemic range-restricted species found in sections 42 and 43, was not found by us in the Kei MPA, but is predicted to occur there. Section 47 is exceptional in having five range-restricted (including two endemic) species, all of which were found in the Pondoland MPA in our survey. These species extend a short distance into southern KZN, and so the Pondoland MPA, which includes the whole of this coastal section, is particularly valuable in terms of conservation, especially since MPA protection in southern and central KZN is minimal, with only the small Trafalgar and Aliwal Shoal MPAs (with shore lengths of 5 and 18 km respectively) along *c.* 380 km of coast between the Eastern Cape border and the adjacent St. Lucia and Maputaland MPAs in northern KZN. Furthermore, a subtidal survey by Celliers *et al.* (2007) showed that Pondoland reefs support a highly diverse benthic biota that is transitional between colder waters to the west (Agulhas Marine Province) and warmer waters to the east, which they refer to as subtropical.

This study shows that over the *c.* 1000 km of coastline comprising the Agulhas Marine Province of southern Africa, effective cover of the full biogeographical range of one group of organisms, which includes three major taxa (seaweeds), requires a number of MPAs. Three MPAs (one each at the centre and near the extremities) are predicted to include over 90% of the seaweed species. The current MPA network, which includes the seven existing and one proposed MPA we surveyed here and three smaller MPAs that we did not survey, is therefore likely to include most or all south coast seaweed species (excluding some that may be restricted to estuaries that we did not survey).

Climate change has become an important and sometimes controversial topic, and projections indicate that effects may become considerable in certain inshore marine systems, for example, in tropical Australian waters (Polaczanska *et al.*, 2007). There is at present little evidence of recent changes in sea surface temperatures causing changes in the distribution of seaweeds, possibly because detailed historical data on the seaweeds are often lacking. An exception is the study by Lima *et al.* (2007), which re-surveyed historical collecting sites on the coast of Portugal and showed some northward movement of warm-water species, but no clear pattern in the response of cold-water species to temperature changes. Circumstantial evidence for recent movements in the boundaries of certain seaweeds in south-eastern Australia is provided by Millar (2007). On the South African south coast, there is evidence of increases in sea surface temperatures in recent decades (Schumann *et al.*, 1995), and some evidence of biological effects on estuarine ichthyofauna (e.g. Mbande *et al.*, 2005; James *et al.*, 2006). Comprehensive distributional data for benthic algae and detailed analyses of biogeographical groups within marine provinces may prove particularly valuable in assessing the effects of climate change in the future.

This study demonstrates the usefulness of reliable distributional data (at least at species level) for marine conservation planning, and we suggest that such information will become increasingly important as planners attempt to meet targets, such as those of the IUCN (1992), for protecting 20% of the world's coastline. Furthermore, such baseline data will become an invaluable tool in understanding the effects of climate change on the distribution of shallow-water marine organisms.

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REFERENCES

Agardy, M.T. (1994) Advances in marine conservation: the role of marine protected areas. *Trends in Ecology and Evolution*, **9**, 267–270.

Anderson, R.J. & Bolton, J.J. (2005) Introduction. *Guide to the seaweeds of Kwazulu-Natal* (ed. by O. DeClerck, J.J. Bolton, R.J. Anderson and E. Coppejans), pp. 12–37. National Botanic Garden of Belgium, Brussels.

Anderson, R.J. & Stegenga, H. (1989) Subtidal algal communities at Bird Island, Eastern Cape, South Africa. *Botanica Marina*, **32**, 299–311.

Attwood, C.G., Harris, J.M. & Williams, A.J. (1997a) International experience of Marine Protected Areas and their relevance to South Africa. *South African Journal of Marine Science*, **18**, 311–332.

Attwood, C.G., Mann, B.Q., Beaumont, J. & Harris, J.M. (1997b) Review of the state of marine protected areas in South Africa. *South African Journal of Marine Science*, **18**, 341–368.

Bolton, J.J. (1986) Marine phytogeography of the Benguela upwelling system on the west coast of southern Africa. *Botanica Marina*, **29**, 251–256.

Bolton, J.J. (1994) Global seaweed diversity: patterns and anomalies. *Botanica Marina*, **36**, 241–246.

Bolton, J.J. (1996) Patterns of species diversity and endemism in comparable temperate brown algal floras. *Hydrobiologia*, **326/327**, 173–178.

Bolton, J.J. & Anderson, R.J. (1990) Correlations between intertidal seaweed community composition and seawater temperature patterns on a geographical scale. *Botanica Marina*, **33**, 447–457.

Bolton, J.J. & Anderson, R.J. (1997) Marine vegetation. *Vegetation of Southern Africa* (ed. by R.M. Cowling, D.M. Richardson and S.M. Pierce), pp. 348–375. Cambridge University Press, Cambridge.

Bolton, J.J. & Stegenga, H. (1987) The marine algae of Hluleka (Transkei) and the warm temperate/sub-tropical transition on the east coast of southern Africa. *Helgolander Meeresuntersuchungen*, **41**, 165–183.

Bolton, J.J. & Stegenga, H. (2002) Seaweed biodiversity in South Africa. *South African Journal of Marine Science*, **24**, 9–18.

Bolton, J.J., Leliaert, F., DeClerck, O., Anderson, R.J., Stegenga, H., Engledow, H.E. & Coppejans, E. (2004) 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. *Marine Biology*, **144**, 51–59.

Breeman, A.M. (1988) Relative importance of temperature and other factors in determining geographic boundaries of seaweeds: experimental and phenological evidence. *Helgolanders Meeresuntersuchungen*, **42**, 199–241.

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R. & Largier, J.L. (2003) Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications*, **13**(Suppl.), S90–S107.

Celliers, L., Mann, B.Q., Macdonald, A.H.H. & Schleyer, M.H. (2007) A benthic survey of the rocky reefs off Pondoland, South Africa. *African Journal of Marine Science*, **29**, 65–77.

Emanuel, B.P., Bustamante, R.H., Branch, G.M., Eekhout, S. & Odendaal, F.J. (1992) A zoogeographic and functional approach to the selection of marine reserves on the west coast of South Africa. *South African Journal of Marine Science*, **12**, 341–354.

Government Gazette, Republic of South Africa (2005) *Marine living Resources Act No. 18 of 1998*. Proposed declaration of three marine protected areas in the border region under section 43 of the Marine Living Resources Act, 18 of 1998, Vol. 484, Number 28129, pp. 9–16.

Hockey, P.A.R. & Branch, G.M. (1997) Criteria, objectives and methodology for evaluating marine protected areas in South Africa. *South African Journal of Marine Science*, **18**, 369–383.

IUCN (1992) Caracas action plan. *Plenary Session and Symposium Papers of the Fourth World Congress on National Parks and Protected Areas, Caracas, Venezuela*. World Conservation Union (IUCN), Gland, Switzerland, pp. 301–310.

James, N.C., Whitfield, A.K. & Cowley, P.D. (2006) Preliminary indications of climate-induced change in a warm-temperate South African estuarine fish community. *Journal of Fish Biology*, **72**, 1855–1863.

Legendre, L. & Legendre, P. (1983) *Numerical ecology*. Elsevier Scientific Publishing, Amsterdam.

Lima, F.P., Ribeiro, P.A., Quieroz, N., Hawkins, S.J. & Santos, A.M. (2007) Do distributional shifts of northern and southern species of algae match the warming pattern? *Global Change Biology*, **13**, 2592–2604.

Lombard, A.T., Strauss, T., Harris, J., Sunk, K., Attwood, C. & Hutchings, L. (2004) South African National Spatial Biodiversity Assessment – marine component. *South African National Biodiversity Institute Technical Report*, **4**, 96 pp. + appendices.

Lourie, S.A. & Vincent, A.C.J. (2004) Using biogeography to help set priorities in marine conservation. *Conservation Biology*, **18**, 1004–1020.

Lundquist, C.J. & Granek, E.F. (2004) Strategies for successful marine conservation: integrating socioeconomic, political and scientific factors. *Conservation Biology*, **19**, 1771–1778.

Lüning, K. (1990) *Seaweeds: their environment, biogeography and ecophysiology*. Wiley, New York.

Lutjeharms, J.R.E., Cooper, J. & Roberts, M. (2000) Upwelling at the inshore edge of the Agulhas Current. *Continental Shelf Research*, **20**, 737–761.

Maggs, C.A. & Guiry, M.D. (1987) Environmental control of macroalgal phenology. *Plant Life in Aquatic and Amphibious Habitats* (ed. by R.M.M. Crawford), pp. 359–373. Special Publication No. 5 of the British Ecological Society Blackwell, Oxford.

Margules, C.R. & Pressey, R.L. (2000) Systematic conservation planning. *Nature*, **405**, 243–253.

Mbande, S., Whitfield, A.K. & Cowley, P.D. (2005) The ichthyofaunal composition of the Mngazi and Mngazana estuaries: a comparative study. *Smithiana Bulletin*, **4**, 1–22.

Millar, A.J.K. (2003) The world's first recorded extinction of a seaweed. *Proceedings of the Seventeenth International Seaweed Symposium* (ed. by A.R.O. Chapman, R.J. Anderson, V.J. Vreeland and I.R. Davison), pp. 313–318. Oxford University Press, Oxford.

Millar, A.J.K. (2007) The Flindersian and Peronian provinces. *Algae of Australia: introduction* (ed. by P.M. McCarthy and A.E. Orchard), pp. 554–559. Australian Biological Resources Study, CSIRO Publishing, Collingwood, Vic., Australia.

Phillips, J.A. (1998) Marine conservation initiatives in Australia: their relevance to the conservation of macroalgae. *Botanica Marina*, **41**, 95–103.

Polaczanska, E.S., Babcock, R.C., Butler, A., Hobday, A., Hoegh-Guldberg, O., Kunz, T.J., Matear, R., Milton, D.A., Okey, T.A. & Richardson, A.J. (2007) Climate change and Australian marine life. *Oceanography and Marine Biology*, **45**, 407–478.

Pressey, R.L. & Nicholls, A.O. (1989) Efficiency in conservation evaluation: scoring versus iterative approaches. *Biological Conservation*, **50**, 199–218.

Pressey, R.L., Humphriess, C.J., Margules, C.R., Vane-Wright, R.I. & Williams, P.H. (1993) Beyond opportunism: key principles for systematic reserve selection. *Trends in Ecology and Evolution*, **8**, 124–128.

Proches, S. & Marshall, D.J. (2002) Diversity and biogeography of southern African intertidal Acari. *Journal of Biogeography*, **29**, 1201–1215.

Rindi, F. & Guiry, M.D. (2004) A long-term comparison of the benthic algal flora of Clare Island, County Mayo, western Ireland. *Biodiversity and Conservation*, **13**, 471–492.

Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M. & Warner, R.R. (2003) Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications*, **13**(Suppl.), S199–S214.

Santelices, B., Bolton, J.J. & Meneses, I. (in press) Marine algal communities, Chapter 7. *Marine macroecology* (ed. by J.D. Whitman and K. Roy). Chicago University Press, Chicago.

Schumann, E.H., Cohen, A.L. & Jury, M.R. (1995) Coastal sea surface temperature variability along the south coast of South Africa and the relationship to regional and global climate. *Journal of Marine Research*, **53**, 231–248.

Shears, N.T., Smith, F., Babcock, R.C., Duffy, C.A.J. & Villouta, E. (2008) Evaluation of biogeographic classification schemes for conservation planning: application to New Zealand's coastal environment. *Conservation Biology*, **22**, 467–481.

Stegenga, H., Bolton, J.J. & Anderson, R.J. (1997) Seaweeds of the South African west coast. *Contributions from the Bolus Herbarium*, **18**, 655 pp.

Stephenson, T.A. (1948) The constitution of the intertidal fauna and flora of South Africa, Part 3. *Annals of the Natal Museum*, **11**, 207–324 + 2 plates.

Turpie, J.K., Beckley, L.E. & Katua, S.M. (2000) Biogeography and the selection of priority areas for conservation of South African coastal fishes. *Biological Conservation*, **92**, 59–72.

BIOSKETCH

The three authors have been collaborating for almost three decades in documenting the seaweed flora of southern Africa. Their publications have substantially contributed to the increase in the known seaweed flora of South Africa from about 500 species in the early 1980's to around 900 species at present. They are currently documenting diversity of the seaweeds of the Agulhas Marine Province, and carrying out biosystematic studies in the southern African region. Their data have been widely used in national and regional marine conservation planning initiatives. They work in a true collaboration, although for this particular contribution HS led the collection and identification of specimens and compilation of lists, R.J.A. and J.J.B. analysed the data, and R.J.A. led the writing.

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