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BIODIVERSITY RESEARCH

Distribution of South African marine benthic invertebrates applied to the selection of priority conservation areas

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Abstract. Available data on species distributions and endemicity were compiled and examined for 11 groups of South African marine invertebrates (2533 species). For five groups species richness adhered to a well-documented pattern, increasing from west to east, but for the other groups species richness was highest along the south coast. Endemicity was generally highest along the south coast, and lowest along the east coast. The data base was then analysed using several types of complementarity analyses, each producing a minimum set of potential reserve areas, which cumulatively represent all invertebrate species analysed. Approaches based solely on rarity, species richness and endemicity demonstrated individual biases, suggesting a need to combine all three interests. Combining the three techniques produced similar results to the individual analyses, showing conservation priorities to be highest along the east coast. Specifically, the areas of Port Elizabeth and Durban were ranked high in all analyses. Consistently, a total of 16 sites was necessary to represent all species analysed. Comparisons with similar analyses on fish and seaweeds revealed similar findings. Existing invertebrate records were shown to be biased towards centres of high sampling activity, demonstrating a need of future sampling attention in under-represented areas.

Key words. Marine invertebrates, South Africa, endemism, biogeography, marine reserves.

INTRODUCTION

Following the early works of Thompson (1917, 1921, 1924), Clark (1923) and Stephenson (1939, 1944, 1948), much attention has been focused on documenting the distribution patterns of South African marine invertebrates (Day, 1967a,b, 1974; Millard, 1975; Clark & Courtman-Stock, 1976; Griffiths, 1976; Kensley, 1978, 1981; Gosliner, 1987; Williams, 1992a,b; Monniot *et al.* in press). The wealth of available species records continues to grow, providing a powerful tool for conservation-orientated analyses. The overall pattern and trends of invertebrate distributions have been well described (Emanuel *et al.*, 1992; Field & Griffiths, 1991), but direct comparisons between the distributions of different invertebrate taxa are lacking. The South African coast is divided into three biogeographical provinces, influenced by the flow of the Benguela upwelling system (west coast), and the south-flowing Agulhas current (east coast) (Ekman, 1953; Branch & Branch, 1981). Water temperatures have the strongest influence on the biogeographical division into the cool temperate west coast province, the warm temperate south coast province, and the subtropical east coast province (Ekman, 1953; Stephenson & Stephenson, 1972). Conventionally, and for the purposes of this study, the south coast is delimited by Cape Point to the west and Port Elizabeth to the east. A splitting of the east coast into two subprovinces

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has been proposed following recent biogeographical analyses (Emanuel *et al.*, 1992). In many taxa there is a trend of increasing species richness along the coast from west to east. Endemicity is generally thought to be highest along the south coast, which is not surprising as this region is the farthest from the political boundaries. This analysis compared the distributions and endemicity patterns for the invertebrate groups that have been adequately sampled, in order to ascertain whether the conventional biogeographical patterns hold at the taxon level.

An analysis of this sort is particularly useful in conservation, as it can highlight regions of high species richness, endemicity, or range overlap, factors often considered in the selection of protected areas (Kerr, 1994). South Africa has maintained a progressive policy towards the establishment and management of marine reserves, which continue to be the focus of conservation efforts within this complex and threatened environment (Hockey & Buxton, 1989; Emanuel *et al.*, 1992; Hockey & Branch, 1994, 1997; Attwood *et al.*, 1997; McQuaid & Payne, 1998; Turpie *et al.*, 2000). This analysis will provide baseline information valuable to the selection and management of marine reserves, as well as highlighting areas for future research.

The network of existing South African marine reserves is extensive when compared to other southern African nations, but small when compared to South Africa's system of terrestrial reserves (Hockey & Branch, 1994). The need for new marine reserves, and more efficient management of them, has previously been expressed (Emanuel *et al.*, 1992; Hockey & Branch, 1994, 1997; Attwood *et al.*, 1997), and recently proposed National Parks in Namaqualand and the Cape Peninsula are the first step in addressing these concerns. The issues regarding reserve management are not included in this study, but are nonetheless vital to the effectiveness of the existing and proposed reserve network. Instead the invertebrate distribution patterns are analysed in order to provide an overview of the current protection afforded to these species, and the potential for increasing the level of representation. Findings are compared with similar analyses conducted by others on coastal fish and seaweeds.

METHODS

Data set

The distribution and endemicity patterns of 11 distinct groups of South African marine invertebrates were examined. These taxa, chosen because of the relatively good state of taxonomic and distributional information, were octocorals, chitons, bivalves, gastropods, opisthobranchs, polychaetes, isopods, amphipods, brachyurans, echinoderms and ascidians. The coastline was divided into twenty eight 100 km units (Fig. 1), within which the presence or absence of each species was recorded. The units correspond to those used by Emanuel *et al.* (1992). However, whereas Emanuel *et al.* extended their study into Namibia and Mozambique, this analysis was restricted to the current political borders of South Africa. For nine of the taxa selected, information was derived from the original spreadsheets compiled by Emanuel *et al.* (1992), who list the original sources of these data. Species that have not been recorded within South African waters were eliminated, as were those found only at depths of more than 100 m. A total of 657 additional species (not previously analysed by Emanuel *et al.*, 1992) were added to the data set by incorporating polychaetes and ascidians, based on distributional data in Day (1967a,b) and Monniot *et al.* (2001). Any doubtful or incomplete records were omitted.

Endemicity data were added from the literature for 10 of the groups analysed. No endemicity data were available for the Brachyura. For the purposes of this study, endemicity is defined as endemic to the political boundaries of South Africa. Where necessary, previous determinations regarding endemicity were updated if a broader definition had been used. Data on octocoral and echinoderm endemicity were added from Williams (1992a,b,c), and Clark & Courtman-Stock (1976), respectively.

Since records of marine invertebrates in South Africa are not nearly as complete as those for the vertebrates, species ranges were assumed to be continuous between their limits, i.e. the distribution is presumed to extend from the most westerly documented record to the most easterly record. Suitable habitat is assumed to be present within each 100 km unit where such interpolations were made.

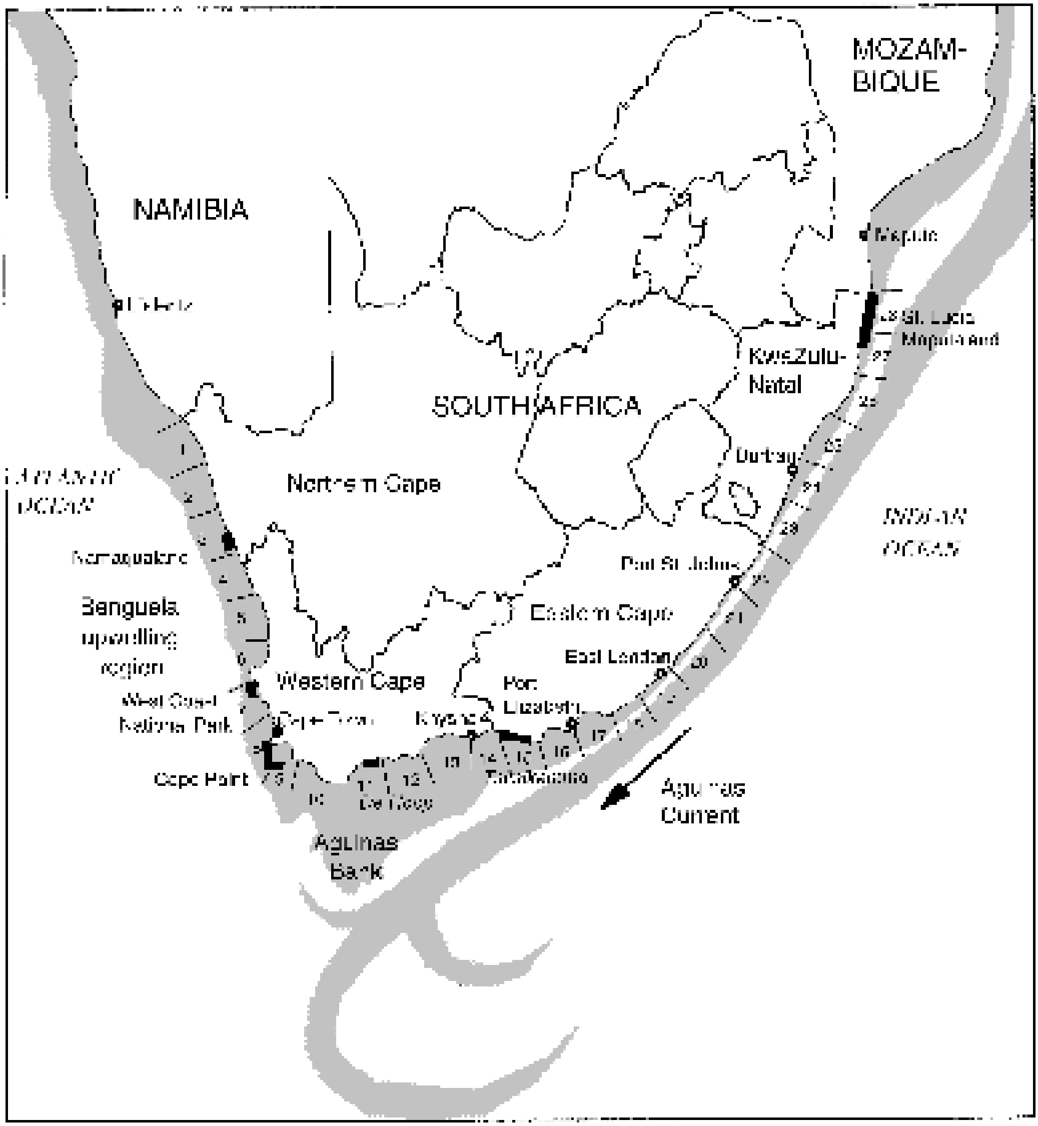

Fig. 1 Map of South Africa showing the twenty-eight 100 km units used in the analysis, and the positions of the major marine reserves along the coastline.

Conservation strategy

The data set was analysed using a series of manual complementarity analyses. Each analysis used an iterative selection technique to identify the minimum number of sites necessary to conserve all the species in the set. Species represented in the existing network of large 'no-take' reserves were thus considered to be adequately conserved, and were removed from the data base. Reserves meeting the criteria were considered to be those located at St Lucia/Maputaland (Units 27 and 28), Tsitsikamma (Unit 15), De Hoop (Unit 11), West Coast (Unit 7), and the proposed National Parks on the Cape Peninsula (Units 8 and 9) and in Namaqualand (Unit 3). Three separate approaches were taken for these analyses in order to produce scenarios that prioritize rare species, species richness and endemic species, respectively.

The first analysis was based on a rarity algorithm, which selects sites in order of those that contain the highest number of range-restricted species. A rarity value was calculated for each of the 100 km units using:

Rarity = k/a_i where k is the total number of unreserved sites, and a_i is the number of unreserved sites containing the ith species (Rebelo & Siegfried, 1992). When the first area with the highest rarity value is selected, all of the species contained therein are removed from the data base. The rarity values are then recalculated, and the process is repeated until all of the species have been accounted for. Effectively, this method weights range-restricted species over those with broader distributions, based on the degree of restriction. The result is a set of potential reserves that together contain all of the invertebrate species included in this analysis. The list is a prioritization of sorts, in that each successive site added recruits fewer species into the 'reserved' total.

The second approach used a similar iterative selection technique to choose sites that contained the highest species richness. This 'greedy algorithm' selects the site with the greatest number of species first. The species present in that site are then removed from the data base, and each successive iteration adds the site with the next highest number of species, until all species are represented at least once. This produces a prioritization of sites for conservation based purely on species richness.

A similar approach was taken for a third complementarity analysis, which was performed on all the endemic species first, before including the rest of the invertebrate fauna. Any non-endemic invertebrates that were present in the sites selected for the endemics were removed from the data base. This approach ensures that the set of reserves chosen conserves all of the South African endemics before considering species that are present, and possibly conserved, in other countries.

RESULTS AND DISCUSSION

Octocorals

The distributions of 54 octocoral species were analysed (Fig. 2). These species are concentrated along the south coast. This stretch along the extensive Agulhas Bank may be a centre of radiation for this group (Williams, 1992c). Maximum species richness was observed at Port Elizabeth (Unit 17) where 25 octocoral species have been documented. The lowest species richness occurred at Kosi Bay, where only one species was recorded. The low east coast species richness is likely due to a lack of sampling, and the small peaks at Durban (Unit 24) and St Lucia (Unit 27) may be more representative of realistic species numbers for this stretch of coast.

A total of 30% (16 species) endemicity was observed for the octocoral species analysed. The highest proportional endemicity was 50%, recorded at Saldanha Bay (Unit 7) and Port St Johns (Unit 22). The highest absolute endemicity was 7 species recorded at Cape Town (Unit 8) and at Port Elizabeth (Unit 17). The lowest proportional and absolute endemicity occurred along the west coast, north of Saldanha Bay, and at Kosi Bay (Unit 28) on the east coast, where no endemic species were observed.

Chitons

With only 23 species occurring in South Africa, the chitons were the smallest group represented in this study (Fig. 2). These species were concentrated along the south and south-east coasts. Peaks in species numbers were evident at the Cape Peninsula and at the area between East London and The Haven (Unit 20), which contained the highest species richness with 15 species. Species richness was lowest along the northern west coast, between the Orange River and Lamberts Bay (Units 1–5), and the eastern-most 300 km stretch of the east coast, each unit containing only six species.

A total of 78% (18 species) of the chitons were endemic to South Africa. False Bay (Unit 9) contained the highest absolute endemicity, with 13 species. Proportional endemicity was highest between False Bay and Tsitsikamma, at 100%. The lowest absolute and proportional endemism occurred along the east coast with 67% (4 species) between Richard's Bay (Unit 26) and Kosi Bay.

Bivalves

The species richness of 208 South African bivalve species increases steadily from west to east

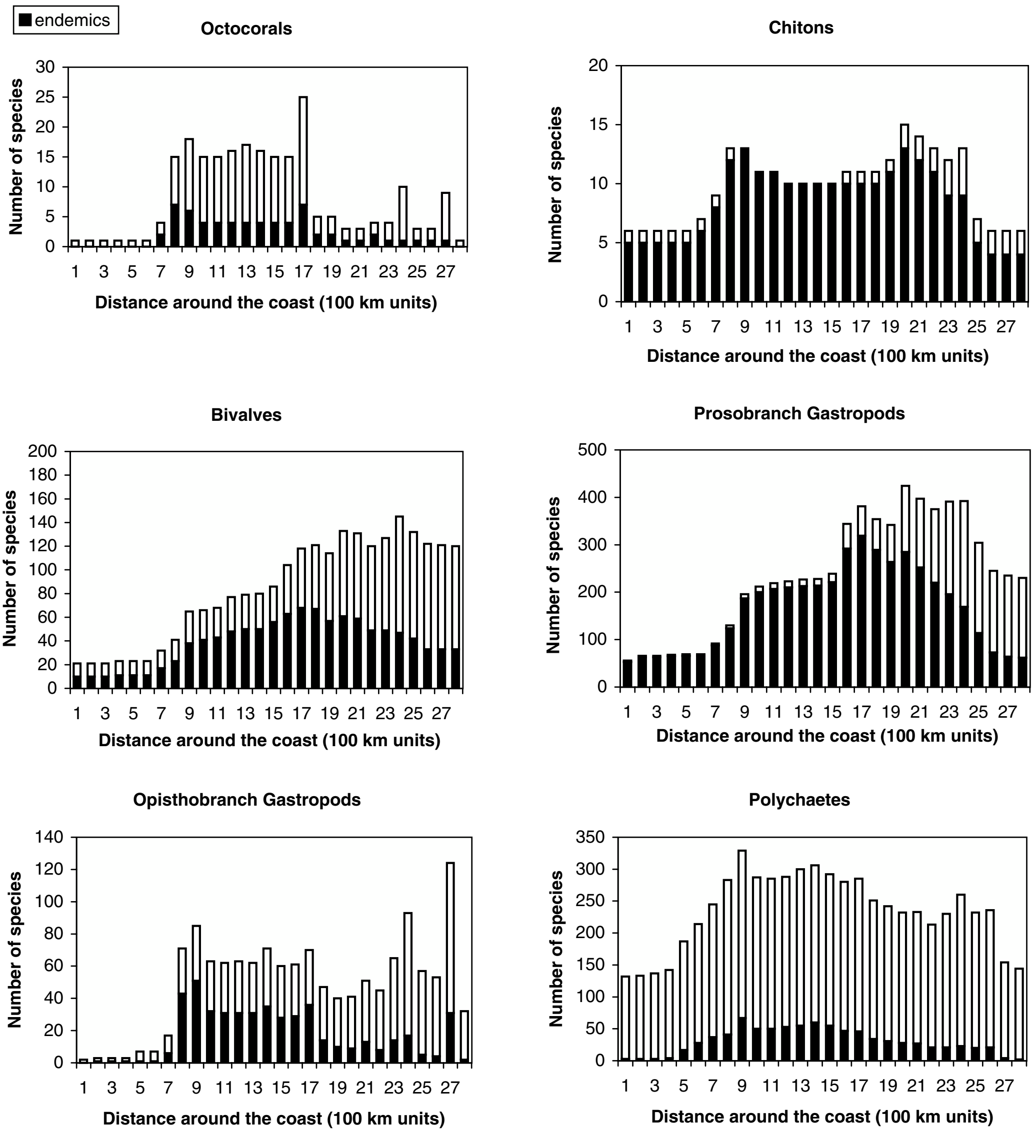

Fig. 2 Distributions for six invertebrate groups showing species richness and endemicity.

(Fig. 2), demonstrating a pattern that has been documented for many South African marine taxa (Branch & Griffiths, 1988; Bustamante *et al.*, 1997). The lowest species numbers were recorded from the 600 km of coast to the north of Saldanha Bay, where 21–23 species occur per 100 km unit. Moving east from this point, species richness increased steadily to a peak of 145 in the Durban area, and remained relatively high up to Mozambique.

Overall, 45% (93 species) of the bivalve species analysed were endemic to South Africa. Endemicity within this group demonstrated a predictable pattern, increasing with distance from the political borders. The highest proportional endemicity was 65%, at Tsitsikamma, and the highest number of endemics was 68 species at Port Elizabeth. The lowest proportional endemicity was 27%, occurring between Richard's Bay and

Kosi Bay, and the lowest numbers of endemics observed was 10 along the west coast between the Orange River and Namaqualand (Units 1–3).

Prosobranch gastropods

The prosobranchs were the largest group in this study, with 692 species analysed from South African waters. This mirrors the global pattern of high gastropod diversity relative to most marine invertebrate taxa (Hickman *et al.*, 1993). Species richness rose steadily from west to east, before falling slightly along the north-east coast (Fig. 2). The highest number of prosobranch species, 424, was recorded from Unit 20, located between East London and The Haven. The west coast had the fewest species, with a low of 56 at the western-most 100 km unit.

The overall proportion of prosobranch gastropods endemic to South Africa was 62% (422 species). Endemism in this group followed a unique pattern, not seen in any of the other groups examined. The proportion of endemic species was very high in the west and dropped steadily to the east. Endemicity levels were 95–96% along the entire west coast, and remained above 92% all the way to Tsitsikamma. From this point the percentage of endemic prosobranchs fell steadily eastwards, until finally reaching 27% at Kosi Bay. Absolute endemicity was highest at Port Elizabeth, with 319 species, and lowest at the Orange River mouth where 53 endemics were observed.

Opisthobranch gastropods

The distributions of 306 opisthobranch species were analysed (Fig. 2). This group had few west coast representatives, with an average of just 4 species per 100 km unit as far south as Saldanha Bay. Species richness increased sharply at False Bay, and remained relatively high along the south and east coasts, reaching a maximum of 124 species at St Lucia (Unit 27). Overall, the pattern of opisthobranch species richness appeared erratic, primarily because of the patchy sampling effort for this taxon.

Of all the South African opisthobranch species analysed, 48% (130) were endemic. The percentage of endemic species was erratic along the west coast due to the low number of species present. Proportions ranged from 0% at the Orange River to 35% at Saldanha Bay. Proportional endemicity was highest along the south coast, with 61% observed at the Cape Peninsula. The highest number of endemic species was 51 at False Bay.

Polychaetes

The distributions of 523 polychaete species were examined (Fig. 2). The fewest species were observed along the west coast, with 132 species reported from the northern-most 100 km unit. The number of species gradually increased south-east from there, reaching a high of 329 at False Bay. Species richness remained relatively high along the south coast, but declined slightly along the east coast. A sharp drop was observed north of Richard's Bay, possibly reflecting the change in dominant habitat types.

Of the polychaete worms analysed, 21% (108 species) were endemic to South Africa. Endemicity was highest along the south coast, with the peaks of 20% at False Bay and Plettenberg Bay (Unit 14). False Bay also contained the highest absolute endemicity, with 67 species. The lowest proportional and absolute endemicity was observed at the northern limits of the west and east coasts. Two endemic species were recorded from Kosi Bay, representing 1% of the invertebrate fauna located there. Globally, the polychaete worms have been well sampled, which may explain the overall low endemism reported here.

Amphipods

The distribution of 194 amphipod species along the South African coast was perhaps the most interesting of all the groups addressed, demonstrating a pattern completely dissimilar to the overall trend for marine invertebrates (Fig. 3). However, this pattern should not be surprising, as amphipods are known for their cool temperate affinities (Barnard, 1960). The highest species richness occurred in False Bay, where 135 species have been recorded. A sharp drop occurred immediately to the east of False Bay, and species richness continued to decline to the east, reaching a low of only 20 species at Kosi Bay.

Overall, 40% (77 species) of the South African amphipods analysed were endemic. This figure is low compared to most of the other taxa analysed, most notably the isopods that have very similar life histories, and that show similar patterns of

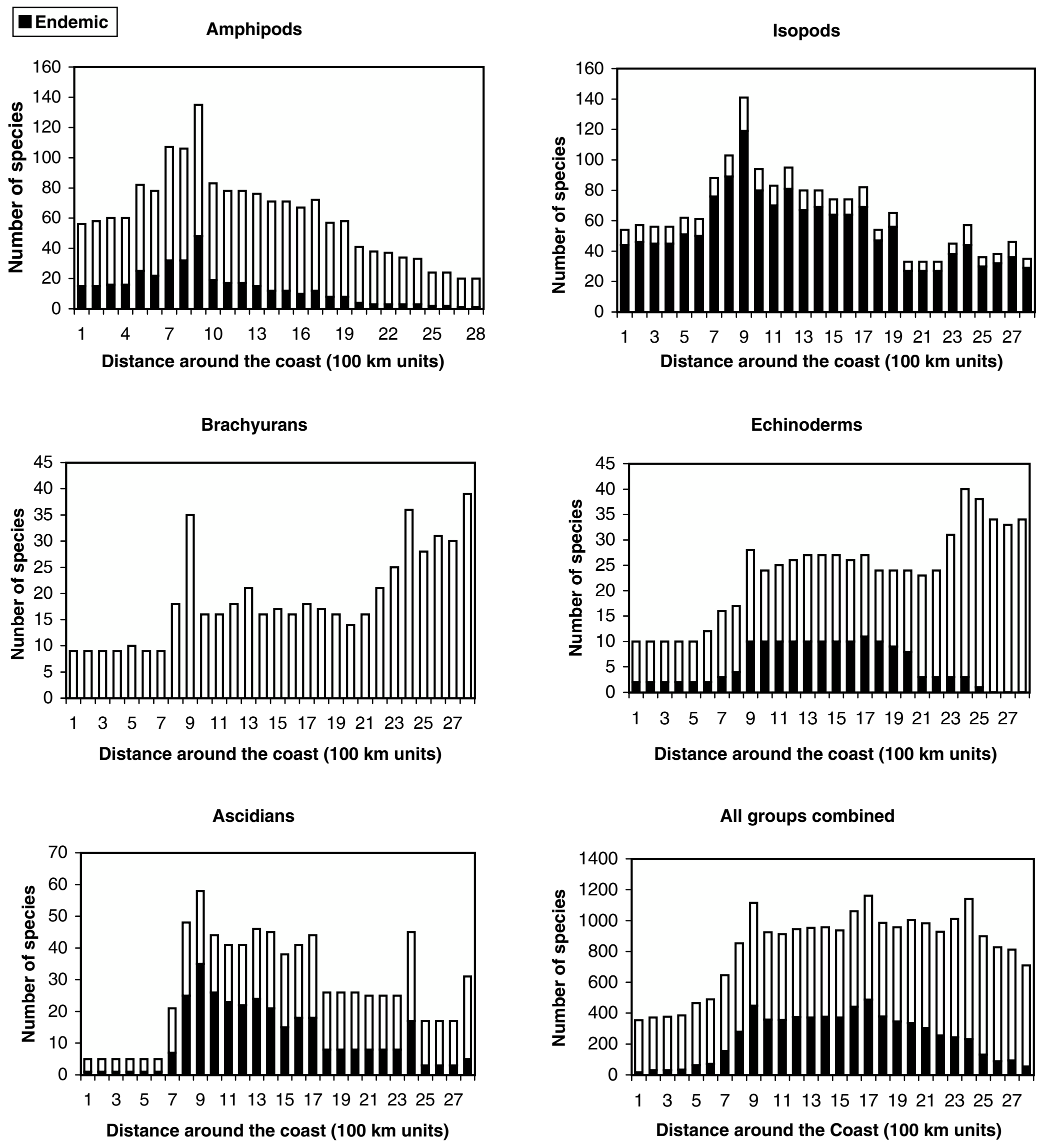

Fig. 3 Distributions for five invertebrate groups, and all 11 groups combined, showing species richness and endemicity.

distribution. Such other groups may not be as well sampled internationally, artificially raising their levels of endemicity. The pattern of amphipod endemicity tended to mirror the species distribution, decreasing steadily from west to east. The highest proportional and absolute endemicity occurred in False Bay, with 48 species representing 36% of the local invertebrate fauna. The decrease was pronounced along the south and east coasts, where endemicity fell continuously to a low of only 5% (one species) at Kosi Bay.

Isopods

The distribution of species richness for the 252 isopod species analysed was almost identical to the pattern shown for the amphipods (Fig. 3). This is likely a reflection of the similar life histories of these taxa. False Bay had the highest number of isopod species (141), and the lowest species richness was observed to the east of East London, where 33 species occurred in units 20–22.

Isopods showed the highest endemicity of all groups analysed, with a total of 84% (224) species endemic to South Africa. This endemicity is notable, in that it was evenly distributed along the entire South African coastline. The proportion of endemic isopod species fluctuated between a high of 87% east of Port Elizabeth, and a low of 77% at Durban. The highest number of endemics was 119 in False Bay, and the lowest absolute endemicity was 27 species occurring at units 20–22, east of East London. The overall high endemicity could, in part, be due to a general lack of isopod taxonomists, outside of South Africa, in the Southern African and Indian Ocean region.

Crabs

The distributions of 99 brachyuran species were analysed (Fig. 3), showing a pattern of species richness that increased from west to east. The highest species richness was observed at Kosi Bay, where 39 species were present, and significant peak of 35 species occurred at False Bay. The entire west coast down to Cape Town contained the lowest species richness, with between 9 and 10 species per 100 km unit.

Adequate endemicity data were not available for this group.

Echinoderms

The 65 species of South African echinoderms analysed followed a distribution pattern similar to that of the brachyurans (Fig. 3). Durban hosted the highest species richness with 40 species, and the west coast, from the Orange River down to Lambert's Bay, contained the lowest number of species, with only 10 species per 100 km unit. The boundaries of the biogeographical provinces were reflected with stepped increases in species richness moving east along the coast.

A total of 19% (12 species) of the South African echinoderms analysed were endemic, the lowest of all groups examined. Endemicity was highest along the south coast, from False Bay to East London, where 36%–42% of the species were endemic. The highest number of endemics was 11, recorded at Port Elizabeth. Due to the broad Indo-Pacific ranges of many echinoderm species, endemicity levels were lowest along the northern east coast, and no endemics were recorded from Richard's Bay northwards.

Ascidians

The distributions of 134 ascidian species were examined (Fig. 3). Due to the relatively low species numbers and patchy sampling effort, this distribution pattern was the most uneven of all the groups. Ascidian species were concentrated along the south coast, with the highest species richness occurring at False Bay (58 species). The west coast was species poor with only 5 species per 100 km unit from the Orange River down to Saldanha Bay. Although much of the coastline is undersampled, the data suggest a consistent decline in species to the east of False Bay.

A total of 54% (72 species) of the ascidians analysed were endemic. The highest levels of proportional and absolute endemism were observed at False Bay, with 35 endemic species representing 60% of the fauna. The lowest endemicity occurred nearest the political boundaries, with 20% (one species) endemicity along the west coast as far south as Saldanha Bay, and 16% (5 species) at Kosi Bay, on the east coast.

All groups combined

A total of 2533 marine invertebrate species from South African waters were included in this analysis. The pattern of distribution for all the groups of species combined (Fig. 3) showed the lowest diversity along the west coast, increasing steadily to the south, reaching a peak at False Bay. Moving eastwards, species richness remained relatively consistent as far as Durban, with peaks evident at Port Elizabeth and Durban, before falling steadily towards the Mozambique border. Obviously, the invertebrate taxa containing the highest numbers of species had the strongest influence on the overall distribution pattern. Therefore, it was not surprising that the pattern seen for all groups combined was quite similar to those of polychaetes and prosobranch gastropods, the two largest groups. The highest overall species richness

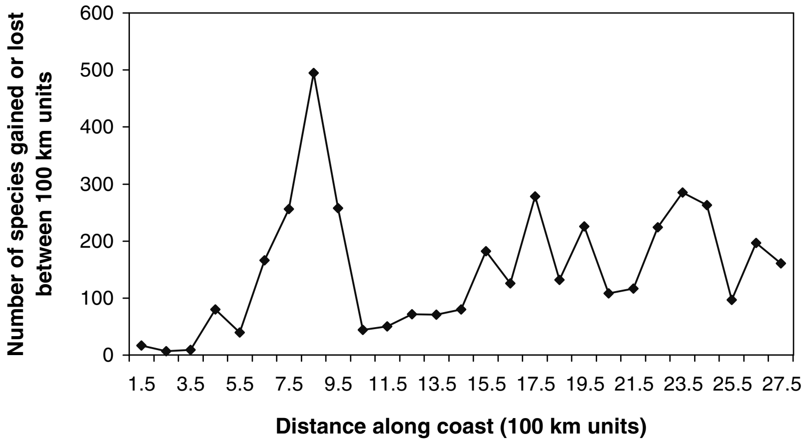

Fig. 4 Change in species composition along the South African coast (beta diversity), for all invertebrate groups combined.

occurred at Port Elizabeth, where 1161 species were recorded, followed closely by Durban (1141 species) and False Bay (1116 species). The west coast had the lowest species richness with only 355 species occurring at the Orange River mouth. An increasing trend, from north to south, was nonetheless observed within the west coast region. Though sampling bias was undoubtedly a factor, it is probable that this trend was real, considering many south coast species reach their eastern limits at Cape Point, while others extend some distance up the west coast away from Cape Town.

Of the marine invertebrates analysed here, 26% (931 species) were endemic to South Africa. The overall distribution of endemic species followed a marked and predictable pattern, remaining low near the political boundaries of the region, and increasing with distance from them. Hence, the south coast hosted the highest absolute and proportional endemicity, with highs of 45% (488 species) at Port Elizabeth and 44% (449 species) at False Bay. Endemicity levels fell swiftly to the west of False Bay, dropping to 5% (17 species) near the Namibian border. Likewise, a steady decline was observed east of Port Elizabeth, falling to 9% (55 species) near the Mozambique border.

General observations

Further analyses are being conducted on the invertebrate distributions in order to seek ecological explanations for the patterns found and to explore the various biases inherent in the available data. In the present study several consistencies have emerged. Strong peaks in species richness were recurrently apparent at the Cape Peninsula/False Bay, Port Elizabeth and Durban. These localities coincide with centres of high sampling activity, suggesting a strong sampling bias in the data. However, the peaks should not be completely discounted because they also coincide with the boundaries of the biogeographical provinces, where overlap in species ranges tends to be high (Emanuel *et al.*, 1992; Gibbons, 1999; Bolton & Stegenga in press). In order to determine the extent to which range overlap influenced the peaks, beta diversity, or change in species composition over distance, was examined for the entire coastline (Fig. 4). This showed the peak at the Cape Peninsula to be highly correlated with species turnover. The peaks at Port Elizabeth and Durban also manifested as a function of beta diversity, but not to the magnitude demonstrated at the Cape Peninsula. The number of endemic species restricted to 3 or fewer 100 km units (Fig. 5) also demonstrated obvious peaks at the Cape Peninsula, Port Elizabeth and Durban. Generally range-restricted endemics would be expected to be more abundant at the centres of biogeographical provinces, suggesting that the observed pattern was strongly influenced by single-species records at areas of high sampling intensity. Subsequent analysis of the data base showed single-species records to be high in these areas, relative to the

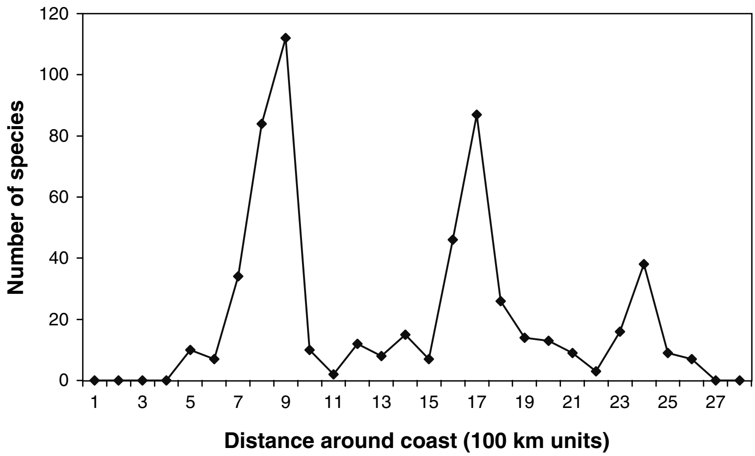

Fig. 5 Distribution of range-restricted endemics (defined as those observed in 3 or fewer units) along the South African coast.

rest of the coastline. No ecological rationale for this trend seemed evident, furthering the suggestion that sampling bias has strongly influenced the distribution of invertebrate species records along the South African coast.

A marked decline in species richness north of Durban was observed for several of the groups analysed (chitons, prosobranch gastropods, ascidians, echinoderms and polychaetes), as well as for all groups combined. This drop coincides with the discontinuity, recognized by Emanuel *et al.* (1992) that separates the subtropical east coast into two subprovinces. However, it is likely that lower sampling intensity and decreasing abundance of rocky shore habitat contribute to this trend.

Endemicity levels varied considerably between the groups analysed. In some cases it is likely that observed levels are biased by the lack of international sampling in the rest of southern Africa. For example, whereas the amphipods and isopods showed very similar distribution patterns, and share similar life histories, their respective overall endemicity levels were 40% and 84%. This discrepancy may be the result of relatively good sampling for amphipods in neighbouring countries, and a relative undersampling of isopods. Such artificially high endemicity is not only an artefact of disproportionate sampling, but also a result of the definition of endemicity used in this analysis. Given that the endemism was limited to the political boundaries of South Africa, and that the physical nature of the marine habitats does not change immediately to the north or south of the Orange River or of Kosi Bay, it is unlikely that the number of endemic species observed close to the borders is an accurate reflection of reality. Because it is likely that the species recorded as endemic immediately south of the borders also occur to the north of the borders, the distributions of all groups combined were recalculated after reclassifying the endemics that occur in the most westerly and most easterly 200 km as non-endemic (Fig. 6). Although this truncated distribution shows a more realistic pattern of endemicity along the South African coast, all conservation-based analyses were conducted on the original data base, due to the unavailability of data to contest accounts of endemism.

Conservation strategy

Using complementarity analysis based on the rarity algorithm, a total of 16 additional sites are necessary to represent all of the South African marine invertebrates, not already conserved in the existing reserve network (Table 1). The greatest contribution would be made by a reserve in the area of Durban (Unit 24), which contains 542 species not present in the current reserve network. A source of bias, specific to this analysis, is produced by the restriction of the analysis to the

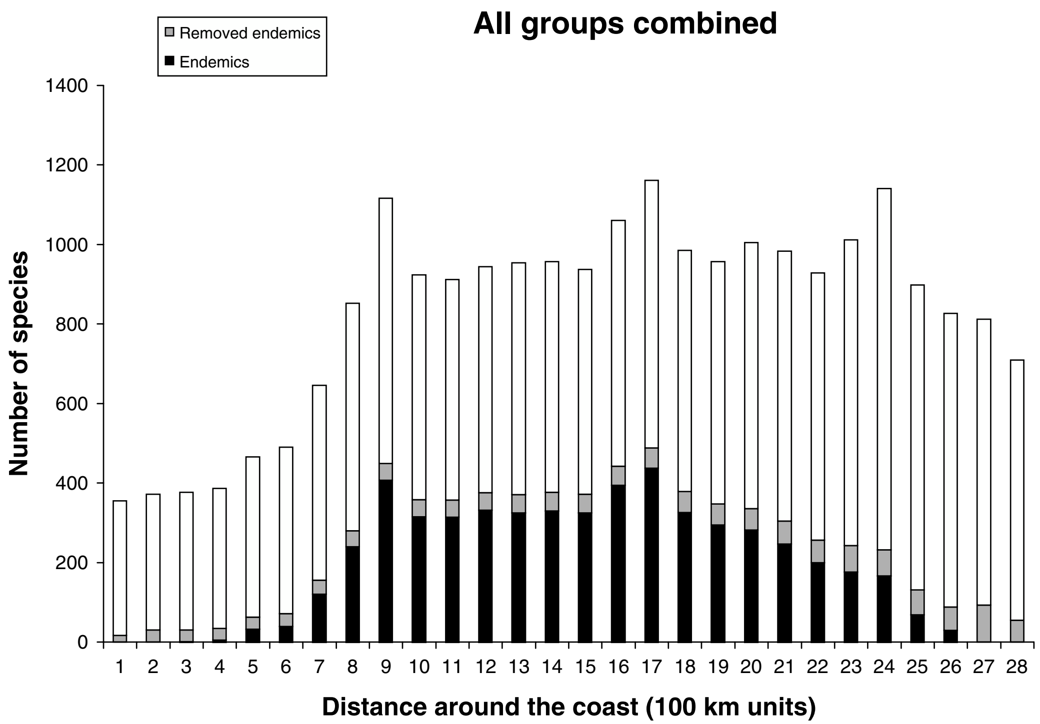

Fig. 6 Distribution of species richness and endemicity for South African marine invertebrates, following the removal of all endemic species occurring within the most westerly and most easterly 200 km of coastline.

political boundaries of South Africa. Species that occur near the borders, and whose ranges extend up the coasts into Namibia and Mozambique, will appear to be more range-restricted than they actually are. Likewise, non-endemic species that have only been documented within short ranges in South Africa will be weighted higher than South African endemics with broader distributions. Because the focus of this project targets the issue of conservation at a national scale, this concern is not seen as a shortcoming of the analysis, but should nonetheless be recognized.

Based on the 'greedy algorithm', Durban emerged again as the area of highest priority (Table 1). Using this analysis 16 new sites are necessary to represent all of the invertebrate fauna, with the order of priority differing slightly from the analysis based on rarity. By using only species richness, this algorithm eliminates any bias, which may result from the weighting used in the other analyses. However, treating all species equally is not a realistic representation of conservation priorities. Rare, endemic or commercially valuable species often take priority in conservation decision-making.

In order to conserve all the endemic species not present in the current reserve system, 15 new reserves would be necessary, with Port Elizabeth and Durban representing areas of highest priority (Table 1). This network of new reserves would leave only one non-endemic species unreserved. The endemicity-based analysis is only valuable under the premise that non-endemics are afforded additional protection in other countries. While this may be the case for species with Pan-African or Pan-Oceanic distributions, it is not a safe assumption for those restricted to southern Africa. South Africa hosts the majority of marine reserves in Africa south of 20°S (Attwood *et al.*, 1997), and species that are endemic to southern Africa are less likely to be conserved elsewhere. In the interest of optimal conservation, the analysis should include a concession that weights southern African endemics higher than other non-endemic species.

Table 1 Results of complementarity analyses showing prioritization of potential new reserve locations. The percent of total invertebrate fauna conserved is shown cumulatively, with the addition of each new site

Priority	Rarity algorithm		Species richness		Endemicity	
	Unit no.	Fauna conserved (%)	Unit no.	Fauna conserved (%)	Unit no.	Fauna conserved (%)
	Existing reserves	78.6	Existing reserves	78.6	Existing reserves	78.6
1	24	87.4	24	87.4	17	86.3
2	17	93.8	17	93.8	24	93.8
3	23	95.2	23	95.2	20	95.1
4	19	96.1	20	96.2	19	95.8
5	14	96.7	12	96.8	12	96.4
6	12	97.4	14	97.4	14	97.0
7	20	98.0	19	98.0	23	98.0
8	22	98.4	22	98.4	5	98.3
9	13	98.7	5	98.7	10	98.6
10	5	99.0	10	99.0	21	98.9
11	10	99.2	13	99.2	13	99.2
12	21	99.5	21	99.5	26	99.4
13	26	99.7	26	99.7	22	99.7
14	18	99.8	18	99.8	18	99.9
15	16	99.9	16	99.9	16	99.9
16	25	100.0	25	100.0	25	100.0

The limitations of each of the above complementarity analyses suggest that none of these approaches alone represents the interests of optimal conservation. Species richness, rarity and endemicity are nonetheless essential parameters to an ideal conservation strategy. In light of these conclusions, a fourth complementarity analysis was conducted using species richness as the selection mechanism, but adding weight to endemic species. All non-endemics were given a weighting of one, and endemics were weighted using the rarity algorithm described above. This method allows both species richness and endemicity to contribute to the selection of conservation areas, and uses rarity only where appropriate. The minimum set of reserve areas produced by this analysis (Table 2) differed in the order of priorities from the other three sets of results. This complementarity analysis was then repeated on the entire invertebrate data set (i.e. without removing the species already conserved in the existing reserve network). The minimum set of sites produced (Table 2) demonstrate the ideal reserve network, against which the locations of existing reserves can be compared.

In the absence of abundance data, complementarity analysis has been shown to be more effective than hotspot analysis or biogeographical zonation for the selection of priority conservation areas (Turpie *et al.*, 2000). Although flexible in its approach, this tool is constrained by parameters programmed by the user. In this analysis, species needed to be represented only once for each site selection. The abundance of each species, within a prioritized area, was not considered as a factor of its conservation. Furthermore, the level of conservation afforded to each species within the 'reserved' 100 km units was not addressed. These shortcomings represent promising areas for potential future analyses.

This type of complementarity analysis is specifically intended for reserve site selection (Rebelo & Siegfried, 1992; Underhill, 1994). However, given the myriad threats facing marine invertebrates, reserves may not always provide the best management option. Management that targets specific threats or species operates at a finer scale than the approach to conservation presented here. While addressing such specific interests is an important aspect of reserve function (Bohnsack, 1993; Agardy, 1994), such management is initially based on reserve size, location and purpose. A reserve must be large enough and situated in such a way that it achieves adequate representation of all the habitats found within the given 100 km unit (Clark, 1996). Furthermore, the design and management of the reserve must target the specific threats facing the species found within it. The priority areas presented here represent a coarse network of potential reserve locations within which a finer analysis can delineate optimal reserve boundaries and functions.

Comparisons with other studies

Recent literature has presented results from similar analyses conducted on other marine taxa. It is both interesting and valuable to note the congruence, or lack thereof, in the patterns that were demonstrated. Turpie *et al.* (2000) examined the distributions of 1239 fish species, and prioritized coastal areas for conservation using complementarity analysis with a rarity-based algorithm. Their analysis was also restricted to the political borders of South Africa, and was hence subject to the same biases as this study. Although the distribution and endemicity patterns shown were not taxon-specific, the overall trend for the fish showed a consistent increase from west to east, with endemicity levels highest along the south coast. The decrease in invertebrate species richness along the north-east coast was not mirrored by the fishes, possibly because fish have been sampled more thoroughly in that region. Endemicity levels for both groups were highest in the south, and lowest along the west coast.

The results of their complementarity analysis showed Durban to be the highest priority for fish conservation, using separate analyses for total species and endemic species. The area east of Port Elizabeth also scored highly for fish, as it did for invertebrates. If reserves were established at the 15 sites chosen for vertebrates, 95% of the currently 'unreserved' invertebrates would be protected (Table 2).

A survey of 803 seaweed species was conducted by Bolton & Stegenga (in press). The distributions of three taxa (Phaeophyta, Chlorophyta and Rhodophyta) were plotted and showed patterns similar to those presented here for invertebrates, reflecting the boundaries of the biogeographical provinces. The trends within the three groups of

Table 2 Results of complementarity analyses performed by (A) applying priority fish areas to invertebrate data base; (B) weighting endemic species, and (C) including species present in existing reserves to produce an ideal reserve network

Priority	A		B		C	
	Unit no.	Fauna conserved (%)	Unit no.	Fauna conserved (%)	Unit no.	Fauna conserved (%)
	Existing reserves	78.6	Existing reserves	78.6		
1	24	87.4	17	87.4	9	44.1
2	8	87.4	24	93.8	17	59.9
3	22	89.0	19	95.2	24	82.5
4	18	91.6	23	96.2	8	87.0
5	24*	91.6	14	96.8	27	91.2
6	7	91.6	12	97.4	14	92.1
7	10	91.9	20	98.0	7	93.1
8	20	92.7	10	98.4	19	94.0
9	25	92.7	5	98.7	23	95.4
10	22*	92.7	21	99.0	12	96.0
11	21	92.9	13	99.2	20	96.7
12	2	93.0	26	99.5	28	97.8
13	13	93.6	22	99.7	10	98.1
14	16	94.9	18	99.8	5	98.5
15	3	94.9	16	99.9	21	98.9
16			25	100.0	13	99.1
17					26	99.4
18					22	99.6
19					18	99.8
20					16	99.9
21					15	99.9
22					25	100.0

* Areas 22 and 24 each appear twice because Turpie *et al*. (2000) used 50 km units.

seaweeds did not differ greatly, with the exception of a peak in green algae species east of Durban. The species richness of invertebrates and seaweeds was lowest on the west coast, and both showed the same peak at the Cape Peninsula. The south coast contained the highest numbers of species from both groups. To the east of East London the number of seaweed species dropped abruptly, whereas the invertebrates maintained high species richness as far east as Durban, north of which a gradual decrease occurred. The analysis of seaweeds did not prioritize conservation areas, but six coastal sections were presented, that together contain 80–90% of the west and south coast seaweed flora, and 60% of the South African species total. These areas included Durban, which was also demonstrated as a high priority for both invertebrates and fish. Three of the existing National Parks reserves (The West Coast, De Hoop, Tsitsikamma) were also included, as well as Cape Hangklip (Unit 10) and the Hluleka Nature Reserve (Unit 21), neither of which ranked highly in either the invertebrate or the vertebrate analyses.

CONCLUSIONS

The data base created for this analysis provides a foundation that can be expanded upon, and used for subsequent analyses. Although the results obtained are clearly a function of the groups selected for analysis, a broad range of taxa was included. It would be beneficial to add some groups not represented here (e.g. sponges and cephalopods), should such taxonomic data become available. Endemicity data is incomplete for many South African invertebrates, and a lack of consensus on the most appropriate definition for endemicity further complicates the issue. By focusing sampling effort on these 'holes' in the existing data, some of the biases and artefacts of this analysis could be removed, clarifying the real distribution patterns, thus strengthening the subsequent conservation decisions.

Based on the analyses of invertebrate distributions, and those conducted by others for fish (Turpie *et al.*, 2000) and seaweeds (Bolton & Stegenga in press), the establishment of a marine reserve in the Durban area would provide protection to the greatest number of presently 'unreserved' species. Setting a reserve in the region between Port Elizabeth and East London would also be highly beneficial to the South African marine fauna. However, the selection of priority conservation areas addressed here does not consider the relative importance of different species, or other practical considerations such as land ownership and exploitation pressures. This first step is important, as it is based on 'big-picture' analyses of species distributions. The level of protection actually offered by existing or potential reserves, and the abundance of species present within them are equally important issues. Attwood *et al.* (1997) reviewed the state of South Africa's marine reserves, summarizing the levels of protection afforded to the various taxa found therein. A synthesis of their findings with available abundance data, and the results presented here, is the next obvious step towards a real conservation application of these data.

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