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Biogeography and the selection of priority areas for conservation of South African coastal fishes

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Abstract

Prioritisation of areas for biodiversity conservation has been debated largely in the terrestrial realm. In response to the increasing need for conservation efforts in the marine environment, this study compiles and analyses available data on species distributions and compares different approaches to the selection of marine protected area sites for the conservation of South Africa's coastal fish diversity. Species richness decreases from Mozambique southwards to the Cape, due mainly to a subtropical subtraction effect, and is uniformly low along the west coast. The number of species endemic to southern Africa is also higher in the east than the west, and peaks in the region of Port Elizabeth. Hotspot analysis does not provide a useful site-selection tool in a linear (coastal) analysis, at least in the absence of abundance data. Cluster analysis shows that coastal fishes conform to the same three biogeographical provinces as other marine taxa, although the zonal boundaries vary between groups and are particularly difficult to determine for fishes. Multidimensional scaling better illustrates the fairly even rate of species turnover east of Cape Point. The selection of sites at the centre and boundaries of vaguely-defined biogeographical zones is thus relatively difficult, and excludes several localised endemics. These problems can be resolved by using complementarity analysis. In the absence of abundance data, to avoid "reserving" species at the periphery of their ranges, a pragmatic approach is developed, in which data are refined to include species' core distributions only. The roles of existing marine protected areas are also considered in assessing future conservation needs.

Keywords: Complementarity analysis; Hotspots; Biogeography; Marine protected areas

1. Introduction

The convention on biological diversity (UNCED, 1992) calls for signatory countries to "develop national strategies, plans or programmes for the conservation and sustainable use of biological diversity". This, and the increasing necessity for rationalisation of conservation efforts in general, has led to a recent proliferation of studies which address the identification of high priority sites and the selection of 'hotspots' and efficient protected area networks for biodiversity conservation (Bibby et al., 1992; Pressey et al., 1993; Margules et al., 1994). Marine biodiversity conservation research and action has, however, generally lagged behind terrestrial conservation efforts (Agardy, 1994; Irish and Norse, 1996). This terrestrial bias is partly because of a traditionally limited view of marine resource conservation which necessitates little more than restrictions in commercial take (Ray, 1984) and partly because of limited information and inaccurate perceptions regarding the ecology and dynamics of marine systems and their biodiversity (Griffis and Kimball, 1996).

Protected areas are a major element in terrestrial conservation strategies, where they are essential in preventing habitat loss or degradation. Although important in the case of coral reefs and estuaries, these threats are less prevalent in marine systems, and marine protected areas have been concerned mainly with protection from overexploitation. It has only relatively recently been recognised that marine protected areas act as valuable, and probably essential, core refuges for the conservation of representative, functional ecosystems and biodiversity, as well as the conservation of source stocks of exploited species (Robinson, 1989; Plan Development Team, 1990; Bennett and Attwood, 1991;

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Bohnsack, 1993; Buxton, 1993a; Bohnsack and Ault, 1996; Eichbaum et al., 1996; McClanahan and Kaunda-Arara, 1996; Attwood et al., 1997a).

Although protected areas may fulfil both of these objectives to some degree, the criteria for their selection, and strategies for resource protection, can differ substantially. Protected area systems for fish stock conservation, sometimes driven by single-species needs, are most likely to be established in response to existing pressure by identifiable stakeholders. Protected area systems for biodiversity conservation, on the other hand, address a much broader range of current and future uses of species than would be the case with fishery-oriented protected areas. South Africa now has to address biodiversity conservation in terms of its commitment to the Biodiversity Convention, and more attention needs to be given to the role of marine protected areas in protecting biodiversity per se.

This study addresses the selection of marine protected areas for the conservation of coastal fish diversity in South Africa. South Africa has 57 marine protected areas, but their designation has largely been an ad hoc, opportunistic process and currently only three of these are considered to offer substantial protection to coastal biota including fishes (Hockey and Buxton, 1989; Robinson, 1989; Bennett, 1991; Attwood et al., 1997b). Part of the reason for a lack of conservation strategy for coastal fishes has been the limited availability of information. Although taxonomic studies on South African fishes are well advanced, effort in terms of thorough ichthyofaunal surveys has not been uniformly spread along the coast. As a result, there have been few studies of the broad distribution of fishes (Smith, 1949; Penrith, 1976), and most distributional studies have been based on restricted groups (e.g. Penrith, 1970; Prochazka, 1994; Whitfield, 1994). An understanding of biogeographical patterns is a prerequisite for identifying priority areas and efficient protected area systems for conservation (Ray, 1984; Emanuel et al., 1992; Turpie, 1995). In this study, we collate existing fish distribution data and apply and compare 'hotspot', biogeographical and iterative, or 'complementarity', approaches to the selection of marine protected areas for the conservation of South Africa's coastal fish diversity. These techniques have seldom been applied or compared for a linear, coastal situation.

2. Methods

2.1. Data set

This study was restricted to marine fish species that occur regularly on the South African coast and continental shelf. Species that occur in the open ocean, mostly at depths greater than 200 m, were not included. Further, doubtful records and vagrants (species recorded only once or twice in South Africa and unlikely to occur regularly) were omitted. In total, 1239 fish species of the approximately 2200 species that have been recorded from southern African waters (Smith and Heemstra, 1986) were included in the analysis. Taxonomic and distributional data were taken primarily from Smith and Heemstra (1986, with 1993 and 1995 additions and corrections). This was augmented by Compagno et al. (1989) for chondrichthyan species, and Griffiths and Heemstra (1995) for sciaenids.

Each species was categorised according to its worldwide distribution as global, Atlantic, Indo-Pacific, western Indian Ocean, endemic to southern Africa or endemic to South Africa. The broad habitat preference of each species was also recorded as intertidal, demersal (sandy, rocky or coral reef) or pelagic.

Based on distributional ranges, each species was recorded as present or absent in each of 50 52-km sections around the coast of South Africa (Fig. 1). Not all species' distributions are documented at this level of resolution, however, and in some cases, certain assumptions had to be made where descriptions of distributional limits were vague. For example, those species documented only to extend 'southwards to Natal' were recorded as occurring to the southern border of the KwaZulu-Natal province. Similarly, species that were reported to 'extend to the Cape' were recorded as occurring to Cape Point.

In using presence/absence data only, there is an implicit assumption that species conserved at a particular site are sufficiently abundant to ensure their long term survival and breeding at that site. A refined data set was created in which only the core distributions of species were included in presence/absence data. Species were taken as being absent in the peripheral 25% of the South African part of their ranges so that the core range was taken as the mid 50% of the range for species whose distributions fell entirely within South Africa, and 75% of the range from the border for species whose ranges extended further north to either Namibia or Mozambique. Species that range from Namibia to Mozambique were not affected.

2.2. Species richness patterns and 'hotspot' analysis

In terrestrial protected area selection, conservation 'hotspots' are usually defined as areas of peak value in terms of criteria such as species richness, endemism or rarity. Thus, as a first step, and using full distributional ranges, we examined the patterns of species and endemic species richness around the coast in order to investigate whether any 'hotspots' could be identified for fishes.

2.3. Biogeographical analysis

It has been suggested that the design of protected area systems should be based on biogeographical zonation (Hockey and Branch, 1994). Cluster analysis and multidimensional scaling (MDS) were performed on the full

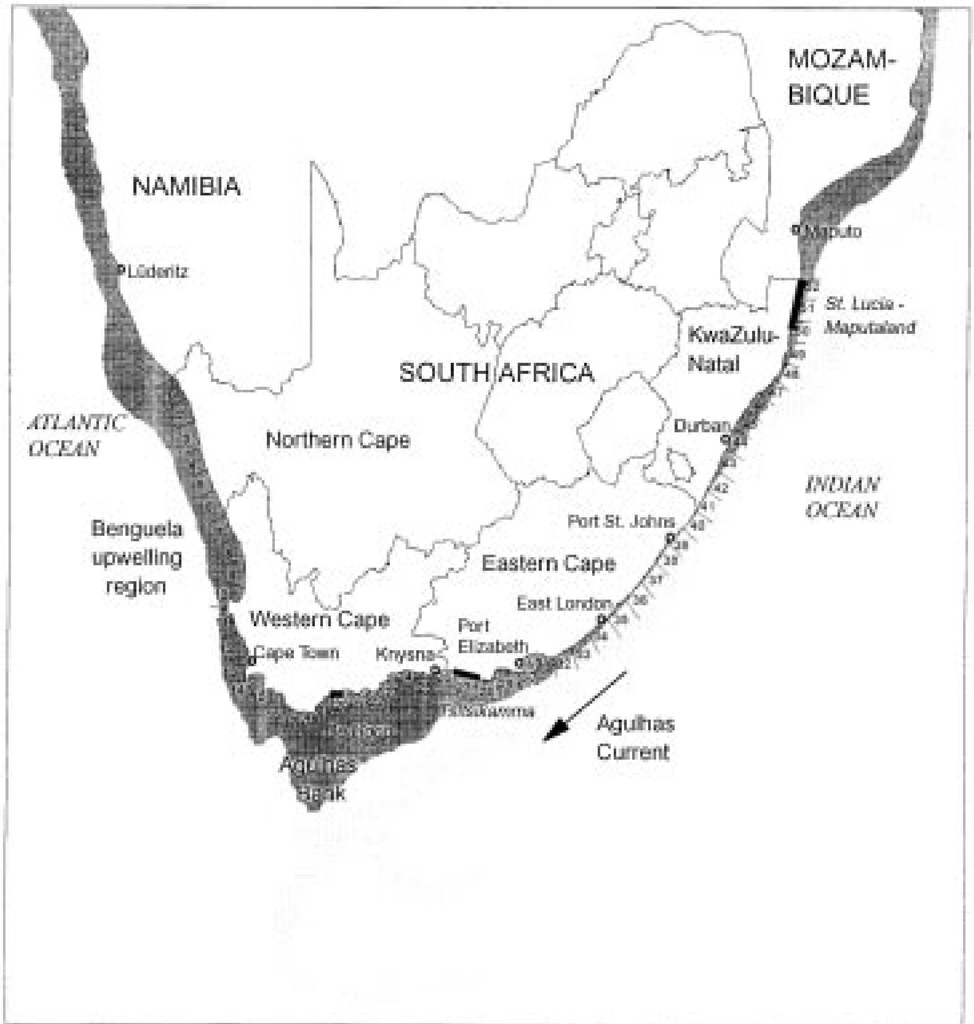

Fig. 1. Map of South Africa showing the location of the 52 50-km coastal sections used in the analysis and the position of major coastal towns or features, the extent of the continental shelf and the major offshore currents.

distributional data, at the scale of the 50 km sections, in order to identify major biogeographical zones for South African fishes. The Bray–Curtis measure of similarity, using an unweighted group-average method, was used in cluster analysis to identify hierarchical similarity among groups of coastal sections. The validity of quadrat grouping recognised by the cluster analysis was assessed by producing a two-dimensional ordination, using MDS. This is a less constraining approach than cluster analysis, because the data are not forced into a hierarchy (Shepard, 1980).

Protected area sites were selected in the centre of biogeographical zones and at the boundaries between zones. In this case, biogeographical zonation had to be considered beyond South Africa's political boundaries. The northern boundaries of the West and East Coast provinces have not been well defined in the past because marine fauna become less known towards the tropics (Penrith, 1976; Brown and Jarman, 1978). Published fish distribution data are still inadequate to perform reliable biogeographical analysis in these regions. Based mainly on invertebrate distributions, the northern boundaries of the two provinces are thought to be in the vicinity of Luderitz, a short distance north of the South African border, and central or southern Mozambique (Emanuel et al. 1992; Branch et al. 1994; Fig. 1). These boundaries were assumed to apply to fishes when defining the zones at the boundaries of the South African coast.

The number of species conserved within their full ranges and within their core distributional ranges was compared for the different sets of protected areas selected based on the biogeographical zones identified at three levels of percentage similarity: 50, 75 and 90%.

2.4. Iterative protected area selection: complementarity analysis

Complementarity analysis is an iterative selection technique which identifies how the target set of species can be conserved at the minimum number of sites (Pressey et al., 1993). Although complementarity analyses can be based on 'greedy algorithms', which choose the sites with the highest number of species first, this study uses one based on a 'rarity algorithm' which favours sites that score highly in terms of rare species at each iteration. A program ('Preserve', A. Rebelo) was used, which incorporates Rebelo and Siegfried's (1992) rarity algorithm and assigns each section the rarity value:

$$\text{Rarity} = \sum k/a_i$$

where k is the total number of unreserved sites, and a_i is the number of unreserved sites containing the ith species. After selecting the site with the highest rarity value, the 'reserved' species in that site are removed from the matrix, rarity values are recalculated, and the process is repeated until all species are represented at least once. The complementarity analysis was repeated using the refined data set in which species were only considered present in the core of their ranges.

3. Results

3.1. Patterns of richness and endemism

There is a progressive decrease in species richness of shelf-inhabiting fishes from the Mozambican border south-westward to Cape Point, and a consistently low number of species on the west coast (Fig. 2). This trend is largely a result of decreasing numbers of tropical Indo-Pacific and western Indian Ocean species (Fig. 2a), most of which are demersal species (Fig. 2b).

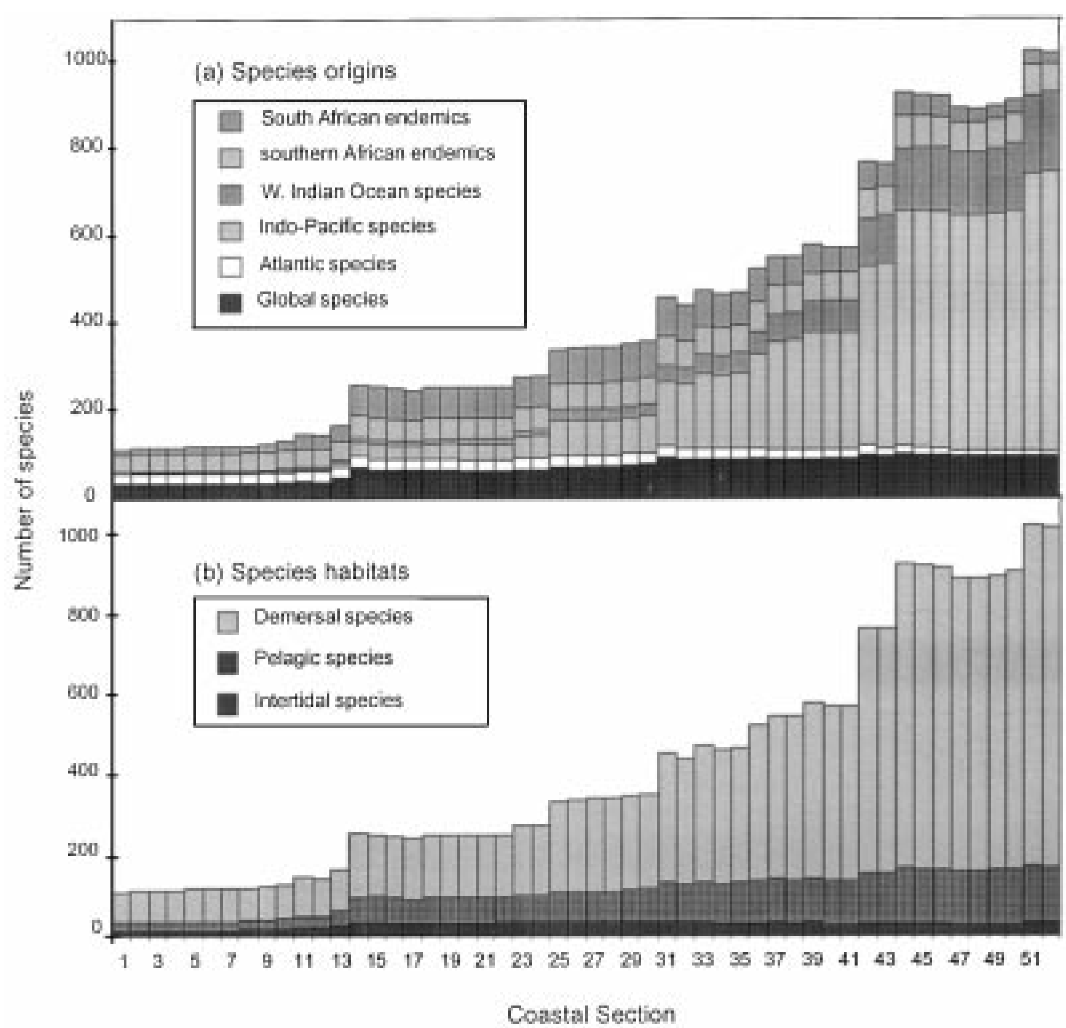

Fig. 2. (a) The numbers of fish species that occur on the coastal shelf from the Orange River to Kosi Bay. Numbers are per 50-km section of coastline and are based on distributional information from Smith and Heemstra (1986). Fish species are divided into different origin groups based on their worldwide distribution. (b) The numbers of fish species which are mainly associated with each of three habitat types: intertidal, demersal (sand or reef) and pelagic.

Stepped increases in numbers of species from west to east (Fig. 2) correspond to well-studied and often-fished areas as well as to biogeographical boundaries. Disproportionately well-sampled sites exist around Knysna (Section 25), Port Elizabeth (Section 31), Port Alfred (Section 35), Durban (Section 45) and St Lucia-Maputaland protected areas (Sections 50–52). The large increase in the number of species at the Eastern Cape/KwaZulu-Natal border is probably an artefact of incomplete distribution data (see Methods). Numbers of species to the west of the above-mentioned sections are therefore likely to be underestimates. The sharp increase in the number of species at Cape Point corresponds to a biogeographical boundary, the nature of which is discussed further below. Nevertheless, the high species richness in this section, relative to sections immediately to the east, is also partly an artefact of many poorly-known species distributions being described as 'extending to Cape Point'.

A total of 227 coastal fish species are endemic to southern Africa, of which 101 are endemic to South African waters. The numbers of southern African endemics increase with increasing distance from the country's borders, as expected, with a peak near Port Elizabeth (Fig. 3a). A similar pattern is found when the analysis is restricted to South African endemics, except that numbers are proportionally lower on the east coast (Fig. 3b). The total number of endemic species is higher on the east coast than the west coast, however, reflecting the pattern of total species richness. The proportion of shelf-inhabiting species that are endemic to southern Africa decreases from about 45% on the west coast to 34% at Port Elizabeth and 9% in northern KwaZulu-Natal.

Southern African endemic fish species are dominated by two families, the Clinidae (klipfishes) and Sparidae (seabreams), and the Gobidae (gobies) are also well represented. The majority of species in these families are found in relatively shallow water, with very few species living at depths in excess of 200 m. Many have limited distribution ranges, making them susceptible to habitat loss or overexploitation. The sparids, important in the

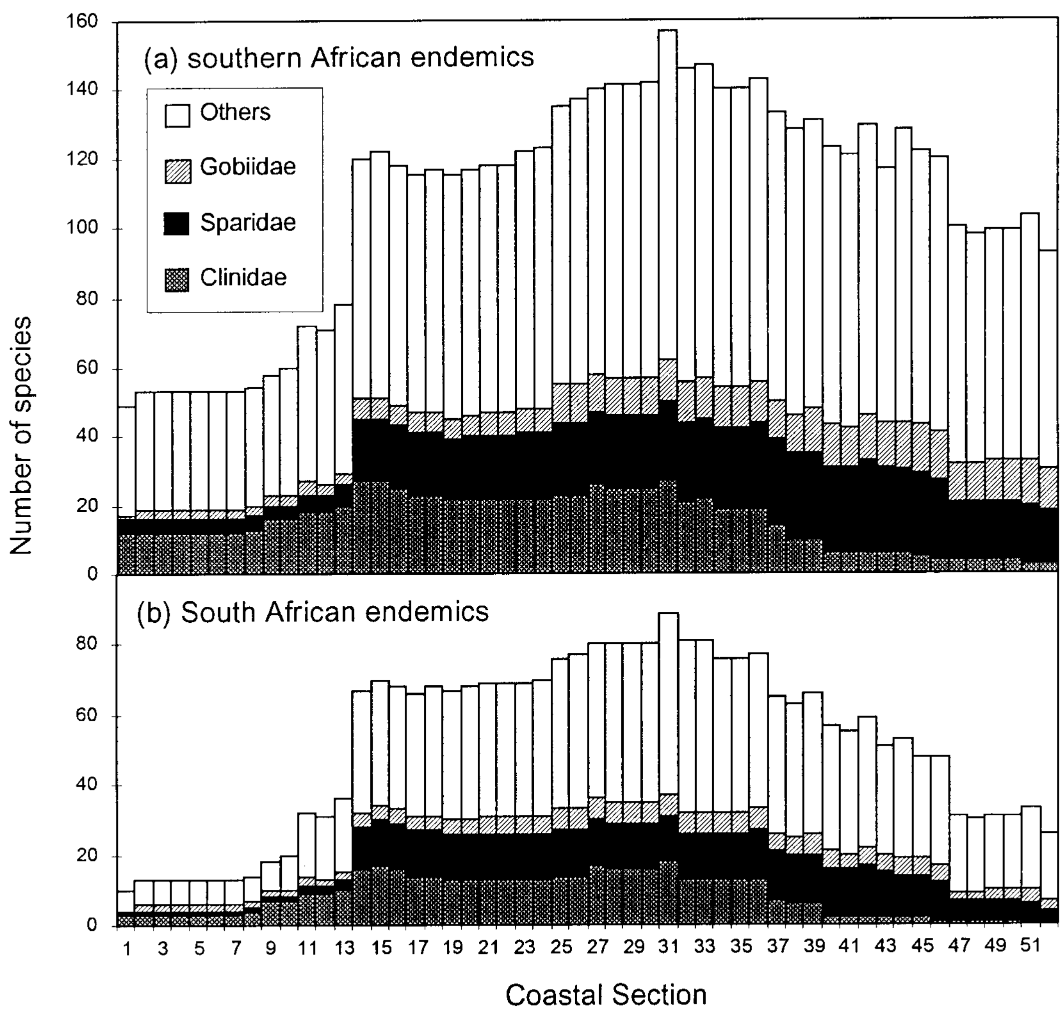

Fig. 3. Patterns of species richness of (a) southern African and (b) South African endemic fish species, indicating numbers of the three most represented families, Clinidae, Sparidae and Gobiidae.

hook-and-line fishery, are especially vulnerable, as life-history characteristics such as longevity, sex-change and residency make them susceptible to overfishing (Penney et al., 1989). Southern African endemic clinids occur mainly between Cape Point and Port Elizabeth, but endemic sparids occur mostly between Cape Point and Durban, with the highest number of species on the Kwazulu-Natal south coast (Fig. 3).

3.2. 'Hotspots' for conservation?

No discernible 'hotspots' exist for fishes in terms of species richness, but section rankings tend to increase from west to east, with the top 10 sections in KwaZulu-Natal. In terms of endemism, Section 31 ranks highest, and rankings decrease to the west and east of this section. However, it is doubtful whether Section 31 could be considered a hotspot, because of the likelihood of disproportionately high sampling effort at this site. Rather, the whole southern coastal area from Sections 14 to 36 could be considered to be important in terms of its relatively high numbers of endemic species. Thus 'hotspots' which are often easily determined for terrestrial biota, are less discernible in a linear, coastal system.

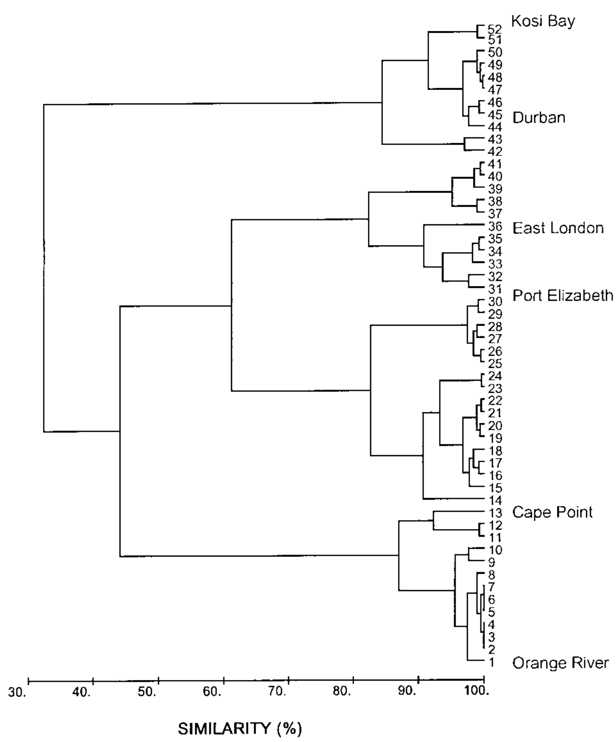

Fig. 4. Dendrogram of the 52 coastal sections from Orange River to Kosi Bay, showing the major groupings indicated by the cluster analysis.

3.3. Biogeographical zonation and the selection of marine protected area sites

Three provinces were identified for shelf-associated fishes in this study (Fig. 4): a west coast zone extending from Cape Point northward, a south coast zone, and an east coast zone from the KwaZulu-Natal border northward. Whereas the break at Cape Point is clearly repeated by the ordination (Fig. 5), it does not show as clear a break between the south and east coast provinces. Instead, the ordination suggests a gradual, even turnover of species east of Cape Point and identifies the whole of the Transkei region in the Eastern Cape (from Section 37 to 41) as being closer to the south coast sections than to those further north.

Assuming that fishes conform to the major zonal boundaries in Namibia and Mozambique (see Methods), then on the basis of the three major biogeographical zones identified at the 50% level of similarity, zone-centre protected areas would be placed in the vicinity of Section 6 on the west coast, Section 26 on the south coast and at or beyond the northern KwaZulu-Natal border. For the latter, zonal representativeness would thus best be achieved within South Africa near Section 52. Two zone-edge protected areas would be required. The first would be in the region of Cape Point (Section 14). The placement of the second would be more difficult, because of the diffuse zonal boundary in the Eastern Cape. It might be most logically placed in the centre of this boundary, around Section 39. Thus five sections

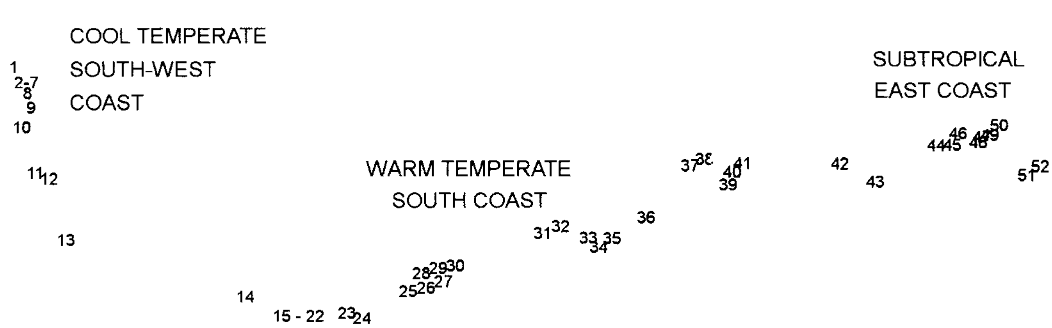

Fig. 5. Two-dimensional ordination plot based on the species composition of the 52 coastal sections.

were required to represent zonal edges and centres at the 50% level of similarity, seven at the 75% level, and 14 at the 95% level (Table 1).

Does the biogeographical approach yield a satisfactory solution in terms of representativeness and diversity? The set of five protected areas listed above accounts for 97% of species. However, of the 31 species not included in these sites, 17 are endemic to southern Africa, 15 of these being endemic to South Africa. If species are only considered to be adequately represented within the core of their ranges (see below), then the above protected area set excludes a further 21 species, including nine species endemic to South Africa (Table 1). Increased resolution of this approach led to an increased proportion of fishes being represented, with 99% of species being represented within their core ranges at the highest level of resolution, requiring 14 protected areas. Nevertheless, even this scenario will require additional protection measures for 12 species, including six South African endemics (Table 1).

3.4. Iterative protected area selection: complementarity analysis

The results of the complementarity analyses for the representation of all species and for southern African endemic species only are listed in Table 2 and illustrated in Fig. 6a. Theoretically, all coastal shelf species in South Africa could be represented in 14 marine protected areas, and if one were to make provision for southern African endemic species only, they could be represented in a minimum of 12 protected areas (Fig. 6a, Table 2). At each iteration, the number of new species for which an area is selected decreases (Table 2), so that the final choices of the programme are increasingly flexible. At the last iteration, the programme scored Sections 3–8 equally, and a west coast protected area could thus be sited anywhere along this stretch of coast. Because the programme is based on a rarity algorithm, there were only slight differences in the outcome for all species and for endemic species alone.

A larger set of protected areas was selected for all species to be represented within the core areas of their ranges than by the analysis based on full distributional ranges (Table 3, Fig. 6b).

4. Discussion

4.1. Patterns of richness and endemism

The decrease in species richness from east to west, also found for most other coastal taxa (Burger, 1990; Emanuel et al., 1992; Prochazka, 1994; Hockey and Turpie, 1999), is largely due to the subtropical subtraction effect. This southward progressive loss of the tropical Indo-Pacific and Western Indian Ocean species results from intolerance of changing oceanographic conditions, particularly decreasing water temperature (Smith, 1965). Three main factors are considered to govern fish distributions along the South African coast: temperature, geology and biological interactions (Penrith, 1976). The most important factor, temperature, is in turn affected by the warm southward-flowing

Table 2
The minimum set of sites in which all 1239 species and 227 endemic species can be represented, as determined by complementarity analysis

	All species			Southern African endemics		
Number	Section	Number of species	Cumulative species reserved	Section	Number of species	Cumulative species reserved
1	52	1019	1019	44	128	128
2	44	926	1089	31	157	199
3	14	259	1201	51	103	206
4	32	441	1221	14	120	218
5	43	765	1223	16	118	219
6	51	1023	1225	27	140	220
7	39	580	1229	46	120	221
8	27	344	1232	39	131	224
9	16	250	1233	32	146	225
10	40	573	1234	24	123	226
11	46	920	1235	2	53	227
12	24	279	1236			
13	33	474	1237			
14	2	117	1239			

Table 1
Protected area systems selected using a purely biogeographical approach, representing zonal centres and boundaries, at different levels of zonal resolution. The level of representativeness of these systems is measured in terms of the percentage of species represented, and the number of species, and of South African endemic species, excluded for both their full and core distributions

			Full distributions		Core distributions	
Level of similarity (%)	Number of reserves	Sections protected	% Species represented	Number outstanding (number of SA endemics)	% Species represented	Number outstanding (number of SA endemics)
50	5	6, 14, 26, 39, 52	97.5	31 (15)	95.8	52 (24)
75	7	6, 14, 22, 31, 36, 42, 52	98.1	24 (11)	97.1	36 (14)
90	14	5, 11, 12, 14, 19, 25, 28, 31, 34, 37, 39, 42, 44, 52	99.3	9 (5)	99.0	12 (6)

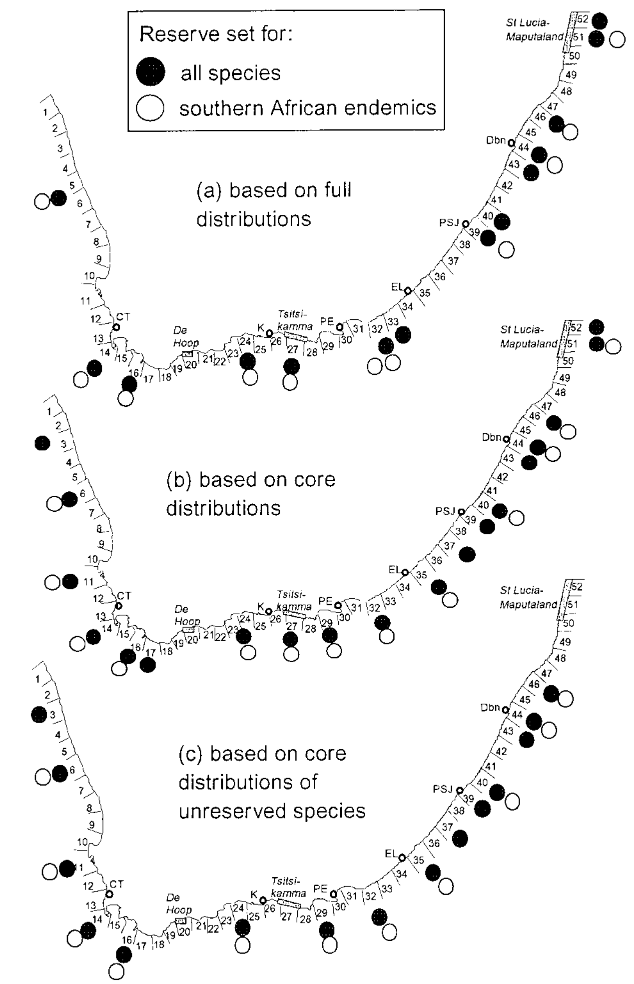

Fig. 6. Positions of reserves selected by complementarity analysis for all species (solid circles) and southern African endemics only (open circles), based on (a) full distributional data, (b) core distributions, and (c) for species not already represented in theory by the three main marine reserves illustrated.

Agulhas current on the east coast and the cold Benguela upwelling system on the west. These currents control fish distributions primarily through their influence on sea temperatures (van der Elst, 1981; Crawford et al., 1987), and also because they disperse fish eggs and larvae (van der Elst, 1988). However, the pattern of lower species richness on the nutrient-rich west coast is probably inversely related to productivity, as has been found for rocky-shore invertebrates (Hockey and Branch, 1994). The relatively high fish species richness in the east is also due to a higher diversity of inshore habitats (Smith, 1980), with the southernmost coral reefs in the Western Indian Ocean extending into KwaZulu-Natal. Habitats are themselves affected by sea-temperature as well as geology and wave action, e.g. coral reefs on the east coast (Schleyer, 1995), and kelp beds on the south-west coast (Branch and Branch, 1981).

Table 3
The minimum set of sites in which all 1239 species and 227 endemic species can be represented within their core ranges, as determined by complementarity analysis

	All species			Southern African endemics		
Number	Section	Number of species	Cumulative species reserved	Section	Number of species	Cumulative species reserved
1	52	1019	1019	51	95	95
2	44	874	1038	27	117	168
3	27	310	1143	44	95	176
4	14	177	1171	32	111	188
5	32	395	1186	16	74	205
6	39	511	1195	46	93	207
7	43	716	1198	35	100	212
8	16	186	1205	14	69	215
9	51	1014	1207	11	54	221
10	11	126	1222	40	85	223
11	35	416	1226	29	114	225
12	46	882	1228	24	116	226
13	40	510	1229	4	52	227
14	39	313	1231			
15	24	267	1234			
16	37	489	1235			
17	3	116	1236			
18	17	191	1238			
19	4	115	1239			

The South African ichthyofaunal complement has a relatively high level of endemism when compared to other regions of the world. This is illustrated by the fact that the proportion of endemism in KwaZulu-Natal (around 15%), which is the lowest along the South African coast, is similar to other more isolated areas such as the Red Sea and the Mediterranean, which have 15 and 14% endemism, respectively (van der Elst, 1988). Contributing to the high numbers of endemic species on the east coast is the fact that the southwestern Indian Ocean is a centre of endemism for Indian Ocean fishes (Cohen, 1973). South Africa's high level of endemism is probably partly due to its connection to the Southern Ocean. Clinids, and a few other endemic taxa, are of sub-Antarctic origin, with related fishes mainly in South America and Australia (Smith, 1965).

4.2. 'Hotspot' analysis

Ray (1984) suggested a type of hotspot approach for marine protected area site selection be used, based on overlays of the "critical habitats" of a set of "indicator species", i.e. the areas essential to the conservation of species deemed ecologically or economically important. The use of "indicator species" makes implicit (and dangerous) assumptions about species redundancy. Furthermore, the notion of "critical habitats", while providing an ideal theoretical measure, is often difficult to apply in practice, largely due to insufficient knowledge of species distributions and survival requirements. These requirements, where known, are thus better tackled during the subsequent phase of setting precise protected area location and design and identification of supplementary site requirements.

The identification of priority areas or 'hotspots' for conservation is usually achieved by scoring sites on one or more attributes, of which the most important are usually measures of species diversity and endemism. In the case of prioritising a set of discrete sites (e.g. wetlands, forest patches), this may include criteria such as site naturalness and overall abundance of the target taxa. The selection of protected area sites in geographically continuous areas is more difficult in that abundance data and other data are often more difficult to collect or deal with, and protected area selection is a two-step process; hotspots are identified by dividing the area into units and scoring each according to a set of criteria, and the size and position of protected areas is determined a posteriori. In marine systems abundance data are difficult to collect, let alone score. The coastal zone also presents an interesting case in that it is geographically continuous, but linear.

The South African coastal sections scored in terms of species richness, would simply imply increasing priority of sites from west to east. The top 10 sites would all be in Kwazulu-Natal, and species overlap between them would be very high. Indeed, the hotspot approach is known to be inefficient for selecting a set of (high-scoring) sites, in that some species may be over-represented and others excluded (Pressey and Nicholls, 1989). Sites scored in terms of percentage endemism, would indicate decreasing priority from west to east. This frequently-applied measure is rendered fairly meaningless in this case by the strong subtropical subtraction effect. In terms of numbers of endemic species, the Port Elizabeth area is identified as a priority area. If the endemic species are further broken down into families, then different hotspots would be identified for clinids, sparids, etc. It is not clear, however, whether prioritisation should be in terms of endemism or richness patterns (see Prendergast et al., 1993; Kerr, 1994).

In this analysis, species are weighted equally. A more comprehensive approach might be to weight species according to their distributional range, whereby, for example, globally distributed species might be assigned one point, Indo-Pacific species two points, and so on. One might also go one step beyond South African endemics, assigning higher weightings to species with restricted ranges (narrow endemics — Williams et al., 1993) within South Africa. However, these relative weightings are arbitrary, and it is easy to see that the hotspot approach could be very sensitive to the criteria and weights used.

The hotspot approach probably does not provide a useful starting point for the design of protected area systems, particularly when analysing a continuous coastline. However, hotspot analysis can be useful when used in conjunction with other methods, especially where subjective decisions have to be made in selecting a set of protected areas (Turpie, 1995). For example, in a study such as this it would be pertinent to check that the final outcome of the analysis includes the identified hotspot areas for endemic species.

4.3. Biogeographical zonation

Three main biogeographic zones are recognised around the southern African coast: a Cool Temperate South-West Coast Province, a Warm Temperate South Coast Province, and a Subtropical East Coast Province (Stephenson and Stephenson, 1972; Brown and Jarman, 1978). These patterns have more recently been verified using better data and more sophisticated analytical techniques for rocky shore invertebrates (Emanuel at al., 1992), intertidal fishes (Prochazka, 1994) and waterbirds (Siegfried, 1981; Hockey and Turpie, 1999).

Although there is broad agreement on South Africa's marine biogeographical zones, there is still some debate as to the location of the interzonal boundaries. In this study, the boundary between the first two zones was found to lie in the vicinity of Cape Point (Fig. 4). A break at Cape Point has been proposed by many authors (e.g. Stephenson and Stephenson, 1972; Emanuel at al., 1992) although the most sensible view is probably to consider the region from Cape Point or Kommetjie (in Section 13, Fig. 1) to Cape Agulhas (in Section 18), which undergoes large temperature fluctuations associated with upwelling (Penrith, 1976), as a transition zone (Day, 1969; Brown and Jarman, 1978). The position of this boundary for intertidal fish, however, was found to lie within the De Hoop Marine Reserve (Prochaska, 1994; Fig. 1), ca. 50 km east of Cape Agulhas. Biogeographical zones are often less distinguishable in the marine environment, and are strongly influenced by the ocean depth to which the analysis extends. For example, the Indian Ocean fauna penetrates further west on the Agulhas Bank than it does nearer the coast (Brown and Jarman, 1978). As analyses extend further offshore, biogeographical boundaries will become increasingly blurred by the dynamics of ocean currents: the boundary between the Benguela upwelling system and the Agulhas current retroflection area shifts periodically (Crawford et al., 1987; Lutjeharms and van Ballegooyen, 1988).

The position of the boundary at the KwaZulu-Natal border is probably largely an artefact of the quality of data used in the analysis, with several distribution limits being set at the border due to insufficiently detailed information available on the extent of distribution into KwaZulu-Natal or the Transkei coast of the Eastern Cape. The South Coast province extends only as far east as Port Alfred for intertidal fish (Prochazka, 1994), and slightly further to East London in the case of rocky shore invertebrates (Emanuel at al., 1992). Smith (1949) and Penrith (1976) considered the boundary to lie near the Kei River 50 km northeast of East London.

Biogeographical zones are normally verified by the distribution patterns of 'characteristic species' (Field et al., 1982; Turpie and Crowe, 1994), or those species whose ranges most closely fit the range identified by cluster analysis or ordination. The eastern distributional limits of the species endemic to the South Coast Province are highly variable, suggesting that this boundary is very diffuse. The lack of clarity of zonation in the east is due partly to many species recorded as present outside their 'normal' ranges because of southward transport by the Agulhas current (Beckley, 1996). In addition, there are numerous temperate species which migrate northwards (mainly in winter) up to KwaZulu-Natal (van der Elst, 1988). It is also difficult to define a boundary in the absence of physical barriers to movement or obvious changes in habitat. We therefore suggest that this boundary occupies a broad transitional zone between Sections 37 and 41. A persistent thermal front has been found to occur on the shelf immediately to the south of this region, with distinctly lower water temperatures south of the front as a result of dynamic upwelling associated with the inshore edge of the Agulhas current (Beckley and van Ballegooyen, 1992).

4.4. A biogeographical approach to protected area-site selection

Hockey and Branch (1994) suggested that a set of protected areas for biodiversity protection be sited near the centres and edges of biogeographical provinces to cover aspects of representativeness and diversity, respectively. In the case of coastal fishes, because of the strong increase in numbers of species from west to east, zone-edge protected areas contain fewer species than zone-centre protected areas further east. However, the number of species uniquely represented within any part of their distributional range by each protected area is lower for both zone-edge protected areas than for the protected areas to the east and west of them, and together make up 5% of species represented only once.

The biogeographical approach yielded a result of apparent high efficiency, in that few protected areas represented a high percentage of the target set of species. However, the species missed were those of limited distributional range, which are often the species most in need of protection. Theoretically appealing, because all biogeographic zones must be conserved in a representative protected area network, this approach only necessarily takes care of species that are widespread or characteristic of biogeographical zones (species whose distributions closely follow zonal boundaries). Furthermore, it is a somewhat dangerous assumption that the most representative site would be located at the centre of a biogeographical zone. This study also provides no evidence that there is greater advantage in siting additional protected areas at zonal boundaries than elsewhere in terms of maximising species representation, although there are other ecological advantages of doing so (Hockey and Branch, 1994).

4.5. Complementarity approach to protected area selection

Iterative reserve-selection approaches have been shown to produce a more efficient result than the above approaches, in that they lead to the selection of a minimum, or near-minimum (Underhill, 1994), set of reserves that conserves all target species at least once (Pressey and Nicholls, 1989; Williams et al., 1993). In doing so it must necessarily be representative of biogeographical zones, and in this study the same sections, or an adjacent section in one case, that would be selected on biogeographical criteria were also selected by the complementarity analysis. These form only part of the overall protected area set selected by complementarity analysis, however, and the latter approach can be considered superior in that it achieves (at least in theory) the conservation of all targeted species. Interesting to note is the relatively high number of sites selected by the complementarity analysis in the broad zonal boundary area of the east coast.

Predictably, and importantly, the analysis using core ranges led to the selection of a higher number of protected areas to represent all species at least once than did the analysis based on full distributions, because of the reduced incidence of overlap among species distributions. Given that relative abundance along the coast is still poorly known for most South African fish species, this is probably the most parsimonious way of avoiding the selection of reserve sites for species in areas of relatively low abundance.

Despite performing well relative to other methods as a primary reserve-selection tool in the marine realm, the limitations of complementarity analysis need to be recognised. Firstly, the sequence of site choice is biased westwards, in that the program chooses the first out of a series of same-scoring sites, should this situation arise. The tendency for same scoring sites to occur increases at each iteration as remaining diversity decreases. Secondly, the outcome of the complementarity analysis is affected by the scale of the analysis, and is also driven to some extent by the number and scatter of species which have very limited distributional ranges. Scale issues include the geographical limits of the analysis, and inclusion of Namibia and Mozambique may result in a somewhat altered protected area configuration. This may be superior in terms of siting certain protected areas optimally (i.e. further north) within biogeographical zones. Nevertheless, the more limited analysis in this study aims to maximise the conservation of biodiversity at a national scale and does not require international collaboration.

4.6. Complementing existing protected areas: a necessary pragmatic approach

It is useful to design theoretically ideal protected area networks which can be compared with existing conservation efforts. South Africa's three main existing marine protected areas are the De Hoop Marine Reserve in the southern Cape (Section 20, Fig. 1), the Tsitsikamma National Park further east (Sections 27 and 28, Fig. 1) and the St. Lucia and Maputaland Marine Reserves near the Mozambique border (Sections 50–52, Fig. 1).

The St. Lucia and Maputaland Marine Reserves lie at the southern extremity of coral reefs in the western Indian Ocean (Chater et al., 1995). Together they extend for 155 km along the coast and 5.6 km out to sea. Angling is permitted in the protected area, but offshore capture of bottom-dwelling reef fishes is forbidden. Some 400 species of fishes have been recorded here during research dives on offshore reefs that took place over the period 1987–1990 (Chater et al., 1993). However, over 800 species have been recorded in all habitats in the area including the marine protected areas and the St Lucia estuary since the turn of the century (Smith, 1980; Chater et al., 1993).

The Tsitsikamma National Park, proclaimed in 1964, includes a marine protected area extending 65 km along the coastline and 5 km seawards (Robinson, 1989). This protected area, which has a small area open to fishing, is important for the protection of several linefish species and the conservation of reef biodiversity, with a total of 119 fish species from 47 families having been positively identified in the reserve (Buxton, 1993b). Being centrally located in the Warm Temperate South Coast province, it is well-placed for the protection of the species of this zone (Burger, 1990). Also fully protected, the 50 km De Hoop Marine Reserve was opportunistically proclaimed in 1985. Nevertheless, it has since proved valuable in protecting heavily exploited fish stocks, including endemic species, in the area (Bennett and Attwood, 1991). At least 65 fish species have been recorded in the reserve (C. Burgers, Cape Nature Conservation, pers. comm.), but no comprehensive survey has been published.

The 'ideal' protected area network identified in the complementarity analysis incorporates two out of three of these protected areas. This may imply that the third, the De Hoop Marine Reserve, is not well sited, and is possibly redundant in terms of contributing to such a primary protected area set. Because of the gradual nature of turnover of fish species along the coast, however, this is not necessarily the case, and a more pragmatic approach may be to account for existing protected areas in the analysis in order to identify additional protected areas that would be required to represent all species once. The flexibility of the complementarity approach is one of its noted advantages.

The complementarity analysis was thus repeated for all species whose core ranges did not already coincide with one of South Africa's three main marine protected areas. Indeed, the outcome, in terms of protected areas required in addition to these three, differed only marginally from the previous results (Table 4, Fig. 6c). The main difference lay in the siting of south coast protected areas: the De Hoop reserve provides a subsititute for a protected area in Section 17, without requiring an additional protected area (i.e. no species were missed in this case).

In summary, the complementarity analysis suggests that a number of areas require conservation measures in order to represent fully South Africa's coastal fish diversity. The areas selected include the 'hotspot' of endemism at Port Elizabeth, the Transkei region of the Eastern Cape coast, an important transitional zone as well as an area of high endemism, and the west coast where percentage endemism is high. Emanuel et al. (1992) and Prochazka (1994) have similarly noted the need to establish a coastal conservation area on the west coast in order to conserve its unique resident fauna, and plans for establishment of a National Park are at an advanced stage. In some cases, marine protected areas (offering varying levels of protection) already exist in selected areas, such as at Cape Point (Robinson and De Graaff, 1994), but their adequacy in protecting target

Table 4
The minimum set of sites in which all 85 species and 43 endemic species not currently represented in reserves can be represented within their core ranges, as determined by complementarity analysis

	All species			Southern African endemics		
Number	Section	Number of species	Cumulative species reserved	Section	Number of species	Cumulative species reserved
1	44	18	18	44	8	8
2	14	11	29	32	11	19
3	39	18	42	16	3	22
4	32	14	51	46	4	24
5	43	12	54	35	12	29
6	11	17	69	14	5	32
7	16	6	73	11	7	38
8	35	18	77	40	10	40
9	46	4	79	24	1	41
10	40	17	80	29	4	42
11	37	18	81	4	7	43
12	3	16	82			
13	24	1	83			
14	29	5	84			
15	4	15	85			

species or representative ecosystems would have to be investigated.

It must be stressed that the broadscale siting of protected areas is only the first step, and that there is a need to ensure that the protected areas are sited and sized in such a way to that they do indeed protect all targeted species. To illustrate this point, the numbers of fish recorded to date in each of the St. Lucia-Maputaland, Tsitsikamma and De Hoop marine protected areas are only 78, 34 and 26%, respectively, of the numbers of fish whose full distributions are thought to coincide with each. These discrepancies are probably due to inadequate sampling effort and under-representation of certain habitats; none of these three protected areas include estuaries, although all are near or adjacent to estuaries. In other cases, small or partially-protected marine protected areas (usually with limited or no protection to fish) already exist in selected areas, such as at Cape Point (Robinson and De Graaff, 1994), and their requirements (e.g. area or legislation) for achieving adequacy in protecting target species or representative ecosystems would have to be investigated. Because environmental requirements often change for fish, with ontogeny and reproductive condition, marine protected areas need to be large enough to incorporate a variety of habitats (Carr and Reed, 1993), and in general, once the sites for protected areas are decided, they should be designed to represent the full diversity of habitat types in the area, most notably including estuarine, rocky and sandy intertidal and subtidal habitats and coral reefs.

This study provides a rough guide to the siting of a baseline set of fully-protected marine protected areas for the conservation of coastal fish diversity, which can then be supplemented to meet further conservation and socio-economic needs and objectives (see Beaumont, 1997). The next steps in the process involve incorporation of the conservation needs of other coastal marine biota (e.g. invertebrates) in order to maximise the efficiency of biodiversity conservation efforts, the additional needs of fishery protection, and then finer-scale selection of protected area sites and sizes through examination of the pertinent criteria (e.g. Kelleher and Kenchington, 1991; Scott et al., 1993; Salm and Price, 1995; Hockey and Branch, 1997). 'Ground-truthing' is required to make sure the protected areas can achieve their objective and conserve the species that they are theoretically supposed to protect.

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