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Conservation of coral reef biodiversity: a comparison of reserve selection procedures for corals and fishes

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Abstract

A range of different biodiversity-based selection methods for nature reserves has been tested for terrestrial environments, including those based on diversity hotspots, endemicity hotspots and complementarity. In this study, we investigate the utility of these approaches for a coral reef embayment. We compare coral and fish species richness in a random accumulation of reserve sites with (a) hotspots analysis, (b) stratified selection of hotspots, and (c) complementarity. Cumulative species-site curves indicated that complementarity maximized the rate of accumulation of species of both corals and fishes in reserves, while the hotspot approach performed moderately well. An equivalent number of reserve sites supported a greater proportion of the coral biodiversity when compared to fishes, reflecting the broader distribution of corals. Our results indicate that when choosing an indicator group as a proxy for representing overall diversity in a reserve network, the group with the greatest heterogeneity will provide the best results. Our findings also show that although a modest number of protected sites (20%) will incorporate much of the local diversity (>75%), species-specific approaches must be incorporated to target rare species.
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1. Introduction

Marine protected areas are a widely recognised means for both fisheries management and the conservation of biodiversity (Salm, 1984; Roberts and Polunin, 1991; Jones et al., 1992; Allison et al., 1998; Salm et al., 2000; Hixon et al., 2001). Maximising the biodiversity in protected areas has not played a central role in selecting sites for marine reserves, particularly in the Indo-Pacific region. The role of protected areas in conserving and enhancing fish stocks has received far greater attention, particularly in coral reef environments where increases of stocks inside protected areas have been demonstrated at several locations (Roberts et al., 2001). More often than not, reserve selection has been opportunistic, depending on areas becoming available for conservation, political circumstances and local goodwill (Hatcher et al., 1989; Courtney and White, 2000; Salm et al., 2000). This process is likely to be sub-optimal from the point of view of protecting as many species as possible (Prendergast et al., 1999) and maintaining ecosystem services (Duarte, 2000).

In conservation planning for terrestrial systems, theory relating to biodiversity has played an important role (Prendergast et al., 1999). Different algorithms for establishing priorities in the selection of reserve sites have been developed and tested (Margules and Nicholls, 1988; Pressey et al., 1993; Williams et al., 1996; Howard et al., 1998; Prendergast et al., 1999). Selection approaches have included analysis of bio-geographical distributions (Turpie et al., 2000), hotspots (sites with maximum counts of all or rare species), complementarity of species richness or rarity (Margules and Nicholls, 1988; Vane-Wright et al., 1991) and irreplaceability value (Ferrier et al., 2000; Pressey and Taffs, 2001). These usually perform better than randomly choosing reserve sites. When combinations of these procedures have been compared, complementarity-based methods for both richness and rarity usually minimise the number of sites necessary to represent the greatest number of species (Pressey et al., 1993; Williams et al., 1996; Reyers et al., 2000; Turpie et al., 2000), while selecting hotspots of species richness does

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not usually provide the best representation of all species (Gaston, 1996; Williams et al., 1996; Reid, 1998).

There have been few attempts to establish the best procedures for selecting sites to protect marine biodiversity (Hixon et al., 2001). The best biodiversity-based approach to selecting reserve sites in marine and terrestrial environments may differ, due to differences in the scales of spatial variation in biodiversity (Steele, 1985; May, 1994; Hixon et al., 2001). Recently, some methods of prioritisation have been applied to marine environments (Turpie et al., 2000; Day et al., in press; Leslie et al., in press) but there has been no systematic comparison of the reserve selection approaches.

The use of indicator groups in reserve selection may achieve a reduction of data acquisition effort and cost (Williams and Gaston, 1994). This is particularly applicable when taxa exhibit a high degree of congruency, and spatial overlap of hotspots, endemicity and complementarity. An understanding of these biodiversity patterns can improve the selection process (Gaston, 1996; Howard et al., 1998; Reyers et al., 2000; Moritz et al., 2001). While there is not always a great deal of concordance between different terrestrial taxa (Prendergast et al., 1993; Gaston et al., 1995), indicator groups have proven useful in certain cases (Balmford, 1998; Howard et al., 1998; Reyers et al., 2000; Moritz et al., 2001). Two studies have suggested that indicator taxa can be useful in marine temperate systems (Ward et al., 1999; Gladstone, 2002), but the approach has not been tested for coral reefs.

The application of biodiversity approaches requires detailed species lists from multiple locations (Gaston and Williams, 1996). In practice, this data is usually restricted to a few well-described taxa that have been described to an appropriate taxonomic level (Holthus, 1994; Werner and Allen, 1998). The cost and effort for such surveys are often too high for local organisations to afford, particularly for the developing countries in the global centre of coral reef biodiversity. However, a marine conservation network based on a few key taxa may capture a substantial part of overall biodiversity (Ward et al., 1999; Gladstone, 2002). This may be especially true on coral reefs where there is often a correlation between fishes, coral and reef invertebrate diversity on large spatial scales (Bellwood and Hughes, 2001). However, the degree to which corals can be used as a surrogate for fishes and vice versa is unknown for local marine reserve networks.

In this study, we apply different selection methods for selecting sites that maximise the biodiversity of fishes and corals in protected areas for a tropical embayment (Kimbe Bay) on the island of New Britain, Papua New Guinea. Kimbe Bay is recognised as an area of exceptional coral reef biodiversity with a total of 837 species of fishes and 347 species of coral recorded (Munday, 2000). We use a data set on species diversity of fishes and corals from 35 isolated reefs to answer the following questions: (1) What step-wise selection procedure provides the greatest accumulation of species in protected areas, for a given area of protection? We compare a random choice of reserve sites, with (a) hotspots analysis (including both species richness and rarity hotspots), (b) stratified hotspot selection within bio-geographical zones and (c) complementarity. (2) Does the best selection procedure apply to both fishes and corals? (3) Is there a general concordance between the preferred sites selected for fishes and corals? Finally, (4) if the goal is to provide the best level of protection for both fishes and corals, which taxon serves as the best surrogate for the other?

2. Methods

2.1. The database

The database for this study was compiled during a biodiversity assessment for Kimbe Bay, New Britain (150° 15′E, 5° 15′S), Papua New Guinea, carried out in 1994 (Allen and Munday, 1994; Holthus, 1994; Holthus and Maragos, 1994; Maragos, 1994). Kimbe Bay is located within the Indo-Pacific centre of tropical marine biodiversity and has a low level of anthropogenic impacts (Munday, 2000). Presence–absence species counts from timed swims were available for hard corals and fishes at 35 sites, which are largely discrete coral reef platforms and pinnacles separated by deep water (Table 1).

All timed swim surveys took between 60 and 80 min. During this time, the recorder began at a maximum depth of 25 m, swimming back and forth along a depth contour while slowly moving into shallower water. The survey ended at the reef crest. The survey report lacked information on selection criteria for the reefs assessed, and how well one survey represented their total size (Allen and Munday, 1994; Holthus, 1994; Holthus and Maragos, 1994). However, based on the idea that each survey covered a similar area in the given time, we assume that the area of each site was roughly the same. All species of fishes and corals for which reliable site records were available were included in the analysis. For this study, we refer to the added number of coral and fish species as 'all species'.

2.2. Species distribution

Variation in species distributions are likely to have a major effect on area selection; and the incorporation of bio-geographic patterns have been recommended for large-scale reserve selection (Turpie et al., 2000). In order to verify whether inclusion of such information improves the reserve selection procedures we applied Multi-Dimensional Scaling (MDS) multivariate analysis to fishes and corals. The detected spatial patterns of community structure defined eco-habitats for the bio-

Table 1
List of sites and species in Kimbe Bay

Site	Name	Region	Number of species			Number of rare species		
			All	Fish	Coral	All	Fish	Coral
J26	Restorff Island	OCZ	323	166	157	26	17	9
J29	Kimbe Island south	OZ	287	164	123	18	9	9
J34	Wulai Reef	OZ	280	183	97	10	8	2
J22	Cape Heussner	OZ	279	184	95	28	23	5
J32	Wulai shelter	OZ	273	145	128	7	3	4
J37	Hogu Reef exposed	OZ	271	179	92	6	6	0
J14	Beacon Reef	OZ	268	173	95	11	4	7
J18	Coast south	OCZ	263	133	130	9	3	4
J39	Palanga coast	OCZ	261	148	113	7	2	5
J10	Big Mulumalu Island	OCZ	259	184	75	15	12	3
J36	Hogu Lagoon	OCZ	252	151	101	6	2	4
J25	Tele Reef	OZ	248	142	106	8	6	2
J8	Erna Reef right	OZ	246	144	102	17	12	5
J31	Oto Reef	OZ	244	139	105	6	5	1
J9	Erna Reef left	OZ	241	171	70	3	3	0
J38	Kilu coast	OCZ	240	155	85	7	3	4
J12	Paluma Reef	OCZ	239	134	105	6	1	5
J30	Kimbe Island north	OZ	239	148	91	10	7	3
J35	Hogu Reef west	OZ	235	150	85	11	8	3
J23	Island Heussner	OZ	233	151	82	11	9	2
J3	Lemu Reef	OZ	231	123	108	9	5	4
J19	Fish Reef	OCZ	224	137	87	4	1	3
J17	Numondo Reef	SCZ	223	129	94	25	23	2
J21	Moewen Reef	OCZ	221	131	90	10	5	5
J15	Coast North	OCZ	220	113	107	4	2	2
J24	Coast Heussner	OCZ	214	131	83	6	5	1
J6	Garua Island coast	SCZ	210	136	74	16	12	4
J33	Wulai shelter south	OZ	209	130	79	6	2	4
J27	Garua mud islands	SCZ	205	108	97	5	4	1
J20	Hoskins coast	OCZ	198	130	68	7	6	1
J13	Deception Point	OCZ	192	144	48	17	13	4
J28	Garua south bank	OCZ	190	119	71	0	0	0
J11	Coast near Garua	OCZ	183	119	64	5	3	2
J16	Kimbe coast	SCZ	178	116	62	12	11	1
J5	Schaumann Island	SCZ	128	83	45	9	8	1

OZ, outer zone; SCZ, sheltered coastal zone; OCZ, outer coastal zone. Rare species occur at no more than two sites. Site codes are reef identifiers from Holthus (1994).

geographical selection method. In this study, we used the term eco-habitats to describe a spatially distinct group of reefs that exhibit a distinct community structure owing to different environmental factors such as proximity to shore, water exchange, relief and reef community structure. The analysis was carried out for both coral and fishes. We also assessed concordance patterns in species distribution by testing the similarity of fish and coral data based on a Bray–Curtis similarity matrix using the RELATE programme of PRIMER (PRIMER, 2001).

2.3. Selection procedures

Selection methods were compared in their efficacy and suitability by species–area accumulation curves. Since our sites correspond to an equal sampling area, those curves plot the accumulated number of sites by the cumulative species percentage. Selection methods established the order in which sites were ranked. Species–site number accumulation curves were determined by the six selection procedures listed below.

2.3.1. Random (n = 6)
Random selections of sites without replacement were made and the accumulative species count calculated as a mean of six repeats (precision $P = 0.007$).

2.3.2. Hotspots (richness)
Sites were selected in decreasing order of total species count for each taxon until all sites were included. The accumulative species number was calculated as sites were added. Sites with the same number of species were added in random order. In our data set, such sites had low species numbers, and their order had little impact on the overall shape of the resulting species accumulation curve.

2.3.3. Hotspots (rarity)

Sites were selected in decreasing order of the species present at each site that occurred twice or less within the entire data set (rarity threshold $T=2$), using the reserve selection software WORLDMAP (Williams, 2000).

2.3.4. Hotspots (three eco-habitats—richness)

Areas were selected by alternating between sites belonging to each eco-habitat identified in the species distribution analysis. Within each subset, sites were selected in decreasing order of total species count. The first site was chosen by selecting the site with the highest total species number from all subsets, followed by the site with the higher species number from the two remaining subsets. This predetermined order of subsets was maintained for the entire calculation.

2.3.5. Complementarity (rarity)

Sites were ranked for maximum complementary rarity ($T=2$) by a progressive rarity algorithm in WORLD-MAP; for details of the algorithm, see Williams (2000) and Williams et al. (2000). If there was an alternative set of sites that would achieve the same conservation goal (i.e. there was a tie between sites), the algorithm selected the site with more rare species.

2.3.6. Complementarity (richness)

Areas were chosen by selecting for maximum complementary richness at each step. This was calculated by a simple greedy algorithm in WORLDMAP, based on Kirkpatrick (1993) and Vane-Wright et al. (1991) in Williams (2000).

2.4. Congruency and representativeness

The area required to represent a large number of species from a range of taxa depends on the degree of congruency among the different groups. In order to establish this for fishes and corals, we first compared the spatial overlap in species richness per site using Pearson Correlation coefficients (Howard et al., 1998). Since the selection process depends largely on rare species, we then correlated total species richness and number of rare species per site for fishes and corals using the same method.

The representativeness of a reserve network selected by one indicator group depends on how the distribution of the indicator taxon overlaps with other taxa (Williams et al., 2000). To determine representativeness of selections based on indicator or representative taxa, areas were chosen for each group (fishes, corals and all species) using the complementarity (richness) approach. The order of sites derived was then applied to the remaining taxa and plotted on a graph relating the cumulative species inclusion to the number of sites chosen.

3. Results

3.1. Patterns in species distribution

The inclusion of species in reserves as a function of the area coming under protection partially depends on large-scale patterns in species distributions or heterogeneity in community structure within the area of interest. Multi-dimensional scaling analysis indicated that there was greater spatial heterogeneity in the fish communities on the 35 reefs compared with the corals. Three fish communities were identified (Fig. 1a), which corresponded with a gradient from sheltered coastal reefs to offshore reefs (Fig. 2, Table 1). In contrast, the coral communities were largely homogeneous, except for a small number of sites with unique species composition (Fig. 1b). Hence, on the scale examined there was not a close correlation between fish and coral assemblages ($r=0.345$, $P=0.3$), at least in terms of presence–absence data. The three habitat systems identified by the fish assemblages were used as a basis for a bio-geographically stratified hotspot approach.

3.2. Comparison of site selection procedures

The complementarity-based approaches (based on either richness and rarity) consistently scored the greatest cumulative representation of species in protected areas during the step-wise addition of new reserve sites (Fig. 3). The two complementarity-based methods performed in a similar manner and always achieved higher accumulative species richness than the other methods, regardless of whether the focus was on fishes, corals or both taxa combined. The random addition of new sites was on average the least efficient method. The three hotspot methods scored within an intermediate range between these extremes, although choice of rarity hotspots consistently included more species than richness hotspots. The hotspots (richness) approach for all species and fishes was relatively efficient for low numbers of reserves, but with increasing numbers of sites added, it eventually performed no better than choosing sites on a random basis.

The species accumulation curves differed between fishes and corals for all methods used. Corals displayed the highest initial species inclusion, resulting in higher species percentages protected for fewer sites (Fig. 4). In contrast, fish curves start at lower species percentages and climb gradually, lying below the other curves for all methods. This reflects the greater regional occurrence of coral species at any one site and their broader distribution across the bay. The differences between fishes and corals are most apparent for the hotspots (richness) method and most similar for the best performing complementarity method. When both fishes and corals are combined the curve more closely resembles the pattern for fishes only, which can be attributed to the greater species richness of fishes.
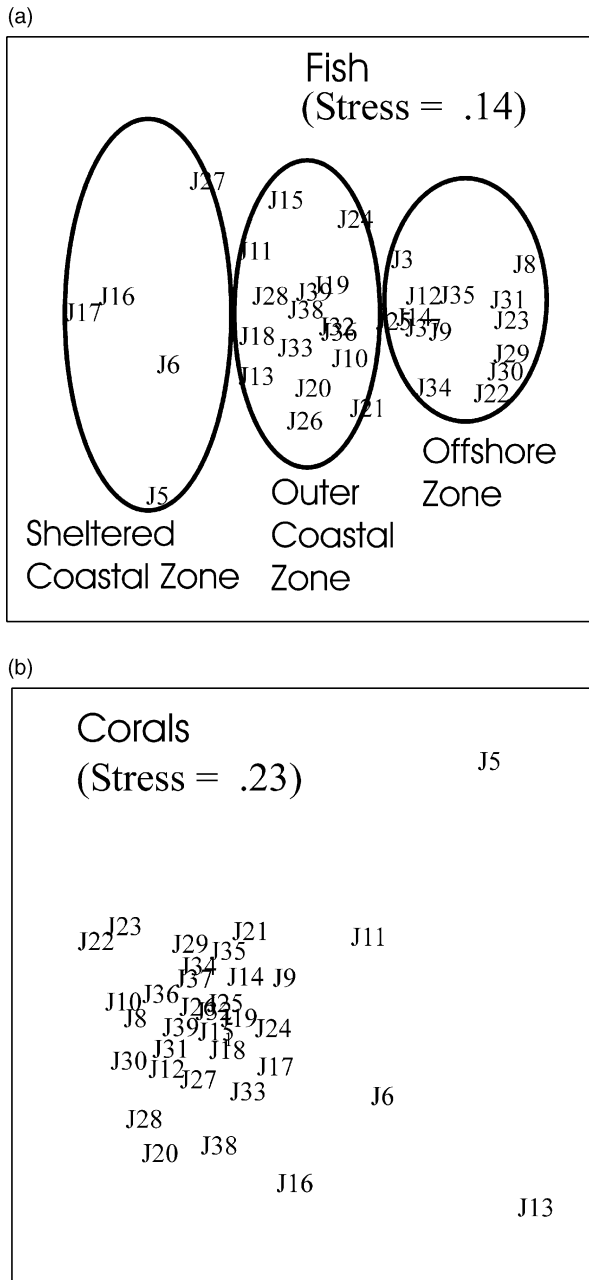
(a)

(b)

Fig. 1. (a) MDS analysis of fish community structure in Kimbe Bay based on presence-absence of species at 35 sites. (b) MDS analysis of coral community structure in Kimbe Bay based on presence-absence of species at 35 sites.

In general, the accumulation of species in reserves with additional sites was rapid, with >50% of the species occurring when less than five of the 35 sites were selected (Figs. 3 and 4). However, once 80% of the species were included by any method, further increases in protected diversity required a substantial increase in the number of sites because of scattered rarities. In practical terms, if we consider seven sites out of the 35 survey sites (20%) as a reasonable and achievable target in terms of the number of protected areas possible in Kimbe Bay, a complementarity approach based on
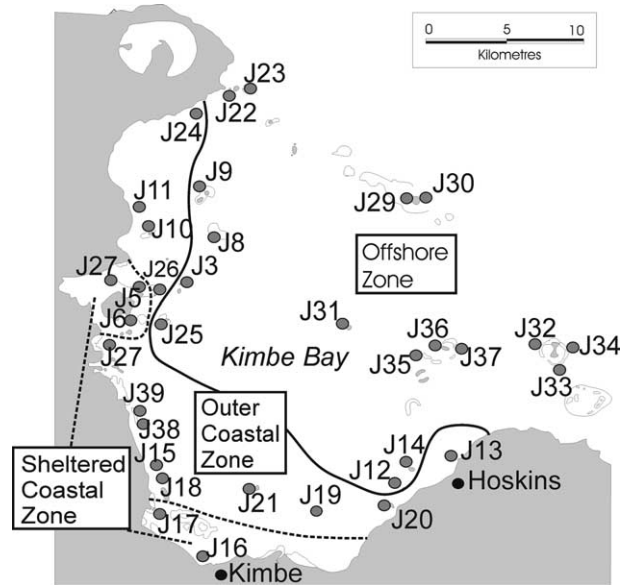

Fig. 2. Sampling sites for fishes and corals in Kimbe Bay, Papua New Guinea, showing the spatial distribution of three eco-habitat zones derived from fish community analysis (see Fig. 1b).

richness would include 76.9% of fish species, compared with only 63.8% for a random protocol (Table 2). The complementarity and hotspot approaches based on rarity provided the same level of improvement over the random protocol. In order to include all species into a reserve network, 34 sites would be required using complementarity-based and rarity hotspot approaches, and all 35 sites for all other approaches. To include all fish species in protected areas would require 31 sites by complementarity (richness), while all other methods would require all 35 sites. At low numbers of protected sites, there was a distinctly higher proportional inclusion of coral species compared to fishes (Table 2).

Protecting 20% of the sites would include 84.6% of corals if based on complementarity and 71.5% if based on a random model. Total coral species representation can be accomplished by 23 sites for complementarity (rarity), whereas 32 or more sites would be needed for all other selection methods. Clearly, a realistic number of reserve sites will fall short of representing a substantial number of the rarer species for both fishes and corals. For 20% of sites included in a reserve network, methods that were based on complementarity and hotspot selection (rarity and 3 regions) performed similarly well for fishes and all species, but not for corals alone. The complementarity-based methods clearly outperformed all others for corals (Table 2).

3.3. Cross taxon congruence

In order to assess cross-taxon congruence between fishes and corals, we compared the distribution and coincidence of (1) species richness hotspots between
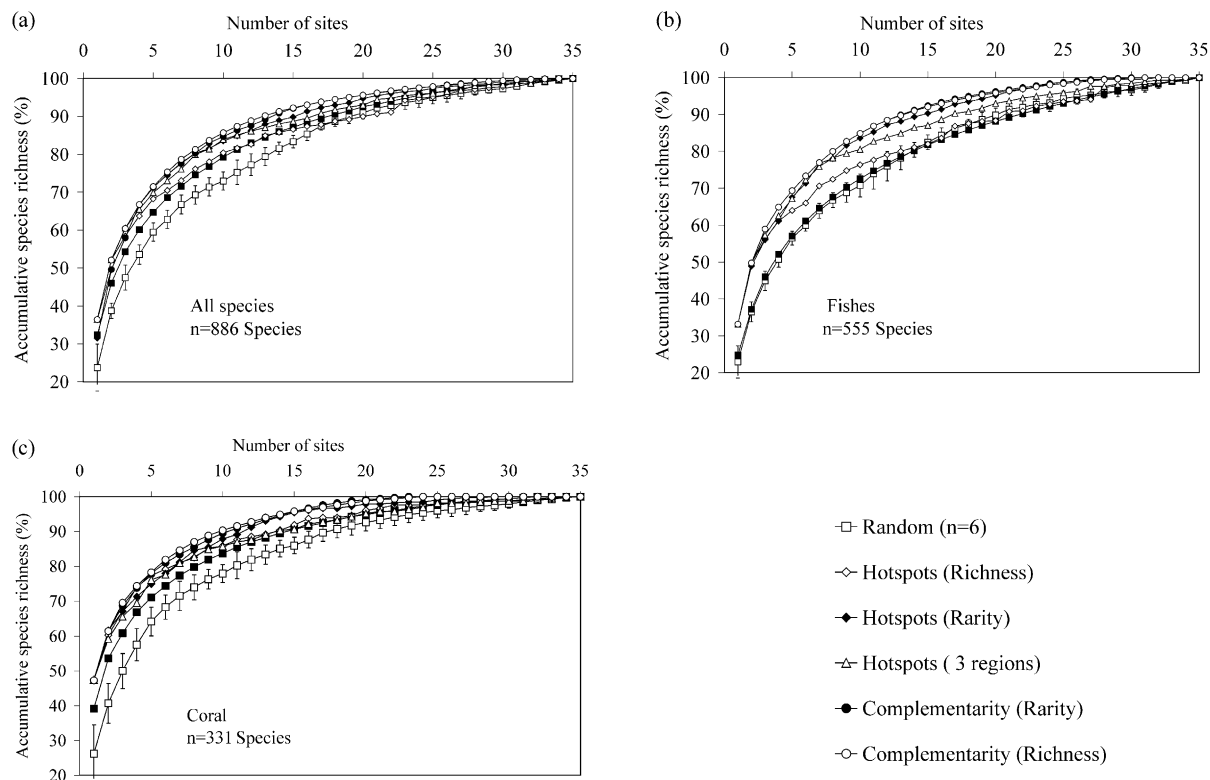
Fig. 3. Species–site accumulation curves for six selection approaches: complementarity (species richness and rarity), hotspots (species richness and rarity), three eco-habitats hotspots and random ($n = 6$). (a) All species, (b) fishes, (c) corals.

corals and fishes and (2) the occurrence of rare species at diversity hotspots. There was no evidence that hotspots in species richness were significantly correlated between fishes and coral species numbers (Pearson correlation coefficient $r = 0.290$, $P > 0.05$), indicating that coral-rich sites do not necessarily harbour a maximum of fish species and vice versa. Fishes and corals also exhibited a different relationship between the distribution of rare species and richness per site. Sites with a high fish species richness do not contain many rare species (Threshold $T = 2$, $r = 0.278$, $P > 0.05$). In contrast, there was a significant relationship between the occurrence of rare corals and coral richness hotspots ($T = 2$, $r = 0.574$, $P < 0.01$). This indicates that both groups are unevenly distributed across the bay.

There was an asymmetry between fishes and corals in the ability of these taxa to serve as an indicator of the species richness of the other (Fig. 5). There is a distinctly lower degree of representation of fishes or all species if sites are selected based on corals (Fig. 5a). Twenty percent of the sites chosen on the basis of coral richness would select 84.6% of coral species for protection, but only 68.5% of fish species and 74.5% of all species included in the study. Conversely, choice of sites based on fishes produces very similar rates of accumulation of coral species in reserve areas (Fig. 5b). Twenty percent of the sites chosen on this basis would protect 76.9% of the fishes and 73.8% of the corals.

4. Discussion

4.1. Selection methods

The selection of sites in Kimbe Bay based on species richness and scarcity has shown that methods proven to represent a greater number of species in terrestrial environments can also be applied to coral reef systems. All selection procedures significantly improved the representation of species in protected areas in comparison to a random accumulation of protected sites.

Complementarity-based methods for both richness and rarity out-performed all other approaches, confirming patterns described for terrestrial species (Williams et al., 1996; Howard et al., 1998). Previous studies found that the complementarity method based on rare species can be more efficient in capturing biotic diversity than the method based on species richness when there is a large number of rare species present (Pressey et al., 1999). However, in this case the complementarity method based on rarity scored not much better than that based on richness. The greatest disparity between methods occurred over the lower range, in terms of the proportion of sites protected. Thus, selection criteria are likely to make a substantial and important difference for any realistic target level of protection in coral reef systems.

The hotspot methodologies were somewhat intermediate in their performance, lying between choice
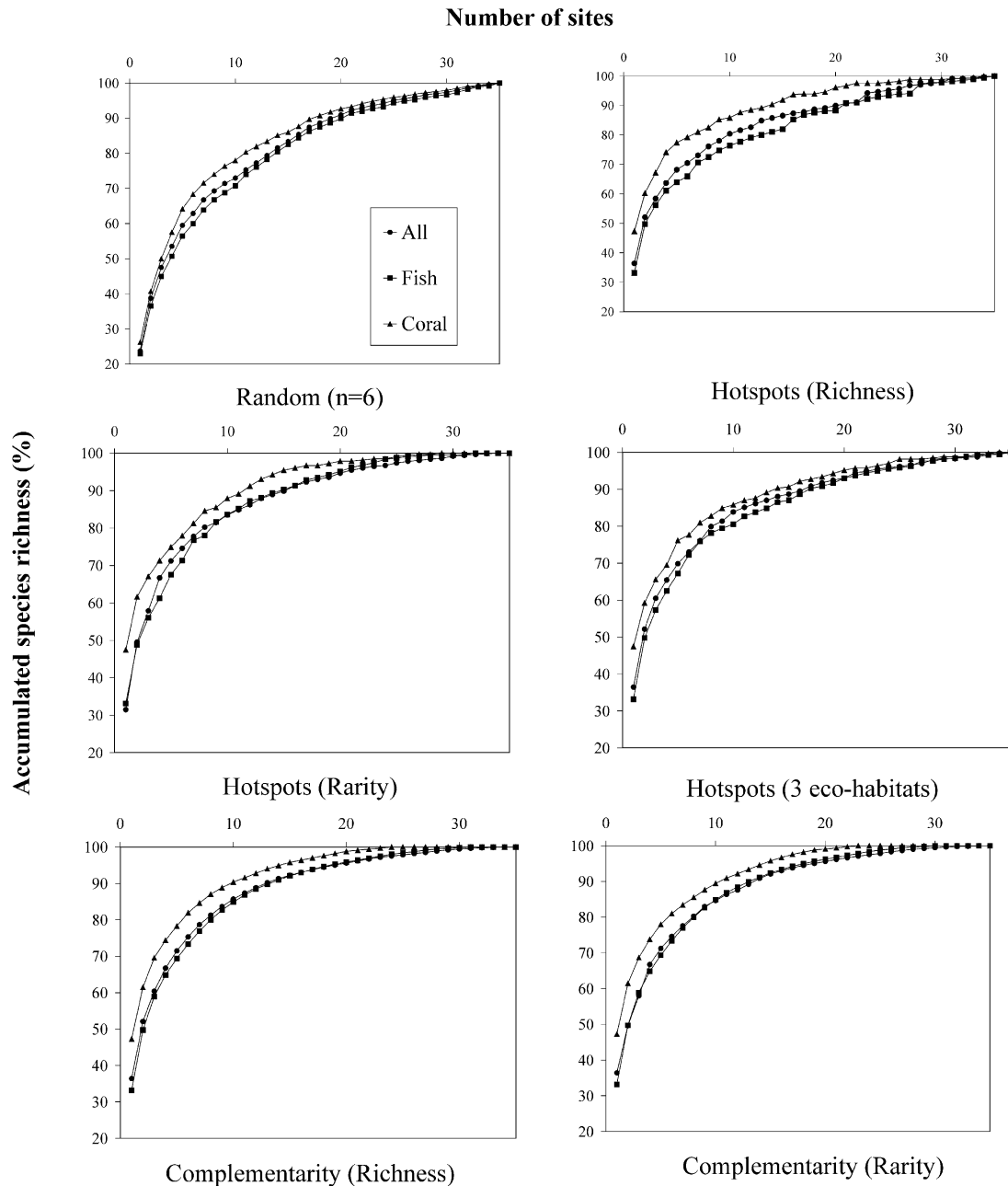
Number of sites

Fig. 4. Site selection for all species, fishes and corals using different selection methods.

based on complementarity and the random model. All methods performed well at low numbers of protected sites and were usually indistinguishable from those for complementarity up to about five protected sites. However, the richness hotspot method was much less efficient in capturing rare species as greater numbers of reserve sites are chosen. The hotspot approach based on rarity hotspots was usually superior to the hotspots methods based on diversity or habitat subdivisions, probably because rare species often occur in sites with low species richness (Prendergast et al., 1993). Although hotspot methods appeared less efficient than complementarity-based approaches, hotspot approaches

could be suitable if only a low number of sites were to be protected.

Alternating sites chosen from three eco-habitats of the bay, based on distance off shore and distinct assemblages of fishes, improved the scores of the hotspots (richness) method for fishes only. This reflects the fact that fish communities but not coral communities changed across this gradient. By selecting sites from each region, all fish communities were represented in the first three choices of reserve sites. As a result, this method scores well for top priority sites. In specific settings where only a small number of sites can be selected for protection, and lack of data and expertise call for a

Table 2
Protection levels in percent achieved by different selection methods when selecting the top seven reserve sites (20% of all 35 sites)

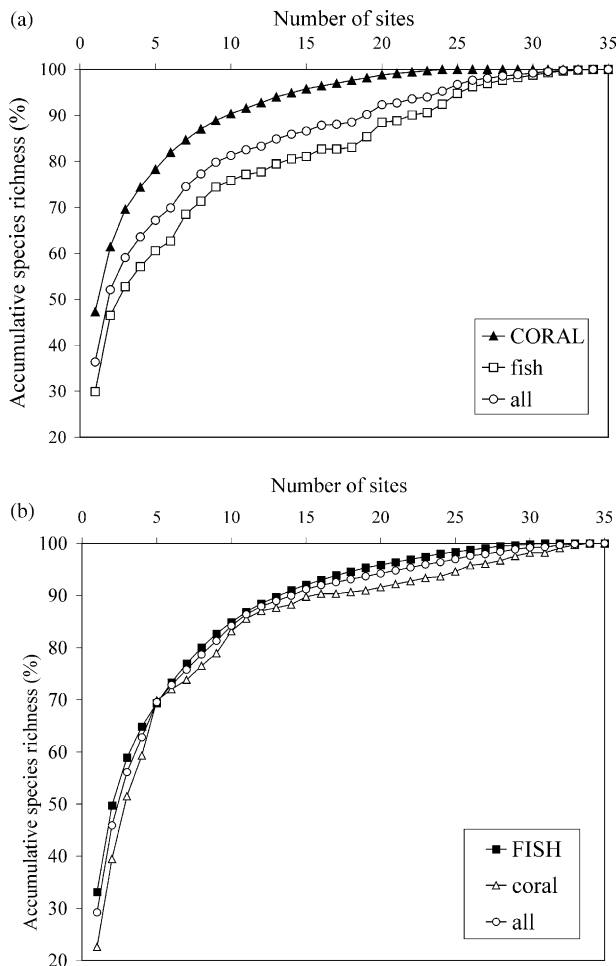| Selection method	Fish	Coral	All species
Complementarity (Richness)	76.9	84.6	78.7
Complementarity (Rarity)	76.9	83.4	77.5
Hotspots (Richness)	70.6	81.0	73.1
Hotspots (Rarity)	76.7	81.3	77.7
Hotspots (three eco-habitats)	75.8	80.9	76.1
Random	63.8	71.5	66.7

Fig. 5. (a) Accumulation of fish species and all species by site selection based on corals using the complementarity richness method. (b) Accumulation of coral species and all species by site selection based on fishes using the complementarity richness method.

simplistic approach, selecting reserves from each known biogeographical zone or habitat could represent a large proportion of biodiversity. Such an approach might appeal to managers and small local organisations with low resources, as it requires minimal data analysis and expertise (Salm et al., 2000). However, if there is a premium on incorporating rare species, this method has limited value.

The same selection procedures differed in their ability to encompass the biotic diversity of fishes and corals. While there was a distinct advantage of using complementarity-based methods over hotspots methods for corals, fishes and all species, the rarity-based and three eco-habitats hotspot methods were close to the performance of complementarity-based methods. For all methods, higher proportions of all coral species were selected for a given number of reserve sites, when compared to fishes. Corals consistently displayed a steeper slope at the start of the protected species-area curve, reflecting the more homogenous distribution of corals, with a greater proportion of all species represented at any one site. Clearly, there is little correlation between fishes and coral distributions on the scale of the whole bay, and each taxon is responding to different environmental cues. Differences among taxa in distribution patterns and responses to environmental gradients have important implications for the efficacy of different selection procedures.

4.2. Cross-taxa congruence

In the literature, cross-taxa congruence established by comparing hotspots coincidence and complementarity scores has been widely used to assess the suitability of taxa as indicator groups in the reserve selection process on a sub-regional scale (Howard et al., 1998; Ward et al., 1999; Moritz et al., 2001; Gladstone, 2002). Groups that display fundamentally similar distribution patterns and biogeography can act as surrogates for overall biodiversity in the terrestrial realm (Prendergast et al., 1993; Gaston, 1996; Williams and Gaston, 1998; Moritz et al., 2001). In Kimbe Bay, however, corals and fishes were not equal in the extent to which they may act as surrogates for one another in the selection of reserve sites. Although there was no significant congruency relationship between hotspots for fishes and corals, selecting sites on the basis of fish biodiversity provided a better representation of coral biodiversity than vice versa, and also represented overall species diversity more efficiently. Similarly, Gladstone (2002) reported that molluscs represent overall species richness better than macroalgae. The better performance of fishes as a surrogate can be explained by their more heterogeneous distribution than corals, and this distribution must be specifically targeted to capture the fish biodiversity. We expect that in general, taxa with homogeneous distributions would be poor surrogates of those with distinct patterns of distributions. This agrees with recent findings in a tropical rainforest, where insects and snails with higher endemism and fine scale distribution performed stronger as surrogates for other taxa (Moritz et al., 2001). However, the situation would be far more complex if reserves were necessary to represent a range of taxa, all with distinct and differing patterns of distribution.

4.3. Considerations for reserve selection

It is important to note that the application of the selection criteria presented here assume that the presence-absence data is accurate for all species, including rare ones (Williams and Gaston, 1994; Rodrigues et al., 2000). Rare species are frequently under-represented when protected areas are selected using species richness hotspots (Prendergast et al., 1993). For coral reef ecosystems, there is little information on rarity and recommendations for the conservation of rare species highlight the need for marine protected areas (Jones et al., 2002). However, the methodologies for collecting coral reef biodiversity data usually involve limited sampling effort at any one site. This is likely to cause an under-estimate of rare species, many of which are cryptic, nocturnal or wide-ranging. The effect of this on the proportion of species represented in reserve sites is unclear. It may lead to an under-estimate of the proportion of species in reserve sites and the diversity of the whole system.

Many factors influence the success of a reserve network in preserving species. While selection procedures based on diversity and rarity are effective for encompassing a large proportion of the species in reserve networks, there are significant limitations to these approaches. Firstly, they do not take into account the likely persistence of species in protected areas (Araujo and Williams, 2000). A species is considered represented when there is only one or a few individuals in a reserve, which is not likely to represent a viable population. In future, selection procedures must take into account the abundance of species and ensure sufficient numbers of individuals of rare species are contained within the same protected area (Nicholls, 1998). This requires information on population size in relation to reef size for a range of species and a better idea of what represents a viable breeding population.

The second problem is that while reserves are the best way to provide some protection for as many species as possible, it is clear that we can never approach a level of protecting 100% of the species in a region. In Kimbe Bay, the area required to protect all species may approach 80–100% of the total area. This level of protection will far exceed what is possible in most societies. At most, a target of protecting 20% of the area may be possible. However, our estimates suggest that this will only cater for 78.7% of the species, and many of these may be poorly represented in terms of numbers. Allison et al. (1998) have argued that marine reserves are a necessary but not sufficient means to protect exploited populations. We concur with this view. To protect rare species, reserve systems must be coupled with species-specific management plans that target rare species of uncertain status. Our study was based on the assumption that selected reserve areas actually receive and sustain protection over a long-term period. In order to sustain such protection and to reduce threats to sites, future efforts should be made to cluster reserves together or improve connectivity between them.

In conclusion, our results support the use of biodiversity-based selection criteria over ad hoc decisions in the establishment of marine conservation areas. We confirm that choosing potential marine reserve sites by complementarity and/or hotspots for rare species will maximise the number of species represented in coral reef reserves. Our comparison of fishes and corals suggests that these techniques achieve different levels of success for different taxa, but a small number of reserve sites ($\sim$20%) can encompass a large proportion of the extant species of all groups (78.7%). When selecting reserves on the basis of a single indicator taxon, care must be taken to choose an indicator that best captures the diversity of other target groups. Although corals are the key habitat-forming organisms on coral reefs, our results suggest that fishes may be more useful surrogates when choosing sites to maximise the protection of both fishes and corals.

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