Requirements for marine protected areas to conserve the biodiversity of rocky reef fishes

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ABSTRACT

1. This study describes spatial patterns in the biodiversity (species, assemblages) of rocky reef fishes at a spatial scale relevant to management, and compared the outcomes for this biodiversity from alternative procedures for selecting marine protected areas (MPAs) and from the selection of MPAs for fisheries-related objectives.

2. The study area included 104 species in two assemblage types; 36 species and 14 species occurred only in one or two locations respectively.

3. MPAs selected by hotspot richness, greedy richness complementarity, and summed irreplaceability included similar percentages of species and significantly more species than randomly selected MPAs. A combined species-assemblage selection ensured representation of assemblage diversity. Representation of all species and assemblage types required 92% of locations.

4. MPAs chosen using density of all fishes or density of exploitable fishes as selection criteria included fewer species (than MPAs selected using species identity) and the percentage of species accumulated did not differ from a random selection.

5. Use of an established MPA as the seed for an expanded network was inefficient, leading to additional locations being required and an accumulation of species that did not differ from a random selection.

6. The smallest MPA network that fulfilled multiple management objectives (representation of assemblage diversity and majority of species, population viability, support for fisheries, connectivity) required 30% of the surveyed locations.

7. This study concluded that: MPAs selected without the benefit of data on intra-habitat variation in species assemblages will be unrepresentative; the upper range of currently promoted targets for MPA establishment (i.e. 30%) should be regarded as a minimum for biodiversity conservation; MPAs selected for fisheries-related reasons may not provide expected benefits for the remainder of the fish assemblage.
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KEY WORDS: habitat; irreplaceability; marine reserve; reserve selection; surrogate

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INTRODUCTION

Marine protected areas (MPAs) have been advocated as a strategy for conserving biodiversity (Agardy, 1994; Lubchenco *et al.*, 2003) and MPA networks have been established in many countries for this purpose (Kelleher *et al.*, 1995; Yurick, 1995; Gladstone *et al.*, 2003). At the scale of individual MPAs the potential benefits for biodiversity include maintenance of habitat diversity, species recovery, and enhanced population sizes (Babcock *et al.*, 1999; Edgar and Barrett, 1999; Shears and Babcock, 2003). Area-protection targets of 10–30% of coastline have been promoted for biodiversity conservation (PDT, 1990; Ballantine, 1997; Reid, 1998; Roberts and Hawkins, 2000; World Parks Congress, 2003); however, there are insufficient data on the distribution of marine biodiversity to assess the adequacy of such targets (Cabeza and Moilanen, 2001; Sala *et al.*, 2002). A range of selection criteria are used to evaluate candidate MPAs for biodiversity conservation including representativeness, species richness, value to threatened species, degree of connectivity, irreplaceability, and population size (ANZECC TFMPA, 1999; Day and Roff, 2000; Stevens, 2002; Roberts *et al.*, 2003). There are few tests in marine systems of the relative benefits for biodiversity from alternative selection criteria (Beger *et al.*, 2003).

MPAs are also advocated for the benefits they can potentially provide for exploitable species and the relevant selection criteria include habitat availability, degree of connectivity, productivity, presence of spawning aggregations, and density of exploitable species (Holland and Brazee, 1996; Hockey and Branch, 1997; Roberts and Hawkins, 2000; Roberts *et al.*, 2003). The similarity of many of the selection criteria for biodiversity and exploitable species, and the results of modelling studies, suggest that selection of MPAs for fisheries-related reasons may provide biodiversity benefits and vice versa (Hastings and Botsford, 2003). In practice, the area likely to be designated as MPAs is relatively small (Roberts and Hawkins, 2000) and sites selected as MPAs need to implement both biodiversity and fisheries objectives in the minimal area (Sala *et al.*, 2002; Roberts *et al.*, 2003). There is limited understanding of the consequences for biodiversity of selecting MPAs using fisheries-related selection criteria.

Target-oriented selection algorithms were developed for conservation planning in terrestrial systems to determine the minimal area required to achieve a representation target, e.g. inclusion of each species in at least one protected area (Margules *et al.*, 2002). These selection procedures have been used only recently for MPA planning (Day *et al.*, 2002; Airamé *et al.*, 2003) and to test theory relating to MPA selection (Ward *et al.*, 1999; Gladstone, 2002; Beger *et al.*, 2003; Gladstone and Alexander, 2005). Systematic approaches to selecting protected areas avoid the inefficiencies that arise from inappropriate site selection (Margules *et al.*, 2002) or from the inappropriate application of generalized targets (e.g. protection of 20% of the coast). The alternative, ad hoc selection, leads to under-representation of biodiversity, increases the area of remaining habitat required to achieve representation targets, and generally compromises efforts in marine protection (Margules and Pressey, 2000; Agardy *et al.*, 2003). Many of the world's MPAs were established in the absence of data on the distribution of biodiversity and relevant ecological processes, prior to the implementation of systematic approaches, and in response to local pressures, and may be inappropriately placed when assessed against currently accepted selection criteria and with more extensive data now available (DeVantier *et al.*, 1998).

Rocky reef fishes have received less attention in the conservation literature than coral reef fishes, despite having higher levels of endemism and being subjected to considerable impacts from large population centres and coastal developments (Wilson and Allen, 1987; Ebeling and Hixon, 1991; Turpie *et al.*, 2000). Rocky reef fishes are functionally significant in the ecology of temperate rocky reefs (Jones and Andrew, 1990; Babcock *et al.*, 1999; Shears and Babcock, 2002) and under some circumstances can be indicators of other groups in MPA selection (Ward *et al.*, 1999). Links between habitat and fish assemblage structure are known (Holbrook *et al.*, 1990; Curley *et al.*, 2002); however, there is little understanding of other elements of the spatial ecology of rocky reef fishes important for the selection and design of MPAs.

The aims of this study were: (1) to describe patterns in the biodiversity of rocky reef fishes at a spatial scale relevant to the establishment of MPAs; (2) to use this data set to compare the biodiversity-related outcomes of alternative approaches to MPA selection for biodiversity including species-related approaches (hotspot richness, complementarity-based greedy richness, irreplaceability), a combined species and assemblage-based selection, and selection based on total fish density; (3) to determine the biodiversity-related outcomes from selection for fisheries purposes using density of exploitable fishes as the selection criterion; (4) to determine the consequences for MPA selection in the study area arising from the presence of an established MPA; and (5) to compare the outcomes of selections in (2), (3) and (4) to a random selection of locations.

METHODS

Study area

This study occurred on the central coast of New South Wales, Australia (Figure 1) in the 'deep reef', a sponge-dominated habitat of temperate rocky reefs occurring at depths of 10–20 m (Underwood *et al.*, 1991). Thirteen locations were sampled in April–June 2002 over a distance of 140 km, which is the spatial scale of most MPAs (Stevens, 2002). Deep reef habitat is patchily distributed in response to the availability of rocky substratum at suitable depth and the locations used in this study represented most occurrences of this habitat in the study area. One location was an existing MPA, Bouddi Marine Extension (covering an area of 287 ha), where fishing has been prohibited since 1973. Bouddi Marine Extension was the first MPA established in New South Wales but broadscale information on the distribution of biodiversity was unavailable at the time the MPA was selected.

Sampling methods

The order in which locations were sampled was randomized. Fishes were surveyed by an underwater visual census technique in which mobile fishes were counted in a 5×25 m strip and smaller, site-attached and juvenile fishes were counted in a parallel 1×25 m strip (Lincoln Smith, 1989). Four replicates of each
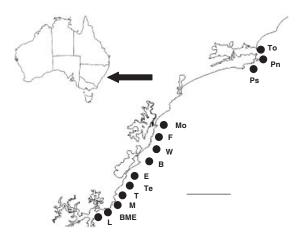

Figure 1. Locations sampled for this study. Location codes: L Lion Island; BME Bouddi Marine Extension; M MacMasters; T Terrigal; Te Terry's Reef; E The Entrance; B Bull Reef; W Wybung Head; F Flat Island; Mo Moon Island; Ps Point Stephens South; Pn Point Stephens Morth; To Tomaree Head. Scale bar = 20 km.

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transect size were done in each of two sites (separated by approximately 200 m) within each location. Replicate transects within a site were separated by at least 25 m from the preceding replicate. Four replicate transects was the maximum that could be done given the depths of the sites sampled (13–20 m) and safety requirements for no-decompression diving. Two sites were sampled in each location to account for the small-scale differences in assemblage composition known to occur in rocky reef fishes (Lincoln Smith, 1989). Surveys took approximately eight weeks to complete and because of the possible variation between locations in settlement over this time period, fishes that had recently settled (near-transparent and < 20 mm total length) were not recorded. All surveys were conducted by one observer (the author) between 0900 h and 1300 h on days when underwater visibility was at least 6 m.

Data analysis

Species richness was the number of species recorded at each location. The density of all fishes in a location was the average of the densities recorded in the eight replicate transects. Prior to this calculation the density of each species of site-attached fish was standardized to number of individuals per 125 m^2. The number of site-attached fishes was then combined with the number of mobile fishes in each transect to give the total density of all fishes in a transect. Species recorded with a maximum range of one or two locations in the study area were called 'uniques' and 'duplicates' respectively, and species occurring as single individuals in locations were called 'singletons' (*sensu* Colwell and Coddington, 1994). Species accumulation curves were constructed from the mean of 100 random selections of locations (without replacement) in the study area using EstimateS software (Colwell, 2001). Range size was the number of locations where a species was recorded. Range size rarity for each location was calculated as the sum of the inverse range size of each species occurring in that location (Gaston, 1994) using Worldmap software (Williams, 1999). A low value for range size rarity indicates a location contained species that occurred in several other locations and a high value indicates a location contained some species that occurred in few, or no other, locations.

Bray-Curtis dissimilarity based on the square-root transformed average density of species in each location was used as a measure of assemblage turnover between locations (Gray, 2000; Ferrier, 2002). Patterns of dissimilarity between locations were visualized by hierarchical clustering and non-metric multidimensional scaling ordination using PRIMER5 software (Primer-E Ltd, Plymouth; Clarke and Warwick, 2001) to distinguish assemblage types present in the study area.

MPA selection

The term 'marine protected area' (MPA) is used throughout this paper to include the suite of spatial management options ranging from no-take marine reserves to multiple-use MPAs. Such use of MPAs thus follows the IUCN definition (Kelleher and Kenchington, 1992) and acknowledges that biodiversity conservation is achievable through a range of spatially based management regimes and not only through no-take marine reserves (Pressey and McNeill, 1996; Agardy *et al.*, 2003). Alternative area selection procedures were used to select candidate locations for MPAs to achieve the target of all species being represented at least once in an MPA. A 'hotspot richness' procedure selected locations in decreasing order of species richness until 100% species had been included in the selected locations. A 'greedy richness' algorithm in Worldmap software selected locations in order of their complementary richness. The algorithm began by selecting the location with the highest species richness, then selected the location with the greatest number of species not already represented in the first location selected. The algorithm continued in the same way until all species were included.

Pressey *et al.* (1994) coined the term 'irreplaceability' as a measure of a location's contribution to a conservation target (e.g. representation of each species at least once in an MPA) in a planning area. Target-orientated protected area selection algorithms can select many alternative sets of locations that will each achieve the conservation target. A location's irreplaceability value is its frequency of occurrence in all

alternative sets of locations. 'Summed irreplaceability' value is the sum of the irreplaceability values of all species in a location and can be used as a relative measure of conservation value when many locations have equal irreplaceability (Ferrier *et al.*, 2000). A selection algorithm in C-Plan software (New South Wales National Parks and Wildlife Service; Pressey, 1998, 1999) was used to calculate the summed irreplaceability of each location for the representation target of each species occurring in at least one MPA and to determine the minimum number of MPAs required to achieve that target. The C-Plan algorithm first selected the location with the highest summed irreplaceability value, then recalculated the summed irreplaceability value of the remaining locations. The algorithm then selected, from among the remaining locations, the location with the highest summed irreplaceability value and, if there was a tie, selected the location with the highest initial summed irreplaceability value. The algorithm continued iteratively until all species were represented in at least one MPA.

Multivariate analyses found that two distinct species assemblages were present in the study area (see Results). The consequences of selecting MPAs to represent both species and assemblage diversity were tested by alternately selecting locations from each assemblage type according to their summed irreplaceability value. Selection continued until all species and assemblage types were represented in the network of MPAs.

The outcomes for species and assemblages of selecting locations according to the density of all fishes and density of exploitable fishes was also determined. The group of exploitable fishes included species targeted by anglers and spearfishers based on the author's observations of the catch at boat ramps and on rock platforms and cross-checked with published sources (Lincoln Smith *et al.*, 1989; Kingsford *et al.*, 1991). Locations were selected separately in decreasing order of their density of all fishes, and their density of exploitable fishes, until all locations had been selected. The percentage accumulation of species and the assemblage type selected were determined for each addition of a location.

A random selection of locations was used as a null model to test the significance of the species accumulated by the alternative selection procedures. Locations were selected randomly until all species were included. One thousand replications of this random selection were used to generate a mean species accumulation curve and 95% confidence limits. The species accumulation curves from the alternative selection procedures were compared with the mean species accumulation curve and the upper 95% confidence limit resulting from the random selection of locations. Selection procedures that produced a species accumulation curve above the upper 95% confidence limit included significantly more species than randomly selected locations.

The effects of the existing MPA on the outcomes of the previous tests were tested by repeating the alternative selection procedures but with the existing MPA specified to be the first location to be included in the expanded MPA network.

RESULTS

Diversity

13 106 individuals belonging to 104 species from 41 families were recorded (Table 1). The families occurring in highest abundance were Plesiopidae (46.7% of total individuals), Pomacentridae (16.1%), Labridae (8.8%), Microcanthidae (6.6%), and Pempheridae (5.9%). One species, *Trachinops taeniatus* (Plesiopidae) represented 46.6% of all individuals recorded. The greatest number of species belonged to the families Labridae (24 species), Pomacentridae (10 species), and Monacanthidae (6 species). Species richness per location varied from 27 to 50 (mean $\pm$ standard error $= 34.8 \pm 1.8$). The species richness of the Bouddi Marine Extension MPA was, along with another location (Wybung Head) the lowest in the study area

Table 1. Summary of the features of each location surveyed in the study area

Location	Species	Uniques[a]	Duplicates[a]	Singletons[a]	Range size rarity[b]	Fish density[c]	Exploited fish density[c]	Assemblage type[d]	Summed irreplaceability
Tomaree (To)	33	3	1	14	14.2	115.1 ± 7.9	25.6 ± 1.6	1	9.7
Pt Stephens North (Pn)	32	3	1	7	14.3	79.0 ± 3.5	13.1 ± 3.4	1	9.9
Pt Stephens South (Ps)	38	4	1	10	17.1	131.2 ± 19.8	19.2 ± 1.2	2	11.5
Moon Island (Mo)	41	6	2	13	22.7	95.5 ± 15.0	15.0 ± 0.5	2	15.2
Flat Island (F)	31	2	0	6	10.8	106.9 ± 6.4	10.9 ± 3.9	2	7.1
Wybung (W)	27	0	3	7	8.4	162.2 ± 16.5	45.0 ± 16.7	2	6.6
Bull Reef (B)	50	5	6	16	26.6	187.5 ± 66.7	24.7 ± 5.5	2	19.7
The Entrance (E)	36	3	2	10	15.5	154.9 ± 33.4	8.2 ± 3.0	2	10.4
Terry's Reef (Te)	37	4	2	10	18.6	225.1 ± 20.4	26.5 ± 12.2	2	13.1
Terrigal (T)	39	3	4	15	17.8	127.2 ± 16.0	8.7 ± 2.5	2	12.0
MacMasters (M)	32	1	2	14	11.1	184.6 ± 28.9	18.7 ± 8.0	2	8.3
Bouddi Marine Extension (BME)	27	0	2	9	8.1	56.6 ± 19.9	8.0 ± 2.3	1	6.3
Lion Island (L)	29	2	2	7	11.9	31.5 ± 11.2	16.0 ± 4.5	1	7.6

[a] Uniques and duplicates were recorded only from 1 and 2 locations respectively; singletons occurred as single individuals in a location.
[b] Σ (range size^{-1}) for each species in each location, where range size is number of locations where species was recorded.
[c] Mean (± SE, $n = 8$) of the number of fish per 125 m^2 in each location.
[d] See Figure 5.

($n = 27$ species). The species accumulation curve for the entire study area did not appear to reach an asymptote (Figure 2).

Thirty-six species (34.6% of all species) were recorded as uniques and 14 species (13.5%) were recorded as duplicates in the study area. The cumulative numbers of uniques and duplicates rapidly approached an asymptote with increasing sampling effort, which indicates these species were adequately sampled (Figure 2). Uniques occurred in all locations except Wybung Head and Bouddi Marine Extension (Table 1). Only six species occurred at all 13 locations (Figure 3): *Trachinops taeniatus* (Plesiopidae), *Cheilodactylus fuscus* (Cheilodactylidae), *Hypoplectrodes maccullochi* (Serranidae), *Parma microlepis* (Pomacentridae),
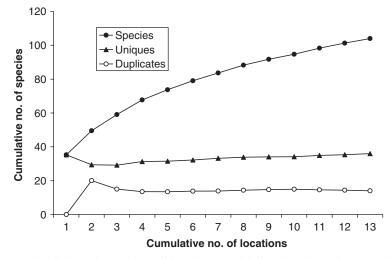

Figure 2. Species accumulated with increasing numbers of locations sampled for all species, uniques (species recorded only from 1 location), and duplicates (species recorded only from 2 locations). Accumulation curves based on the mean of 50 random samplings (without replacement).
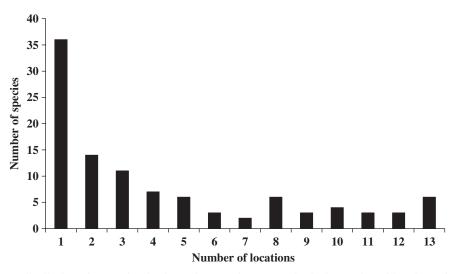

Figure 3. Frequency distribution of range sizes in the study area where range size is the number of locations where a species was recorded.

Notolabrus gymnogenis and *Pseudolabrus psittaculus* (Labridae). Five of these species (*T. taeniatus*, *H. maccullochi*, *P. microlepis*, *N. gymnogenis*, *P. psittaculus*) were among the 10 most abundant species.

Range size rarity values of reefs varied between 8.07 and 26.55 and the range size rarity value of a reef was significantly correlated with its species richness (Spearman rank correlation coefficient = 0.95, $P < 0.001$), i.e. reefs with high species richness also had a greater number of species with a limited distribution. All species recorded from Bouddi Marine Extension were recorded from at least one other location and Bouddi Marine Extension had the lowest range rarity value (8.07) in the study area.

Mean fish density (number per $125\,\mathrm{m}^2$) varied from 31.5 ± 11.2 (Lion Island) to 225.1 ± 20.4 (Terry's Reef). Mean density of exploited fishes varied from 8.0 ± 2.3 (Bouddi Marine Extension) to 45.0 ± 16.7 (Wybung Head). Mean density of all fishes was uncorrelated with species richness ($\rho = 0.40$, $P = 0.17$) and range size rarity ($\rho = 0.37$, $P = 0.22$). Mean density of exploitable fishes was uncorrelated with species richness ($\rho = 0.10$, $P = 0.74$) and range size rarity ($\rho = 0.17$, $P = 0.58$).

The majority of species were recorded at low abundance in the study area: 59.6% of species were represented by <10 individuals in total and 80.7% of species were recorded at an average of <10 individuals per location. The number of species represented by single individuals (i.e. singletons) at a location varied from 6 to 16 (Table 1). Twenty-three species were recorded as singletons in the study area.

Assemblage types

The clustering dendrogram and non-metric multidimensional scaling ordination revealed two assemblages in the study area (Figure 4), occurring at a group of locations consisting of the most northern and southern locations (BME, L, To, Pn), and a group of locations consisting of all other locations. The group of most northern and southern locations (hereafter Assemblage 1) had a combined richness of 55 species and the group of all other locations (hereafter Assemblage 2) had a combined richness of 94 species. Mean species richness of Assemblage 1 (30.2 ± 1.38) and Assemblage 2 locations (36.8 ± 2.21) was significantly different ($t = -2.51$, $P = 0.03$).

Differences in assemblage type occurred over relatively small distances. The two locations Ps (Point Stephens South) and Pn (Point Stephens North) had different assemblages but they occurred on the southern and northern sides, respectively, of the same headland (Point Stephens) and were approximately 1 km apart (Figure 1). The two locations BME (Bouddi Marine Extension) and M (MacMasters) had different assemblages and were separated by 5 km.

MPA selection

Selection of locations by hotspot richness, greedy richness complementarity, and summed irreplaceability included significantly more species than the set of randomly selected locations (Figures 5(a)–(c)). The three selection procedures each required 92% of locations to achieve their representation target and each captured a similar percentage of species at each step of the selection process. The greedy richness and summed irreplaceability procedures included a majority of species (i.e. at least 75%) with the selection of 30% of locations; the hotspot procedure selected slightly fewer species (Table 2). By comparison, an average of 65% of species (upper 95% confidence limit = 73%) had been accumulated by randomly selecting 30% of locations. The three selection procedures gave low priority to locations representing Assemblage 1 in achieving their representation target, i.e. Assemblage 1 locations were generally selected later in the selection order. Only the greedy richness procedure had selected an example of Assemblage 1 in the set of locations representing 30% of total locations. The existing MPA was selected last by the hotspot and greedy richness procedures and was not selected by the summed irreplaceability procedure. The alternate selection of locations from each assemblage type led to inclusion of a similar percentage of species
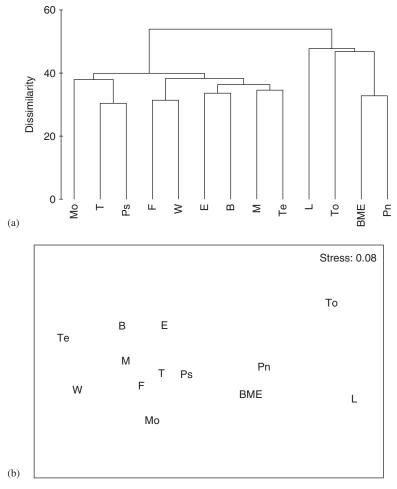
Figure 4. Cluster dendrogram (a) and non-metric multidimensional scaling ordination (b) depicting groupings of locations according to assemblage similarities. Location codes as in Figure 1.

as the other methods and the percentage of species included was significantly greater than a random selection of locations (Figure 5(d), Table 2).

The selection of locations according to either density of all fishes (Figure 5(e)) or density of exploitable fishes (Figure 5(f)) accumulated fewer species, and accumulated them at a slower rate, than the species and species-assemblage procedures (Table 2). The selection of locations according to density of all fishes required 100% of locations to achieve the representation target. Both selection procedures gave a low priority to Assemblage 1 locations and the percentage of species accumulated by both procedures did not differ significantly from a random selection of locations. For example, selection of 30% of locations according to density of all fishes or density of exploitable fishes included, respectively, 63% and 70% of all species of fishes and a random selection of 30% of locations included 65% of species (upper 95% confidence limit = 73%).

Inclusion of the existing MPA as the seed of an expanded MPA network had dramatic consequences for the percentage of species included. Fewer species were included in the locations selected by hotspot richness and the percentage of species accumulated was greater than the percentage of species accumulated from a
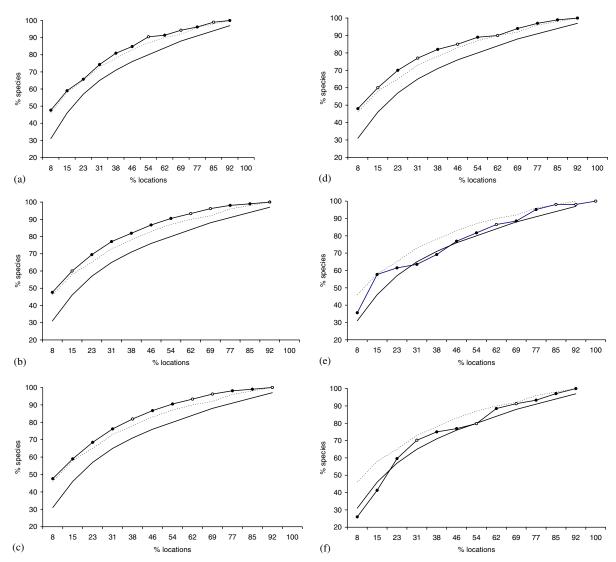
Figure 5. Cumulative percentage of species and assemblage types included in locations selected on the basis of (a) hotspot richness, (b) greedy richness complementarity, (c) summed irreplaceability, (d) summed irreplaceability and assemblage type, (e) total fish density, and (f) density of exploitable fishes. Each selection is compared with the mean and upper 95% confidence limit of percentage of species included from 1000 random selections of locations (solid and dashed curves respectively). Assemblage types of each selected location are indicated by (○) Assemblage 1 and (●) Assemblage 2.

random selection but below the upper 95% confidence limit (Figure 6(a), Table 2). For example, 70% of species had been accumulated after 30% of locations had been selected by hotspot richness compared with 65% of species accumulated by randomly selecting locations (upper 95% confidence limit = 73%). Fewer species were accumulated by the greedy richness, summed irreplaceability, and species-assemblage selection procedures and the percentage of species included was only significantly greater than random selection when more than 60% of locations had been selected (Figures 6(b)–(d), Table 2). The percentage of species accumulated by selecting on the basis of density of all fishes (Figure 6(e)) and density of exploitable fishes

Table 2. Percentage of total species included for combinations of locations from Assemblage 1 and Assemblage 2. Locations are shown in order of their selection and selection was prioritized according to summed irreplaceability value. Selection was done under two scenarios: (a) beginning with the locations of highest summed irreplaceability value in both assemblage types; (b) beginning with Bouddi Marine Extension (BME) as the first example of Assemblage 1. Under scenario (a) the selection of Pn (from Assemblage 1) and B and Mo (from Assemblage 2) led to 70.2% species selected. Location codes are shown in Figure 1

Assemblage 2	Assemblage 1			
	Pn	Pn + To	Pn + To + L	Pn + To + L + BME
(a)				
B	60.6	64.4	70.2	74.0
B + Mo	70.2	74.0	79.8	80.8
B + Mo + Te	76.9	80.8	84.6	85.6
B + Mo + Te + T	82.7	85.6	88.5	89.4
B + Mo + Te + T + Ps	87.5	90.4	92.3	93.3
B + Mo + Te + T + Ps + E	91.3	94.2	96.1	97.1
B + Mo + Te + T + Ps + E + M	92.3	95.2	97.1	98.1
B + Mo + Te + T + Ps + E + M + F	94.2	97.1	99.0	100
B + Mo + Te + T + Ps + E + M + F + W	95.2	98.1	100	100

(b)				
Assemblage 2	Assemblage 1			
	BME	BME + Pn	BME + Pn + To	BME + Pn + To + L
B	55.8	64.4	68.3	74.0
B + Mo	63.5	71.1	75.0	80.8
B + Mo + Te	71.1	77.9	81.7	85.6
B + Mo + Te + T	76.9	83.6	86.5	89.4
B + Mo + Te + T + Ps	83.6	88.5	91.3	93.3
B + Mo + Te + T + Ps + E	87.5	92.3	95.2	97.1
B + Mo + Te + T + Ps + E + M	89.4	93.3	96.1	98.1
B + Mo + Te + T + Ps + E + M + F	91.3	95.2	98.1	100
B + Mo + Te + T + Ps + E + M + F + W	91.3	95.2	98.1	100

(Figure 6(f)) was reduced (compared to selection without specifying the inclusion of the MPA) and was not significantly different from random selection. Selection of 30% of locations according to density of all fishes or density of exploitable fishes included, respectively, 67% and 64% of all species of fishes and a random selection of 30% of locations included 65% of species with an upper 95% confidence limit of 73% of species.

The smallest MPA network that fulfilled multiple management objectives (conservation of a majority of species, multiple examples of each assemblage type, population viability, support for fisheries), required four locations: Tomaree, Bull Reef, Terry's Reef, and Bouddi Marine Extension (Figure 1). This MPA network covered approximately 30% of all locations and included 71% species. Tomaree and Bouddi Marine Extension are examples of Assemblage type 1 and Tomaree has the highest density of all fishes and of all exploitable fishes and the second highest summed irreplaceability in this assemblage. Bull Reef and Terry's Reef are examples of Assemblage type 2; Bull Reef has the highest summed irreplaceability and Terry's Reef has the highest density of all fishes. Selection of locations with high density of all fishes and high density of all exploitable fishes will assist population viability and support for fisheries in adjacent waters. The four locations are evenly distributed throughout the study area (average distance to nearest location = 44.3 km) to maintain connectivity (assuming larvae are transported more than 40 km).
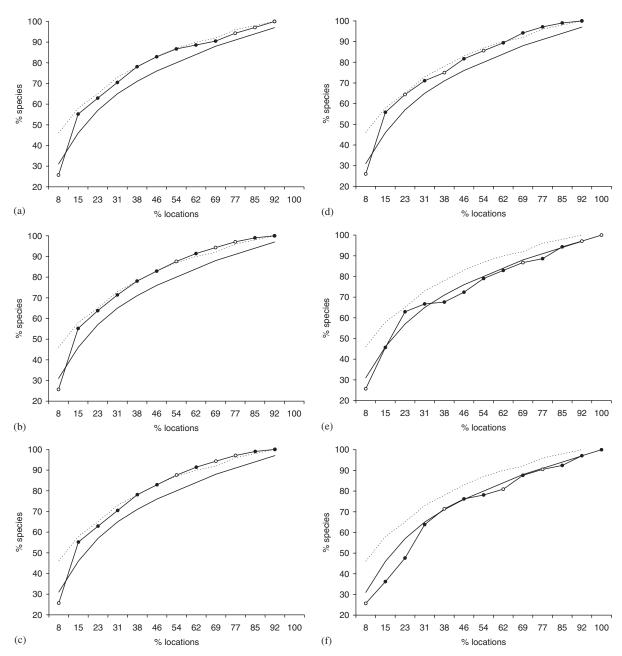
Figure 6. Cumulative percentage of species and assemblage types included in locations selected on the basis of (a) hotspot richness, (b) greedy richness complementarity, (c) summed irreplaceability, (d) summed irreplaceability and assemblage type, (e) total fish density, and (f) density of exploitable fishes with the existing MPA selected first. Each selection is compared with the mean and upper 95% confidence limit of percentage of species included from 1000 random selections of locations (solid and dashed curves respectively). Assemblage types of each selected location are indicated by (○) Assemblage 1 and (●) Assemblage 2.

DISCUSSION

A central question in conservation research and management is the area and number of MPAs required to achieve society's conservation targets. When the conservation target includes representation of all species and assemblage types, and turnover in both variables is high, the areas required will be large. In the present study 92% of locations were required to achieve the representation target of all species and assemblage types being represented and, in spite of differences in biotic group, spatial scale, sampling methodology, and environment, this result is similar to area requirements found in other studies for the same target (Schlacher *et al.*, 1998; Ward *et al.*, 1999; Gladstone, 2002; Beger *et al.*, 2003). Significant areas of coastline will still be required to implement more modest conservation targets. Studies using biodiversity spatial data, similar to the present study, found that 40% (Sala *et al.*, 2002), 30–50% (Airamé *et al.*, 2003), and 38–41% protection (Friedlander *et al.*, 2003) were required for representation of habitat types and significant species. Modelling of larval dispersal and persistence suggests that a minimum target of 40% of the coastline protected was required for persistence (Lockwood *et al.*, 2002). The present study concluded that representation of a majority of species (i.e. 75% of all species) and examples of both assemblage types required the establishment of a network of MPAs that included approximately 30% of locations. Given that locations for this study were randomly selected as representative examples of the deep-reef habitat throughout the study area, it is reasonable to assume that this result (i.e. the requirement for 30% of locations) can be scaled up to the same percentage of the total area of the habitat in the study area. The scale at which the present study was undertaken (140 km) is relevant to the scale of planning for the majority of MPAs (Stevens, 2002). The results of this and other studies indicate that the area of global coastline currently gazetted as MPAs (Roberts and Hawkins, 2000) is likely to be inadequate for biodiversity representation and that general targets for MPAs that are less than 30% of coastline will also be inadequate.

A majority of locations were required to achieve the target of all species being represented at least once in an MPA. This was a result of the large number of species that occurred at a single location (i.e. uniques and singletons), leading to higher summed irreplaceability values for the location where they occurred. One cautionary note that could be added to this conclusion is that the number of locations actually required as MPAs could be artificially inflated by the sampling effort used in this study. The total number of unique species in the study area might decrease with greater sampling effort (e.g. more locations and/or more replicate transects) or with a modified sampling method that targeted rare species. A greater sampling effort may expand the range of species already discovered (thereby reducing the total number of unique species). However, it is also likely to discover additional unique species (see also Schlacher and Wooldridge (1996) and Schlacher *et al.* (1998) for similar findings). The point at which additional sampling fails to find additional species and unique species is likely to be beyond the scope of fieldwork, given the depth of this habitat and practical considerations of dive duration. The relative summed irreplaceability values of locations may also be unchanged by further, more intensive surveys given results from other studies that have found significant correlations between rapid and intensive biodiversity surveys (Benkendorff and Davis, 2002).

In the absence of detailed information on the distribution of marine biodiversity, habitats have been suggested as a suitable surrogate for biodiversity and ecological processes, and habitat representation has been advocated as a selection and design criterion for MPAs (Ballantine, 1997; Roberts *et al.*, 2003; Sobel and Dahlgren, 2004). The available data both support (O'Hara, 2001; Williams and Bax, 2001; Curley *et al.*, 2002; Valesini *et al.*, 2003) and refute (Stevens and Connolly, 2004) the proposition that habitats contain distinct assemblages and should be the focus of MPA selection and design rather than species. A comparison of the effectiveness of using habitats or species assemblages to select and design MPAs (Ward *et al.*, 1999) found that habitats performed best (at representing all species) when the representation target was 40–60%. These levels of protection are unlikely to be achieved in

real-world conservation planning. Species assemblages performed better than habitats at more modest representation targets of 10–20%.

Habitat is one level of a nested hierarchy of ecological units advocated as the planning units for the development of Australia's representative system of MPAs. This hierarchy includes bioregion, ecosystem, habitat, community/population, and species/individual (ANZECC TFMPA, 1999). Use of habitats as a planning unit for MPA selection and design will need to include within-habitat assemblage variability to account fully for both the habitat and community/population levels. Rocky reef habitats occupy a considerable extent of coastline (Andrew and O'Neill, 2000) and it is likely that, in addition to biogeographic variation in species composition, each habitat will vary in its depth, water quality, physical complexity, ecological processes and disturbance regimes, which are likely to contribute to within-habitat differences in assemblage structure. Relying solely on a mapped surrogate (e.g. habitats), without information on intra-habitat variation in assemblage structure, may be an inefficient process for selecting and designing MPAs. Information on the potential sources of variation in assemblage structure will allow future surveys to be targeted and will assist in the goal to represent habitat and community diversity.

Selection of MPAs for fisheries-related reasons may not provide associated conservation benefits for the remainder of the fish assemblage. Density of fishes and density of exploited fishes have been advocated as criteria for prioritizing locations for protection (Winston and Angermeier, 1995; Roberts *et al.*, 2003). However, neither variable was correlated with other measures of conservation value used in this study (species richness, range size rarity, summed irreplaceability value). Locations selected according to density of fishes and density of exploited fishes performed no better in representing total fish biodiversity than a random selection of locations, and their use led to inclusion of a smaller percentage of rare species. Optimal benefits for fisheries management and biodiversity conservation may be achieved by MPAs specifically established for each purpose.

Use of the existing MPA as a seed for an expanded network of MPAs was inefficient as it led to an additional location being required to achieve the same representation target. This result is not surprising as the Bouddi Marine Extension was selected as a marine extension to an established terrestrial national park and without the benefit of systematic biodiversity surveys in other potential areas. There are many other MPAs in Australia and elsewhere in the world that were established in a similar manner (McNeill, 1994; Kelleher *et al.*, 1995). With an increasing emphasis on including representative samples of regional marine biodiversity as a criteria for selecting MPAs (Day and Roff, 2000; Day *et al.*, 2002), the results of this study suggest some existing MPAs may not be the optimal point from which to expand and that surveys of existing MPAs should be done as part of the process for selecting additional MPAs.

In conclusion, this study has demonstrated a high turnover of species of rocky reef fishes between reefs, assemblage variation within a single habitat type, and a significant proportion of species restricted to a limited number of reefs. Accordingly, a large percentage of reefs need to be selected as MPAs or managed sustainably to ensure protection of a representative sample of rocky reef fish biodiversity. The similarity in results of this and other studies suggests that these results can be scaled upwards to larger areas. The use of habitat maps to select candidate MPAs, without supporting data on intra-habitat assemblage variation, may lead to under-representation of reef fish biodiversity within representative MPAs. Finally, the sole use of fisheries-based criteria to select MPAs may not provide optimal benefits for biodiversity of fishes.

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