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Intertidal habitat conservation: identifying conservation targets in the absence of detailed biological information

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ABSTRACT

1. Growing concern associated with threats to the marine environment has resulted in an increased demand for marine reserves that conserve representative and adequate examples of biodiversity. Often, the decisions about where to locate reserves must be made in the absence of detailed information on the patterns of distribution of the biota. Alternative approaches are required that include defining habitats using surrogates for biodiversity. Surrogate measures of biodiversity enable decisions about where to locate marine reserves to be made more reliably in the absence of detailed data on the distribution of species.

2. Intertidal habitat types derived using physical properties of the shoreline were used as a surrogate for intertidal biodiversity to assist with the identification of sites for inclusion in a candidate system of intertidal marine reserves for 17 463 km of the mainland coast of Queensland, Australia. This represents the first systematic approach, on essentially one-dimensional data, using fine-scale (tens to hundreds of metres) intertidal habitats to identify a system of marine reserves for such a large length of coast. A range of solutions would provide for the protection of a representative example of intertidal habitats in Queensland.

3. The design and planning of marine and terrestrial protected areas systems should not be undertaken independently of each other because it is likely to lead to inadequate representation of intertidal habitats in either system. The development of reserve systems specially designed to protect intertidal habitats should be integrated into the design of terrestrial and marine protected area systems.

KEY WORDS: conservation planning; intertidal conservation; marine reserves; reserve design; siting algorithms

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INTRODUCTION

The designation of a system of marine reserves is seen as a mechanism for protecting representative examples of marine biodiversity in the coastal zone (Kelleher *et al*., 1995; Allison *et al*., 1998; Day and Roff, 2000; Thompson *et al*., 2002). In Australia, and elsewhere in the world, there are commitments to the development of representative systems of marine reserves (ANZECC, 1999; Day and Roff, 2000), modelled on the principles of reserve design used for terrestrial systems that aim to maximize the protection of representative examples of ecosystems, habitats and species (Margules *et al*., 1988; Bedward *et al*., 1992; Davey, 1998; Carr *et al*., 2003). Marine reserves are closed to all forms of extraction (e.g. fishing, mining, etc.) and may be a single reserve or be core areas within a larger multiple-use marine protected area (Agardy *et al*., 2003).

A representative system of marine reserves would include the complete range of environmental gradients or habitat types at a given scale to maximize the protection of marine biodiversity (Kelleher *et al*., 1995; ANZECC, 1999; Day and Roff, 2000). The benefits of protecting representative examples of habitats using a systematic, science-based framework are expected to include the protection of the associated biological communities and species, a better understanding of marine systems through the establishment of long-term experimental and monitoring programmes, improved non-consumptive opportunities (e.g. enhanced educational opportunities) and potential fisheries benefits (e.g. increased abundance of overfished stocks) (Sobel, 1993; Day and Roff, 2000).

One of the most controversial issues associated with establishing marine reserves is determining where best to locate these areas (National Academy of Sciences, 2001). This has often led to the opportunistic or ad hoc declaration of marine reserves, an approach considered expensive, inefficient and generally favouring only charismatic fauna (e.g. whales) or habitats that are at least risk because there is a lower demand for their use by extractive industries (Pressey, 1994, 1997; Dee Boersma and Parrish, 1999; Pressey *et al*., 2000). The failure of such historical approaches to the establishment of marine reserves results in the inadequate protection of a truly representative range of habitats (e.g. intertidal areas in Queensland multiple-use marine parks; Banks and Skilleter, 2002; Stewart *et al*., 2003).

One approach to identifying marine reserves to protect representative examples of biodiversity involves the systematic collection of data on the distribution and ecology of the entire biodiversity within a region (Schoch and Dethier, 1996; Rodriguez and Young, 2000; Beck and Odaya, 2001). However, in Australia, and elsewhere in the world, there is often a lack of detailed biological information on the distribution of species over large areas, even for intertidal habitats that have been traditionally well studied (Thompson *et al*., 1996; Ward *et al*., 1999; Roff and Taylor, 2000; Underwood and Chapman, 2001). In response to the lack of knowledge about the distribution of the biota, ecosystem-based 'coarse filter' approaches that use surrogate measures of biodiversity have been developed to support marine reserve identification (Ward *et al*., 1999; Beck and Odaya, 2001; Ardon *et al*., 2002; Ardon, 2003).

Surrogate measures of biodiversity include, for example, the use of biophysical properties, keystone species or indicator species (Banks and Skilleter, 2002; Gladstone, 2002; Warwick and Light, 2002). Biophysical factors have most often been used to define and map habitat types (e.g. Ward *et al*., 1999; Zacharias and Roff, 2000). These habitat types are mapped on the assumption that environments that have similar biophysical properties and environmental conditions predict, or at least correlate with, patterns of biological distributions (Araujo and Costa de Azevedo, 2001; Stevens and Connolly, 2004). The mapping of surrogates to define habitat types and delineate their boundaries requires the development of a consistent classification system, often based on enduring (e.g. abiotic) features of the marine environment (Roff and Taylor, 2000; Zacharias and Roff, 2000; Roff and Evans, 2002). An ability to predict the distribution of biodiversity using surrogate measures would enable decisions about where to locate marine reserves to be made more reliably in the absence of detailed data on the distribution of species (Roberts *et al*., 2003b). There is increasing knowledge about the distribution of species in relation to specific habitats defined using physical properties (e.g. Williams and Bax, 2001; Curley *et al.*, 2002; Valesini *et al.*, 2004), improving the likelihood that marine reserve systems designed on this basis would benefit the protection of representative biodiversity. Schoch and Dethier (1996) partitioned the coastline of San Juan Island (USA) into relatively distinct segments based generally on abiotic characteristics and were able to predict the composition of intertidal communities in the area. This approach has not been applied to other regions though, so there is no information on its general applicability. There is a clear need for further investigation of the relationship between physical properties of habitats and their ability to predict biological distributions (Stevens and Connolly, 2004) for a wide range of species and habitat types.

Banks and Skilleter (2002) described the intertidal habitats along 24 216 km of Queensland's mainland and island coastline as a complex mosaic of intertidal habitat types, which included sandy beaches, rocky shores, mangrove communities, fringing coral reefs and coastal sand flats. The effectiveness of existing protection of multiple-use reserves was assessed and this demonstrated that the existing system of reserves failed to protect the full range of different intertidal habitats, with potential implications for biodiversity conservation if these different habitats support different communities or species (Schoch and Dethier, 1996; Roff and Taylor, 2000).

Here, we explore several reserve design scenarios that incorporate information about cost, reserve boundary length and existing protection of an intertidal habitat surrogate to identify the range of areas that would need to be included in a reserve system. Social, economic and management constraints, including associated costs (e.g. political or management-related costs) are important factors that will influence the choice of sites for inclusion into a system of marine reserves, particularly if large areas are required to protect representative examples of biodiversity. This study is an improvement over the previous attempts to apply a habitat surrogacy approach to reserve selection, as it is based on a fine-scale (tens to hundreds of metres) intertidal habitat classification that has been applied consistently to 24 216 km of the Queensland coastline. We describe a process for the systematic identification of sites for inclusion in a system of marine reserves that would protect representative examples of the full range of mainland intertidal habitats in Queensland. We evaluate the success of different reserve system scenarios in achieving conservation targets and the potential influences of reserve boundary compactness and the relative cost of each solution in identifying sites to be included in a representative system.

METHODS

The first detailed classification of Queensland's intertidal shoreline was recently completed (Figure 1) (Banks and Skilleter, 2002). The information in this classification was used to map the Queensland coast and provide the descriptive information for planning units that could be considered for inclusion in a system of 'candidate' intertidal marine reserves. The shoreline was subdivided into alongshore units that described the physical characteristics of the intertidal habitats at low tide. To consider the mosaic of intertidal habitats along a particular section of the shoreline, alongshore units were partitioned based on changes in the across-shore components, which reflected changes in substratum (e.g. bedrock, gravel), or features of the landscape landward (e.g. sand dunes, road, residential) of the low-tide habitat type.

The shoreline was classified into four major categories: marine (mainland and island) and estuarine (mainland and island). These major categories were then further partitioned into intertidal habitat types (e.g. wide sand flat; narrow rock ramp). A total of 63 intertidal habitat types was included in the initial reserve identification problem for the mainland (marine and estuarine) coast (i.e. 17 463 km) of Queensland to identify priority areas that would contribute to representation of intertidal habitats in a system of 'candidate' marine reserves. There were three artificial habitats (i.e. piles, marina and rock wall) that were not considered part of the marine reserve identification problem because they are highly modified areas and are often associated with locations used for industrial or commercial purposes.

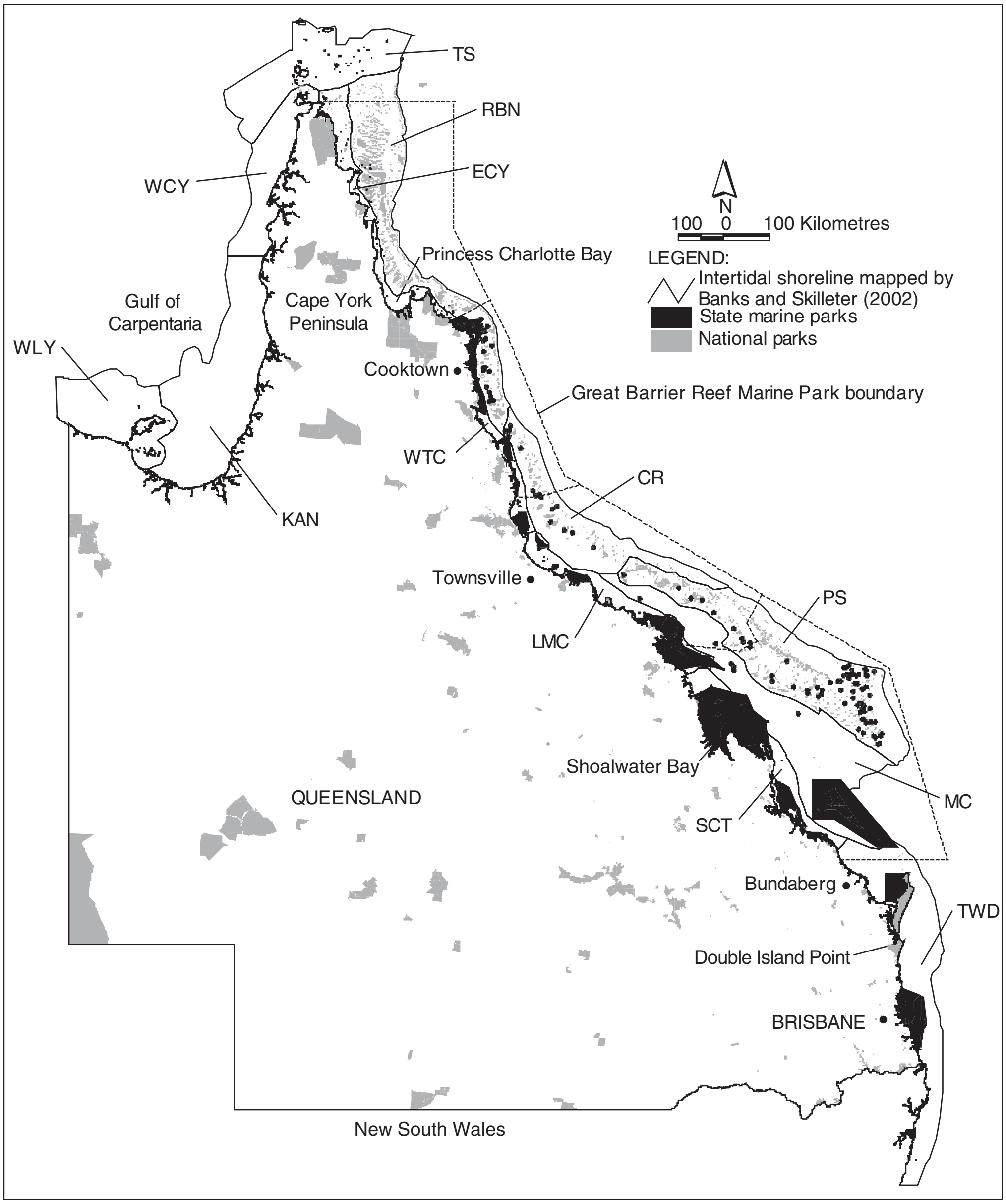

Figure 1. Queensland's mainland coastline that was partitioned into intertidal habitat types by Banks and Skilleter (2002). Ecosystem-scale bioregions: CR, Central Reef; ECY, East Cape York; KAN, Karumba–Nassau; LMC, Lucinda–Mackay; MC, Mackay–Capricorn; PS, Pompey–Swains; RBN, Ribbons; SCT, Shoalwater Coast; TS, Torres Strait; TWD, Tweed–Moreton; WCY, West Cape York; WLY, Wellesley; WTC, Wet Tropics Coast (IMCRA Technical Group, 1998).

The across-shore component (habitat type) described by Banks and Skilleter (2002) for the littoral zone higher on the shore and adjacent to each intertidal habitat type was included as additional conservation features in the reserve identification problem. This enabled variation across the shoreline to be considered as part of the reserve system identification process, increasing the likelihood that the complete range of biodiversity in an area could be included in a marine reserve system solution. The number of conservation features recorded in the adjacent littoral zone was 30, taking the total number of conservation features to 93 for the mainland coast of Queensland.

Reserve-selection algorithm

MARXAN (v1.8.3) was used to identify areas of coastline that are representative of the range of intertidal habitats in Queensland that could potentially be included in a representative system of marine reserves (Ball and Possingham, 2000). One formulation of the reserve system identification problem is to minimize its cost, whilst ensuring that the specific level of representation for each conservation feature is met (Pressey *et al.*, 1993; Leslie *et al.*, 2003). Given reasonably uniform data on species, habitats and/or other relevant biodiversity features and surrogates for a number of planning units, MARXAN was designed to minimize the cost (a weighted sum of area and boundary length while meeting user-defined biodiversity targets) of reserve systems while meeting all targets (Possingham *et al.*, 2000).

Simulated annealing was the optimization method used to find appropriate solutions to the marine reserve identification problem. The simulated annealing algorithm in MARXAN identifies a range of potential solutions to the problem of representing all the habitat types to a predefined percentage, while minimizing total cost (a weighted sum of area and boundary length). The summed irreplaceability of a site is the percentage of times each planning unit is chosen amongst the various solutions. Summed irreplaceability produces a value between zero and one for each planning unit. A unit that was allocated a value close to one is necessary for inclusion to meeting conservation goals, whereas a unit allocated a low value would be one that is unlikely to be required (Ball and Possingham, 2000).

Scenarios explored

Scenarios 1–24 were explored for identifying possible state-wide priorities for the conservation of a representative example (i.e. minimum one) of the intertidal habitat types in Queensland (Table 1). The choice of these 24 scenarios was based on consideration of several features that were varied, including: (i) boundary length modifier (three levels), which puts more or less weight on the cost of the reserve boundaries (free ends) compared with reserve length; (ii) the number of conservation features (63 intertidal habitats; or 93 i.e. 63 intertidal habitats plus 30 adjacent littoral zone habitats); (iii) the conservation feature target (5, 10, 20% of each habitat type); and (iv) an occurrence target (minimum of one or three). We compared the 'best' of 100 runs for each scenario explored using planning units 10 km in length.

Planning units

To determine state-wide conservation priorities, we grouped the mainland, intertidal habitats into 10 km lengths (i.e. 1746 planning units) to delineate the spatial location of potential ('candidate') sites to be included in a marine reserve system. Each planning unit consisted of one or more intertidal habitat types. The length of each habitat type in each planning unit was the basic data matrix for input into the reserve identification problem. Twenty-six planning units were locked into the marine reserve system as they were coastline areas adjacent to or within terrestrial national parks, or they were already protected in a 'no-take' zone within a state multiple-use marine park.

Conservation targets

Conservation targets were set at 5, 10, or 20% representation of each intertidal habitat for the mainland (marine and estuarine) coastline of Queensland (Table 2). Establishing conservation targets remains an area

Table 1. Scenarios explored to identify state-wide conservation priorities for the conservation of intertidal habitats. The table includes details of the features used for each scenario to identify state-wide conservation priorities, including boundary length modifier, number of conservation features, predefined conservation targets and minimum occurrence of each conservation feature

Scenario no.	No. of conservation features	Target (%)	Boundary length modifier	Replication	Separation distance (km)
1	63	5	0	Minimum 1	
2	63	5	0.5	Minimum 1	
3	63	5	1	Minimum 1	
4	63	5	0.5	3	
5	63	5	0.5	3	50
6	93	5	0	Minimum 1	
7	93	5	0.5	Minimum 1	
8	93	5	1	Minimum 1	
9	63	10	0	Minimum 1	
10	63	10	0.5	Minimum 1	
11	63	10	1	Minimum 1	
12	63	10	0.5	3	
13	63	10	0.5	3	50
14	93	10	0	Minimum 1	
15	93	10	0.5	Minimum 1	
16	93	10	1	Minimum 1	
17	63	20	0	Minimum 1	
18	63	20	0.5	Minimum 1	
19	63	20	1	Minimum 1	
20	63	20	0.5	3	
21	63	20	0.5	3	50
22	93	20	0	Minimum 1	
23	93	20	0.5	Minimum 1	
24	93	20	1	Minimum 1	
25	63	5	0	Minimum cost assigned to each planning unit	
26	63	5	0.5		
27	63	5	1		
28	63	10	0		
29	63	10	0.5		
30	63	10	1		
31	63	20	0		
32	63	20	0.5		
33	63	20	1		

of reserve selection that leads to much controversy, particularly as there is currently limited empirical evidence to support the selection of one target over another. There has recently been support for establishing a conservation target of between 20 and 30% related to the reproductive attributes of some commercially exploited species (Bohnsack *et al*., 2002).

The different scenarios also explored a target for the inclusion of a minimum of three examples of each conservation feature to protect against the loss of associated biodiversity arising from any major catastrophes that may affect an area (i.e. oil spills or adjacent land-use development). Buffering a reserve system against such catastrophes involves spreading the risk along the coast or determining an appropriate 'insurance factor' (Allison *et al*., 2003). By building into the reserve-design criteria a minimum separation distance, impacts of a catastrophic event on a reserve locally would not destroy the integrity of the entire reserve system (Ball and Possingham, 2000). The inclusion of these areas was based on a separation distance of 50 km between three or more conservation features protected.

Table 2. The 5%, 10% and 20% conservation targets (in kilometres) for each of the 63 intertidal habitat types

Intertidal habitat type	Total length mapped	5% target	10% target	20% target
Estuarine				
Boulder cliff	0.04	<0.01	<0.01	0.01
Beach rock platform, wide	0.82	0.04	0.08	0.16
Flat boulder field, wide	4.02	0.20	0.40	0.80
Flat cobble beach, narrow	0.23	0.01	0.02	0.05
Flat cobble beach, wide	1.91	0.10	0.19	0.38
Fringing coral reef, wide	0.88	0.04	0.09	0.18
Gravel flat, wide	1.37	0.07	0.14	0.27
Inclined boulder field, narrow	1.80	0.09	0.18	0.36
Inclined boulder field, wide	0.45	0.02	0.04	0.09
Inclined cobble beach, narrow	5.67	0.28	0.57	1.13
Inclined cobble beach, wide	0.28	0.01	0.03	0.06
Inclined gravel beach, narrow	4.08	0.20	0.41	0.82
Inclined gravel beach, wide	0.08	<0.01	0.01	0.02
Inclined mixed fines flat, narrow	1657.18	82.86	165.72	331.44
Inclined mixed fines flat, wide	2373.30	118.67	237.33	474.66
Inclined sand beach, narrow	197.17	9.86	19.72	39.43
Inclined sand beach, wide	17.32	0.87	1.73	3.46
Marina	50.88	–	–	–
Mixed fines flat, narrow	44.42	2.22	4.44	8.88
Mixed fines flat, wide	5947.02	297.35	594.70	1189.40
Piles	20.15	–	–	–
Rock cliff	1.89	0.09	0.19	0.38
Rock platform, wide	19.67	0.98	1.97	3.93
Rock ramp, narrow	4.34	0.22	0.43	0.87
Rock ramp, wide	3.43	0.17	0.34	0.69
Rock wall	93.97	–	–	–
Sand flat, narrow	1.60	0.08	0.16	0.32
Sand flat, wide	730.76	36.54	73.08	146.15
Steep mixed fines flat	1266.91	63.35	126.69	253.38
Steep sand beach	132.68	6.63	13.27	26.54
Unclassified		–	–	–
Estuarine total	**13 014.01**	**620.95**	**1241.93**	**2483.86**
Marine				
Boulder cliff	2.08	0.10	0.21	0.42
Beach rock platform, wide	16.79	0.84	1.68	3.36
Beach rock ramp, narrow	3.84	0.19	0.38	0.77
Beach rock ramp, wide	0.07	<0.01	0.01	0.01
Flat boulder field, wide	43.55	2.18	4.35	8.71
Flat cobble beach, wide	26.40	1.32	2.64	5.28
Fringing coral reef, narrow	0.48	0.02	0.05	0.10
Fringing coral reef, wide	45.47	2.27	4.55	9.09
Gravel flat, wide	19.50	0.97	1.95	3.90
Inclined boulder field, narrow	181.62	9.08	18.16	36.32
Inclined boulder field, wide	23.84	1.19	2.38	4.77
Inclined cobble beach, narrow	44.85	2.24	4.49	8.97
Inclined cobble beach, wide	14.72	0.74	1.47	2.94
Inclined gravel beach, narrow	16.46	0.82	1.65	3.29
Inclined gravel beach, wide	7.46	0.37	0.75	1.49
Inclined mixed fines flat, narrow	33.78	1.69	3.38	6.76
Inclined mixed fines flat, wide	45.20	2.26	4.52	9.04
Inclined sand beach, narrow	201.11	10.06	20.11	40.22
Inclined sand beach, wide	63.74	3.19	6.37	12.75

Table 2 *continued*

Intertidal habitat type	Total length mapped	5% target	10% target	20% target
Marina	3.10	–	–	–
Mixed fines flat, wide	1254.87	62.74	125.49	250.97
Piles	16.07	–	–	–
Rock cliff	73.30	3.66	7.33	14.66
Rock platform, narrow	2.05	0.10	0.21	0.41
Rock platform, wide	121.21	6.06	12.12	24.24
Rock ramp, narrow	82.43	4.12	8.24	16.49
Rock ramp, wide	18.29	0.91	1.83	3.66
Rock wall	16.85	–	–	–
Sand flat, narrow	5.44	0.27	0.54	1.09
Sand flat, wide	2058.03	102.90	205.80	411.61
Steep cobble beach	0.33	0.02	0.03	0.07
Steep mixed fines flat	6.33	0.32	0.63	1.27
Steep sand beach	0.18	0.01	0.02	0.04
Marine total	**4449.44**	**220.64**	**441.34**	**882.70**
GRAND TOTAL	**17 463.45**	**841.59**	**1683.27**	**3366.67**

Boundary length modifier

The boundary length modifier (BLM) was varied to determine the relative importance of system compactness. The algorithm ignores the boundary length of planning units when the BLM is set at zero and the compactness becomes increasingly important as the BLM is increased. To determine the influence of the BLM on the identification of sites for state-wide conservation priorities, BLMs of 0, 0.5 and 1 were used.

Cost

In this exercise, the objective was to minimize the total cost of the system in terms of total length, while ensuring that at least 5, 10 or 20% of every one of the conservation features (i.e. intertidal habitat types) were represented across the entire marine reserve system. The overall cost of the system is a combination of purchase (or compensation), dedication and ongoing management. Although direct measures of cost are hard to obtain, area and boundary length are useful surrogates and were used in this analysis. A relative cost was measured in terms of overall conservation rather than a real cost associated with the exclusion of commercial extraction. The length of each across-shore component of a planning unit that contained road, industry or residential areas or other artificial feature determined the relative cost and all other planning units had a relative cost of zero.

In all scenarios we assume that sites adjacent to residential areas are likely to have greater social or economic cost associated with the planning and management of a multiple-use marine park. Developing a zoning plan would normally involve the closure of certain areas to all forms of extraction (e.g. recreational and commercial fishing). We assume that the process of removing or ceasing exploitation may have a higher cost (i.e. enforcement and compliance or political costs) associated with the implementation of a management regime in areas adjacent to residential or tourist development where use may be higher.

Nine additional scenarios (scenarios 25–33) were explored to determine the influence of relative cost on the intertidal marine reserve system solutions (Table 1). These scenarios were completed with relative cost determined as described above; however, planning units adjacent to terrestrial protected areas were given a zero cost, with a minimal cost provided to all others.

RESULTS

The length of coast identified to be included in a 'candidate' system of intertidal marine reserves ranged from 3476 km (20% of the mainland coastline) to 7500 km (43% of the mainland coastline) for the 24 scenarios analysed (Table 1) where relative cost was only included for those planning units that contained modified across-shore components (e.g. roads, residential areas) (Table 3).

Habitat representation and conservation targets

The full range of intertidal habitats described for the coastline of Queensland were included in the marine reserve system solutions (for scenarios 1–24). A larger reserve system was required to achieve conservation feature targets as these targets increased from 5% (Figure 2), to 10% (Figure 3) and 20% (Figure 4) of each habitat type. The average proportion of mainland shoreline required to be included in a system of intertidal

Table 3. Results of scenarios explored to identify state-wide conservation priorities for the conservation of intertidal habitats (see Table 1 for scenario details)

Scenario no.	Conservation feature targets met	Length of coast protected (km)	Number of planning units
1	Yes	7126.7	713
2	Yes	3476.4	348
3	Yes	5785.6	579
4	33 met	6045.8	605
5	33 met	6375.2	638
6	Yes	7464.8	746
7	Yes	6798.6	680
8	Yes	5878.7	588
9	Yes	6895.2	689
10	Yes	6197.6	620
11	Yes	6885.2	689
12	32 met	5104.1	511
13	33 met	5455.4	546
14	Yes	7216.5	723
15	Yes	7574.9	758
16	Yes	5505.5	551
17	Yes	7226.9	723
18	Yes	6817.3	682
19	Yes	5428.5	543
20	35 met	6795.2	680
21	33 met	6702.9	671
22	62 met	7529.5	752
23	Yes	7204.7	721
24	Yes	6914.9	692
25	Yes	920	92
26	Yes	940	94
27	Yes	910	91
28	Yes	1760	176
29	Yes	1760	176
30	Yes	1760	176
31	Yes	3430	343
32	Yes	3430	343
33	Yes	3440	344

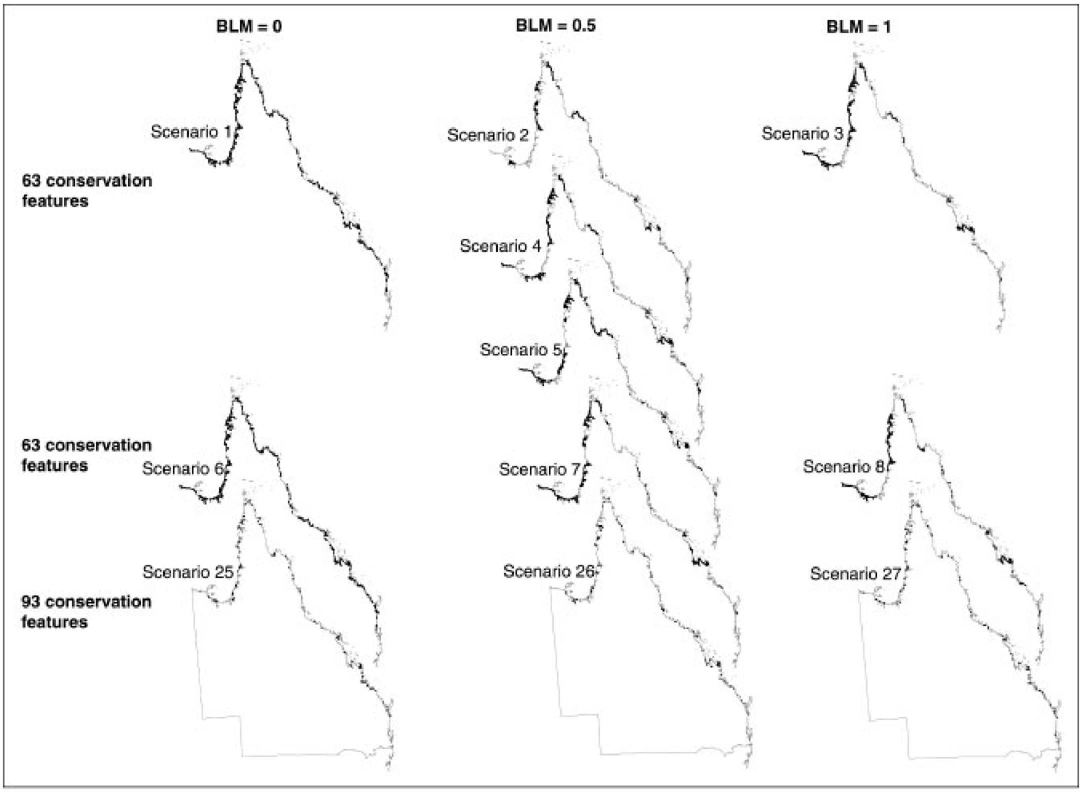

Figure 2. Scenarios that used 5% conservation feature targets (see Table 1 for scenario details).

marine reserves to achieve the conservation feature targets was 35% (for 5% target), 37% (for 10% target) and 38% (for 20% target) of the total shoreline analysed.

Similar lengths of coast were identified for inclusion in a system of intertidal marine reserves whether there were 60 conservation features or 93 conservation features included in the reserve identification problem (i.e. when the adjacent upper shore habitats were included). Increasing the number of conservation features by incorporating this vertical dimension in a shoreline should increase the likelihood that representative examples of intertidal communities and species will be conserved by protecting a mosaic of intertidal habitat types in the reserve system.

The conservation-feature targets were generally exceeded for each intertidal habitat type in all the solutions. For a target of 5%, the proportion of all habitat types selected to be included in a system of marine reserves was $>10\%$ of the available habitat. Similarly, $>50\%$ (for a 10% target) and $>30\%$ (for a 20% target) of each habitat type was selected to be included in the reserve solutions.

In solutions where the targets were not achieved, this outcome generally related to scenarios where the requirement of at least three examples of each conservation feature could not be met.

BLM

As the BLM increased above zero the compactness of the 'candidate' marine reserve systems increases (Figures 2–4). Increasing the BLM from zero to one resulted in a reduction in the overall length of shoreline selected to be included in the reserve solution. Based on targets of 5%, 10% and 20% and 63 conservation

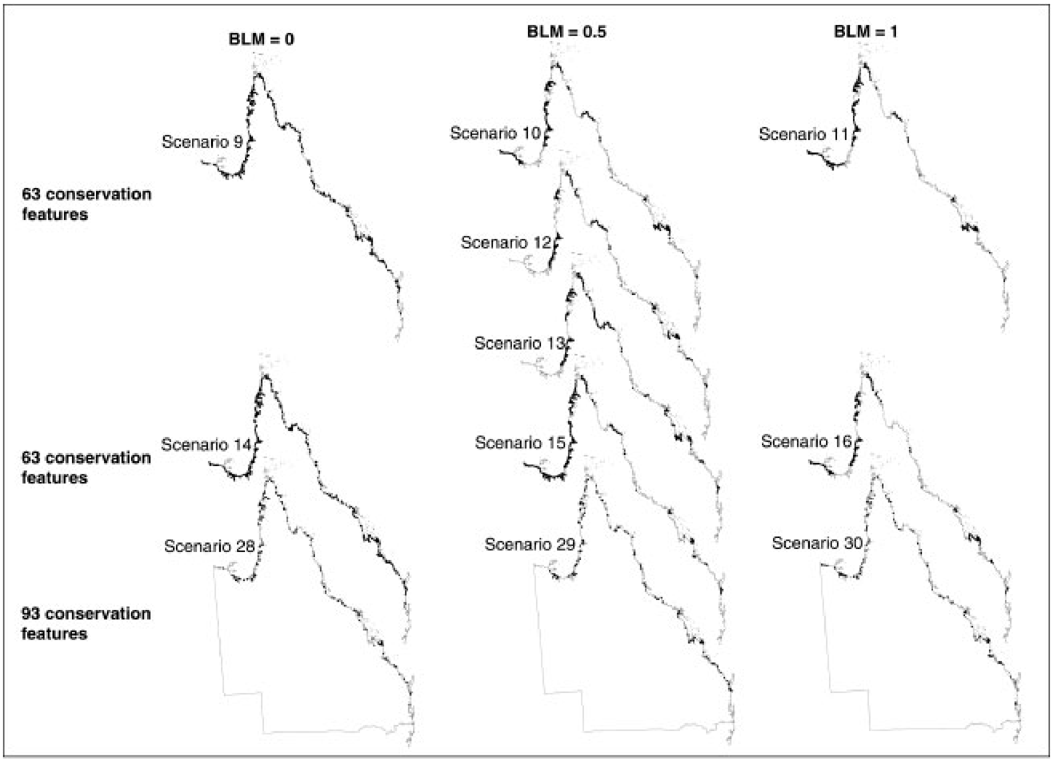

Figure 3. Scenarios that used 10% conservation feature targets (see Table 1 for scenario details).

features, the reduction in shoreline required to achieve these targets was 19%, 0.1% and 24% respectively when the BLM was increased from zero to one. Similarly, when 93 conservation features were included in the analysis, the overall length of shoreline required for protection reduced by 21%, 24% and 8% respectively as the BLM increased.

Cost

Taking relative cost into account resulted in the preferential inclusion of areas that were adjacent to areas that contained natural features in the adjacent across-shore components rather than modified sections of the coastline. Areas close to roads or residential areas attracted a higher relative cost and were, therefore, less likely to be included in a reserve solution. Additional planning units were included in the system, as they were considered to have no relative cost and, therefore, were free to be selected.

For scenarios where a minimum cost was given to all planning units (except those adjacent to terrestrial reserves) the reservation targets were achieved. The average proportion of the mainland shoreline required to be included in the system of intertidal marine reserves to achieve conservation targets was 5% (for a 5% target; Figure 2), 10% (for a 10% target; Figure 3) and 20% (for a 20% target; Figure 4).

DISCUSSION

The design of a system of intertidal marine reserves that meet prespecified goals can be made more efficient through the use of siting algorithms and a consistent fine-scale classification of intertidal habitats. This

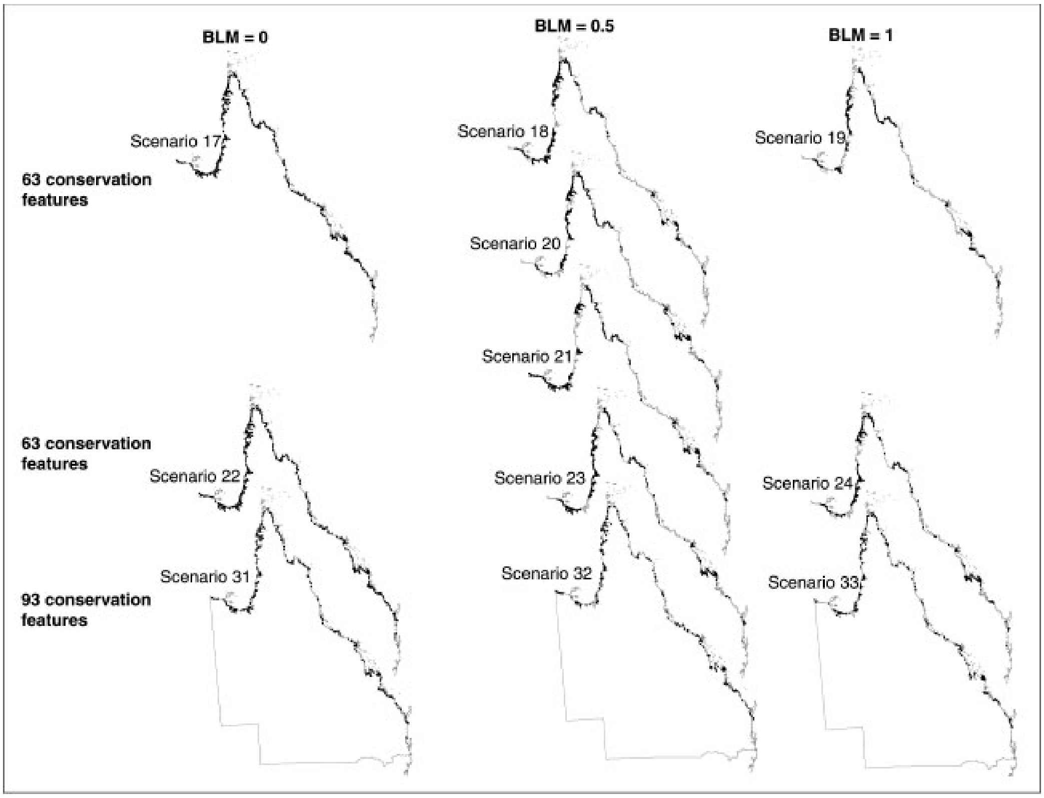

Figure 4. Scenarios that used 20% conservation feature targets (see Table 1 for scenario details).

approach enables marine reserve managers to negotiate a conservation outcome that is more likely to protect the range of intertidal assemblages and species than the historical ad hoc approach. The ability to 'factor in' other features, important to marine reserve selection (i.e. cost and boundary length), into the decision-making process for such a large section of coast represents an important step forward in marine reserve identification and selection. To demonstrate the influence of relative boundary length (i.e. compactness), relative cost and variations in the conservation feature targets would greatly assist the negotiation process with decision makers and stakeholders (Badalamenti *et al*., 2000; Scholz *et al*., 2004). These factors will also provide a sound basis to ensure that stakeholders, marine reserve managers and politicians understand the influence their decisions may have in achieving conservation goals while minimizing costs (management or political) associated with implementing different reserve system solutions.

Conservation feature targets

Determining the area or amount of each habitat to be included in a system of marine reserves remains a challenging problem (Bohnsack, 1998; Pressey *et al*., 2003). Protecting a minimum of 10–50% of the total area of all representative habitats has been recommended based on cultural traditions, social acceptability and the precautionary principle (Ballantine, 1991; Bohnsack, 1993; Dayton *et al*., 1995; Bohnsack *et al*., 2002; Airame *et al*., 2003; Roberts *et al*., 2003b). Targets of 20–30% of total area have been recommended in relation to fisheries management and maintaining fish stocks (Bohnsack, 1998). There has been a trend for targets of between 10 and 30% to be used in reserve-system planning. For example, targets of 20% of reef and non-reef bioregions were used in the rezoning of the Great Barrier Reef Marine Park (Great Barrier Reef Marine Park Authority, 2003), and targets of 10–30% of the area of 26 habitats were used as one of a number of scenarios to design a system of marine reserves in the Florida Keys (Leslie *et al*., 2003). Studies have shown that there are many different combinations of reserve networks that could meet conservation representation targets (Possingham *et al*., 2000; Leslie *et al*., 2003; Stewart *et al*., 2003).

Although there is limited biological/ecological evidence to support the establishment of a particular target for representation of ecosystems, habitats or species in a reserve system, examination of a range of conservation feature targets should be used to assist in a negotiation process with stakeholders. These different scenarios could include varying targets for overall representation (of all habitat types) or for specific habitat types (e.g. rare or unique habitats). A range of reserve solutions using different scenarios provides a sound basis for understanding the implications of conservation outcomes with consideration of cost, planning unit length and reserve system compactness.

Reserve compactness and cost

There are social and political implications for a system of marine reserves where there is an absence of information related to the cost of implementing or managing the system. It is important that an appropriate assessment of cost for each planning unit be made prior to the identification and planning process commencing. The solutions presented in this paper demonstrate the importance of defining cost for each planning unit, which, when not considered, resulted in a much higher average length of mainland coastline required to achieve a conservation feature target of 5% (approximately 6000 km or 35% of the mainland coast). A greater proportion of the planning units, compared with those scenarios when all planning units had a minimum cost, were considered cost free and, therefore, were potentially available for selection in a reserve system solution, resulting in the selection of a larger number of planning units than was necessary to achieve reserve system targets. Closing some areas to harvesting would potentially draw attention from recreational and industrial fishers who generally oppose such closures, particularly if it involves extensive areas of the coastline, thus resulting in higher social and/or political costs (Scholz *et al*., 2004). Therefore, it is imperative that realistic costs are used for each planning unit.

Some areas of coastline, including areas in the southern Gulf of Carpentaria, Shoalwater Bay, Princess Charlotte Bay, east and west Cape York and Double Island Point in south-east Queensland, were consistently identified as a ‘key’ part of the candidate system of marine reserves, but this may have been at the cost of other areas because of the influence of ‘relative cost’. The identification of these areas, many of which are in northern Queensland, were influenced by the relative cost assigned to planning units that contained modified intertidal habitat types or that were adjacent to residential or industrial areas, such as those in south-east Queensland. The cost of including the latter in a representative marine reserve scheme is likely to be greater. Greater relative costs associated with some otherwise similar planning units are likely to have led to the selection of planning units that, for example, contain wide sand flats (i.e. beaches) in the Gulf of Carpentaria, where there is little modification of the shoreline and adjacent terrestrial habitats, rather than similar habitats in south-east Queensland.

The data used by the siting algorithm did not incorporate latitudinal variation when assigning a planning unit to be included in the reserve system. To overcome this problem, analysis of the mainland coastline could be examined in relation to the IMCRA marine bioregions (IMCRA Technical Group, 1998), with the objective of representative coverage of all biogeographic regions in reserves (Roberts *et al*., 2003a,b). This would provide a basis for representation of intertidal habitat types in a latitudinal context and would assist with differentiating intertidal habitats between climatic and oceanographically different areas along the coast of Queensland.

The ability to consider compactness of reserve system solutions and costs associated with either the establishment or management of a system of marine reserves strengthens the ability of decision makers to make an informed decision about where to locate the reserves and provides a sound basis for negotiation with stakeholders. Compactness of the reserve system is important in relation to overall social and political acceptability of a system of protected areas, because people affected by closures to harvesting activities are generally likely to seek minimal protection over small areas and are, therefore, more likely to support a highly compact system.

Planning-unit size

It is likely that the reserve system outcomes shown here have been strongly influenced by the length of the planning unit (i.e. 10 km). To achieve the conservation targets, planning units were selected and/or substituted by MARXAN to determine the 'best' reserve system solution based on 100 runs for a scenario. Where, for example, a particular type of unique or rare habitat (e.g. steep cobble beach) occurs as a unit less than the 10 km length, it will be selected, along with the surrounding, more extensive habitat type (e.g. wide sand flats). Although this ensures the rare habitat type is included in the reserve system, it may lead to overrepresentation (i.e. above conservation targets) of these other habitats. Thus, planning units that contain habitats considered rare or unique should probably be 'locked into' the system during the stakeholder negotiations. Increased representation of habitats that may be desirable from a biodiversity conservation perspective, however, is likely to lead to greater social or political costs in establishing the system. Use of a smaller length of planning unit (e.g. 1 km) would reduce the potential to overrepresent common or extensive habitat types.

Using habitat surrogates in reserve design

The application of reserve solutions derived through the use of decision-support tools and based on a physical habitat surrogate can assist the decision-making process. It has been suggested that the best strategy for conserving intertidal habitats is to conserve patches of habitats of different sizes and shapes and at different distances apart (Underwood and Chapman, 2001). The systematic classification of the coast of Queensland provided a consistent description of the physical intertidal habitat types (Banks and Skilleter, 2002). The problem with such physical classifications of the coastline is that it is not yet possible to predict reliably the biological communities that are associated with each type of habitat (Zacharias *et al*., 1999; but see Valesini *et al*. (2003) for an alternative).

At present, it is assumed that the combination of physical factors used to derive the habitats adequately predicts differences in the diversity and abundance of intertidal organisms between one habitat type and another. This is probably the case when considering differences in the assemblages supported by extremes in habitat types (Valesini *et al*., 2003), such as sandy beaches, rocky shores or biologically derived reefs. However, it is more problematic when considering the variation within broad habitat types, e.g. different types of rocky shore, such as wide rock platforms, narrow rock platforms and rock ramps. There are no detailed empirical data that allow predictions to be made about the relationship between physical attributes of a specific habitat type and the biota found there. If there is sufficient replication within the reserve system then this may not matter; however, there is now the need to test the relationship between the habitat surrogate and the distribution and abundance of intertidal organisms.

Clearly, in the absence of detailed information related to the distribution and abundance of intertidal organisms, conservation priorities must be identified using physical surrogates as the input data for a siting algorithm. The strength of this pragmatic approach is that it can be applied to large sections of the intertidal coastline. It will also assist with negotiation processes with stakeholders who will be better able to understand the implications of selecting one site over another for inclusion in a system of marine reserves.

Marine reserve planning in Queensland

The results represent a small subset of those solutions available to protect a representative range of intertidal habitats in Queensland. Use of 10 km planning units enabled conservation priorities to be broadly identified over a vast length (i.e. 17 463 km) of the Queensland coast. Although the outcomes of the present analysis provided a range of solutions for the identification of a set of priority areas that could be protected in intertidal marine reserves, the marine conservation framework used in Queensland involves the establishment of large multiple-use marine parks. These parks usually have 'core' areas (i.e. zones) that are closed to all extractive activities. As discussed by Agardy *et al.* (2003), there is debate about the value of establishing large multiple-use marine parks that contain 'core' areas as no-take zones versus the establishment of a marine reserve over a specific area that is entirely closed to extraction.

This analysis identified a representative suite of areas of conservation interest in Queensland. From here, marine-park planners and decision makers need to consider a range of other factors at a variety of spatial scales in the context of social and economic impacts of the different options to select the location of reserves (i.e. areas zoned to prohibit extractive activities) within multiple-use marine parks. Following the declaration of a marine park, a zoning plan is required that establishes the spatial management regime that defines marine reserves (areas of 'no-take') to areas where extractive activities can continue. During this process, finer scale (e.g. 1 km) planning units should be used to determine local priorities for zoning areas as 'no-take'. The identification of these 'no-take' zones using a systematic science-based framework will be fundamental to achieving conservation goals by protecting representative examples of intertidal habitats in fully protected 'no-take' zones.

Our findings support the need for Queensland to review zoning arrangements for the current system of multiple-use State marine parks (Banks and Skilleter, 2002). In particular, we need a system of intertidal reserves or 'no-take' zones that include a representative range of intertidal habitats to provide protection from damaging activities. There is also a need for consideration of the establishment of additional multiple-use marine parks in bioregions where no marine park protection currently exists (e.g. Torres Strait and the bioregions in the Gulf of Carpentaria).

The differences between the physical and biological processes operating in the marine and terrestrial environments have been documented and recognized as important for determining the planning response by management agencies (Avery, 2003). This, however, does not necessarily mean that reserve systems to protect representative examples of the range of ecosystems, habitats and species in these environments need to develop independently. Avery (2003) describes the planning approaches to marine and terrestrial reserves systems as being largely the same; this enables the systems to be developed to complement each other, reducing the risk that important habitats in the coastal zone are not protected. In Queensland, there has been little progress in the protection of intertidal habitats in 'no-take' zones in marine parks. The future design and planning of protected-areas systems should ensure that marine and terrestrial system identification and selection is integrated to optimize the likelihood that the range of intertidal habitats is protected. If marine reserve systems continue to be developed without consideration of the adjacent terrestrial reserve system (and the role that system may play in protecting intertidal habitats) then there will continue to be poor representation of intertidal habitats in reserves.

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REFERENCES

Agardy T, Bridgewater P, Crosby MP, Day J, Dayton PK, Kenchington R, Laffoley D, McConney P, Murray PA, Parks JE, Peau L. 2003. Dangerous targets? Unresolved issues and ideological clashes around marine protected areas. *Aquatic Conservation: Marine and Freshwater Research* **13**: 353–367.

Airame S, Dugan JE, Lafferty KD, Leslie H, McArdle DA, Warner RR. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. *Ecological Applications* **13**(1 Supplement): S170–S184.

Allison GW, Lubchenco J, Carr MH. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecological Applications* **8**: 79–82.

Allison GW, Gaines SD, Lubchenco J, Possingham HP. 2003. Ensuring persistence of marine reserves: catastrophes require adopting an insurance factor. *Ecological Applications* **13**(1 Supplement): S8–S24.

ANZECC. 1999. *Strategic Plan of Action for the National Representative System of Marine Protected Areas: A Guide for Action by Australian Governments*. Australian and New Zealand Environment and Conservation Council. Environment Australia: Canberra.

Araujo FG, Costa de Azevedo MC. 2001. Assemblages of southeast–south Brazilian coastal systems based on the distribution of fishes. *Estuarine, Coastal and Shelf Science* **52**: 729–738.

Ardon J. 2003. BC Coast Information Team Marine Ecosystem Spatial Analysis. Version 1.2. Excerpted and revised from Rumsey C, Ardon JA, Ciruna K, Curtis T, Doyle F, Ferdana Z, Hamilton T, Heinemyer K, Iachetti P, Jeo R, Kaiser G, Narver D, Noss R, Sizemore D, Tautz A, Tingey R, Vance-Boland, K. *An ecosystem analysis for Haida Gwaii, Central Coast, and North Coast British Columbia*. Draft, September 22 2003. www.livingoceans.org/library.htm.

Ardon JA, Lash J, Haggarty D. 2002. Modelling a network of marine protected areas for the central coast of British Columbia. Version 3.1. Living Oceans Society, Sointule, BC, Canada.

Avery R. 2003. Marine and terrestrial conservation planning—how different are they? In *Conserving Marine Environments. Out of Sight Out of Mind*, Hutchings P, Lunney D (eds). Royal Zoological Society of New South Wales: Sydney: 18–40.

Badalamenti F, Ramos AA, Voultsiadou E, Sanchez Lizaso JL, D'Anna G, Pipitone C, Ruiz Fernandez JA, Whitmarsh D, Riggio S. 2000. Cultural and socio-economic impacts of Mediterranean marine protected areas. *Environmental Conservation* **27**(2): 110–125.

Ball I, Possingham HP. 2000. Marxan (v1.8.2) *Marine Reserve Design Using Spatially Explicit Annealing*. A manual prepared for the Great Barrier Reef Marine Park Authority, Townsville, Australia.

Ballantine B. 1991. Marine reserves in New Zealand. University of Auckland. *Leigh Laboratory Bulletin* **25**: 1–196.

Banks SA, Skilleter GA. 2002. Mapping intertidal habitats and an evaluation of their conservation status in Queensland, Australia. *Ocean & Coastal Management* **48**(8): 485–509.

Beck MW, Odaya M. 2001. Ecoregional planning in marine environments: identifying priority sites for conservation in the northern Gulf of Mexico. *Aquatic Conservation: Marine and Freshwater Ecosystems* **11**: 235–242.

Bedward M, Pressey RL, Keith DA. 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biological Conservation* **62**: 115–125.

Bohnsack JA. 1993. Marine reserves: they enhance fisheries, reduce conflicts, and protect resources. *Oceanus* **36**(3): 63–71.

Bohnsack JA. 1998. Application of marine reserves to reef fisheries management. *Australian Journal of Ecology* **23**: 298–304.

Bohnsack JA, Causey B, Crosby MP, Griffs RB, Hixon MA, Hourigan TF, Koltes KH, Maragos JE, Simons A, Tilmant JT. 2002. A rationale for minimum 20–30% no-take protection. In *World Coral Reefs in the New Millennium: Bridging Research and Management for Sustainable Development*, Kasim Moosa M, Soemodihardjo S, Soegiarto A, Romimohtarto K, Nontji A, Soekarno, Suharsono (eds). Proceedings of the 9th International Coral Reef Symposium, October 2000. Ministry for the Environment, Indonesian Institute of Sciences, International Society for Reef Studies: Bali, Indonesia.

Carr MH, Neigel JE, Estes JA, Andelman S, Warner RR, Largier JL. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecological Applications* **13**(1 Supplement): S90–S107.

Curley BG, Kingsford MJ, Gillanders BM. 2002. Spatial and habitat-related patterns of temperate reef fish assemblages: implications for the design of marine protected areas. *Marine and Freshwater Research* **53**: 1197–1210.

Davey AG. 1998. *National System Planning for Protected Areas*. IUCN: Gland (Switzerland) and Cambridge (UK).

Day J, Roff J. 2000. *Planning for Representative Marine Protected Areas: A Framework for Canada's Oceans*. World Wildlife Fund: Canada.

Dayton PK, Thrush SF, Agardy MT, Hofman RJ. 1995. Environmental effects of marine fishing. *Aquatic Conservation: Marine and Freshwater Ecosystems* **5**: 1–28.

Dee Boersma P, Parrish JK. 1999. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* **31**: 287–304.

Gladstone W. 2002. The potential value of indicator groups in the selection of marine reserves. *Biological Conservation* **104**: 211–220.

Great Barrier Reef Marine Park Authority. 2003. Background and history: biophysical operational principles as recommended by the scientific steering committee. http://www.gbrmpa.gov.au/corp_site/key_issues/conservation/rep_areas/info_sheets.html.

IMCRA Technical Group. 1998. Interim marine and coastal regionalisation for Australia: an ecosystem-based classification for marine and coastal environments. Version 3.1. Environment Australia, Commonwealth Department of the Environment, Canberra.

Kelleher G, Bleakley C, Wells SC (eds). 1995. *A Global Representative System of Marine Protected Areas: Antarctic, Artic, Mediterranean, Northwest Atlantic and Baltic*. The International Bank for Reconstruction/The World Bank: Washington, DC.

Leslie H, Ruckelshaus M, Ball IR, Andelman S, Possingham HP. 2003. Using siting algorithms in the design of marine reserve networks. *Ecological Applications* **13**(1 Supplement): S185–S198.

Margules CR, Nicholls AO, Pressey RL. 1988. Selecting networks of reserves to maximise biological diversity. *Biological Conservation* **43**: 63–76.

National Academy of Sciences. 2001. *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems*. Committee on the evaluation, design, and monitoring of marine reserves and protected areas in the United States. Ocean Studies Board Commission on Geosciences, Environment, and Resources National Research Council. National Academy Press: Washington, DC.

Possingham H, Ball I, Andelman S. 2000. Mathematical methods for identifying representative reserve networks. In *Quantitative Methods for Conservation Biology*, Feron S, Burgman M (eds). Springer-Verlag: New York.

Pressey RL. 1994. Ad hoc reservations: forward or backward steps in developing representative reserve systems? *Conservation Biology* **8**(3): 662–668.

Pressey RL. 1997. Priority conservation areas: towards an operational definition for regional assessments. In *National Parks and Protected Areas: Selection, Delimitation and Management*, Pigram JJ, Sundell RC (eds). Centre for Water Policy Research, University of New England: Armidale.

Pressey RL, Humphries CJ, Margules CR, Vane-Wright RI, Williams PH. 1993. Beyond opportunism: key principles for systematic reserve selection. *TREE* **8**(4): 124–128.

Pressey RL, Hager TC, Ryan KM, Schwarz J, Wall S, Ferrier S, Creaser PM. 2000. Using abiotic data for conservation assessments over extensive regions: quantitative methods applied across New South Wales, Australia. *Biological Conservation* **96**: 55–82.

Pressey RL, Cowling RM, Rouget M. 2003. Formulating conservation targets for biodiversity pattern and process in the Cape Floristic region, South Africa. *Biological Conservation* **112**: 99–127.

Roberts CM, Andelman S, Branch G, Bustmante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie L, Lubchenco J, McArdle D, Possingham HP, Ruckelshaus M, Warner RR. 2003a. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* **13**(1 Supplement): S199–S214.

Roberts CM, Branch G, Bustmante RH, Castilla JC, Dugan J, Halpern BS, Lafferty KD, Leslie L, Lubchenco J, McArdle D, Ruckelshaus M, Warner RR. 2003b. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* **13**(1 Supplement): S215–S228.

Rodriguez LO, Young KR. 2000. Biological diversity of Peru: determining priority areas for conservation. *Ambio* **29**(6): 329–337.

Roff JC, Evans SMJ. 2002. Frameworks for marine conservation—non-hierarchical approaches and distinctive habitats. *Aquatic Conservation: Marine and Freshwater Research* **12**: 635–648.

Roff JC, Taylor ME. 2000. National frameworks for marine conservation—a hierarchical geophysical approach. *Aquatic Conservation: Marine and Freshwater Research* **10**: 209–223.

Schoch G, Dethier M. 1996. Scaling up: the statistical linkage between organismal abundance and geomorphology on rocky intertidal shorelines. *Journal of Experimental Marine Biology and Ecology* **201**: 37–72.

Scholz A, Bonzon K, Fujita R, Benjamin N, Woodling N, Black P, Steinback C. 2004. Participatory socioeconomic analysis: drawing on fisherman's knowledge for marine protected area planning in California. *Marine Policy* **28**: 335–349.

Sobel J. 1993. Conserving biological diversity through marine protected areas: a global challenge. *Oceanus* **36**(3): 19–26.

Stevens T, Connolly RM. 2004. Testing the utility of abiotic surrogates for marine habitat mapping at scales relevant to management. *Biological Conservation* **119**: 351–362.
Stewart RR, Noyce T, Possingham HP. 2003. Systematic marine reserve design: the opportunity cost of ad hoc decisions. *Marine Ecology Progress Series* **253**: 25–38.
Thompson RC, Wilson BJ, Tobin ML, Hill AS, Hawkins SJ. 1996. Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *Journal of Experimental Marine Biology and Ecology* **202**: 73–84.
Thompson RC, Crowe TP, Hawkins SJ. 2002. Rocky intertidal communities: past environmental changes, present status and predictions for the next 25 years. *Environmental Conservation* **29**(2): 168–191.
Underwood AJ, Chapman MG. 2001. Intertidal ecosystems. In *Encyclopedia of Biodiversity*, vol. 3, Levin SA (ed.). Academic Press: San Diego.
Valesini FJ, Clarke KR, Eliot I, Potter IC. 2003. A user-friendly quantitative approach to classifying nearshore marine habitats along a heterogenous coast. *Estuarine, Coastal and Shelf Science* **57**: 163–177.
Valesini FJ, Potter IC, Clarke KR. 2004. To what extent are the fish compositions at nearshore sites along a heterogenous coast related to habitat types? *Estuarine, Coastal and Shelf Science* **60**: 737–754.
Ward TJ, Vanderklift MA, Nicholls AO, Kenchington RA. 1999. Selecting marine reserves using habitats and species assemblages as surrogates for biological diversity. *Ecological Applications* **9**(2): 691–698.
Warwick RM, Light J. 2002. Death assemblages of molluscs on St Martin's Flats, Isles of Scilly: a surrogate for regional biodiversity? *Biodiversity and Conservation* **11**: 99–112.
Williams A, Bax NJ. 2001. Delineating fish–habitat associations for spatially based management: an example from the south-eastern Australian continental shelf. *Marine and Freshwater Research* **52**: 513–536.
Zacharias MA, Roff JC. 2000. A hierarchical ecological approach to conserving marine biodiversity. *Conservation Biology* **14**: 1327–1334.
Zacharias MA, Morris MC, Howes DE. 1999. Large scale characterization of intertidal communities using a predictive model. *Journal of Experimental Marine Biology and Ecology* **239**: 223–242.