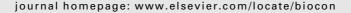# Connectivity of reef fish between mangroves and coral reefs: Algorithms for the design of marine reserves at seascape scales

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A B S T R A C T

Many species of coral reef fish undertake ontogenetic migrations between seagrass beds, mangroves, and coral reefs. A recent study from the Caribbean found that the availability of mangrove nursery habitat had a striking impact on the community structure and biomass of reef fish in their adult, coral reef habitat. The biomass of several species more than doubled when the reefs were connected to rich mangrove resources (defined as having at least 70 km of fringing *Rhizophora mangle* within a region of 200 km^2). Here, the results of this large-scale empirical study are translated into a series of algorithms for use in natural resource management planning. Four algorithms are described that identify (i) the relative importance of mangrove nursery sites, (ii) the connectivity of individual reefs to mangrove nurseries, (iii) areas of nursery habitat that have an unusually large importance to specific reefs, and (iv) priority sites for mangrove reforestation projects. The algorithms generate a connectivity matrix among mangroves and coral reefs that facilitates the identification of connected corridors of habitats within a dynamic planning environment (e.g., reserve selection algorithms).

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1. Introduction

Many aquatic organisms undertake ontogenetic migrations from one habitat to another during their life time. Inter-habitat migrations have been reported for both invertebrate (Hiddink, 2003) and vertebrate fauna (Law and Dickman, 1998) with the majority of studies focused on fishes, including those wholly within freshwater ecosystems (Ruzycki and Wurtsbaugh, 1999), wholly within coastal marine systems (Parrish, 1989; Nagelkerken et al., 2000a) and those that move among rivers, estuaries and the ocean (Lenormand et al., 2004). The reasons for undertaking such a stage-structured lifecycle are varied and include: (i) requirements for different food sources as the organism grows (Werner and Gilliam, 1984; de la Moriniere

et al., 2003a), (ii) changing risks of predation with size, such that sheltered habitats, where predator foraging efficiency is low, are chosen when the organism occupies its smaller, more vulnerable stages (Shulman, 1985; Laegdsgaard and Johnson, 2001), and (iii) a need to reproduce in habitats which offer the greatest dispersal or survival of larvae.

The existence of ontogenetic habitat shifts means that the utilisation of a seascape differs between juveniles and adults (Lindeman et al., 1998). Conservation strategies should therefore protect connected corridors of habitat and facilitate the natural migration of species among habitats. This is conceptually similar to the practice of conserving corridors among habitat patches that may become gradually isolated through habitat fragmentation (Tewksbury et al.,

2002; Haddad et al., 2003; Haddad and Tewksbury, 2005). In the latter case, corridors facilitate the interaction of individuals, thereby increasing genetic exchange and dispersal among patches, and reducing population fluctuations. The first step in creating habitat corridors for ontogenetic migration is identifying the utilisation and importance of specific habitats in the seascape.

Whilst many studies have identified 'nursery' habitats as those occupied by juveniles of a species, the importance of juvenile habitats at a population level is only beginning to emerge. Firstly, just because juveniles of a species are often seen in habitat A, it does not follow that the population would be severely impacted if large areas of habitat A were lost. Juveniles might, for example, switch to using another habitat. Alternatively, the availability of nursery habitat may only become limiting at extremely low levels. For example, if density-dependent mortality (Caley et al., 1996) were acute in adult habitats, the adult population would be relatively insensitive to the number of immigrants arriving from juvenile habitats. Indeed, the vagaries of quantifying the importance of juvenile habitats has prompted some (Beck et al., 2001) to tighten the definition and study of 'nursery' habitats.

A recent study of Caribbean coastal ecosystems attempted to distinguish the importance of seagrass and mangrove habitats to populations of coral reef fishes (Mumby et al., 2004). A number of reef fish, representing herbivores (e.g., *Scarus iserti*, *Scarus guacamaia*), invertivores (*Haemulon sciurus*, *Haemulon flavolineatum*, *Haemulon plumieri*), and piscivores (*Lutjanus apodus*, *Sphyraena barracuda*) use mangroves and seagrass beds as juveniles and coral reefs as adults. Analysis of the size-frequency distribution of several species suggested that some (e.g., *H. sciurus*) utilise seagrass beds first and then occupy mangroves as an intermediate habitat before migrating to coral patch reefs and the outer forereef. Using a large-scale data set comprising four atolls and parts of the Belize Barrier Reef, the authors' concluded that only one species, *S. guacamaia*, the largest herbivorous fish in the Atlantic, has a functional dependence on mangroves. However, the presence of prolific mangroves in the vicinity of coral reefs was found to exert a profound impact on the community structure of 162 species of reef fish and greatly elevated the total adult biomass of several species (Table 1). Since many of these species are economically and/or ecologically important, it is desirable to incorporate their spatial ecology explicitly into criteria for coral reef management. Here, the present state of knowledge of inter-habitat connectivity in Caribbean reef fish is used to design four algorithms for conservation planners. These algorithms represent the spatial distribution of:

(1) Mangroves capable of providing high-quality habitat for juvenile reef fishes.
(2) Reef connectivity to mangrove nurseries.
(3) Mangroves that offer critical nursery habitats to particular reefs. Loss of such mangroves could have a large impact on the connectivity of these reefs to nursery habitat.
(4) Priority sites for use in mangrove restoration (i.e., those sites best placed to enhance the biomass of fishes on coral reefs).

Application of these algorithms will highlight important nursery areas for coral reef fishes, the most critical man-

Table 1 – Impact of extensive mangroves on the biomass of fish in patch reef, shallow forereef, and Montastraea reef habitats (adapted from Mumby et al., 2004)

Species	Mean (s.e.m.) biomass (kg km^{-2})								
	Patch reef			Shallow forereef			Montastraea reef		
	Scarce mang.	Rich mang.	Biomass increase (%)	Scarce mang.	Rich mang.	Biomass increase (%)	Scarce mang.	Rich mang.	Biomass increase (%)
Scarus iserti	–	–		–	–		1530 (118)	2170 (111)	42
Haemulon sciurus	1205 (329)	33349 (9274)	2667	56 (38)	425 (120)	659	288 (53)	447 (55)	55
H. flavolineatum	5256 (1460)	15307 (4114)	191	516 (101)	1600 (249)	210	1398 (149)	1643 (139)	
H. plumieri	5174 (1614)	16280 (3591)	214	317 (72)	843 (304)	165	523 (62)	863 (69)	65
Haemulidae (all)	11636 (2089)	67370 (12971)	478	889 (152)	3031 (497)	240	2288 (188)	3210 (192)	40
Ocyurus chrysurus	769 (441)	410 (95)		659 (150)	892 (187)		3098 (486)	6715 (1323)	116
Lutjanus apodus	739 (354)	6192 (1566)	737	622 (336)	2392 (722)	284	1767 (226)	1898 (259)	
Lutjanidae (all)	2890 (1228)	16707 (4805)	478	1882 (745)	4428 (1055)	135	5883 (796)	12223 (1503)	107

Where mangroves (denoted mang.) exerted significant influence, the increase in mean biomass is expressed as a percentage of the level in mangrove-scarce systems. *Scarus iserti* was not surveyed on patch reefs or shallow forereefs. (all) denotes all species in family not just those in table. Neither the biomass nor density of species in seagrass beds differed significantly by the factor mangrove.

grove forests on the grounds of their nursery function, those reefs that are most likely to benefit from prolific mangrove nurseries and therefore have greater potential fisheries production, and the most strategically valuable sites to restore to a mangrove habitat. These algorithms also provide the basis for establishing connected corridors of marine habitats which is analogous to the identification of habitat corridors for many other taxa including *Acipenser oxyrhynchus*, the Atlantic sturgeon (Niklitschek and Secor, 2005), *Phoenicopterus ruber*, the greater flamingo (Amat et al., 2005), and butterflies (Binzenhofer et al., 2005). Since these algorithms combine physical attributes of the seascape with limited information on the overall dispersal ability of coral reef fishes, they fall under the category 'Potential connectivity' in the classification of connectivity measures undertaken by Calabrese and Fagan (2004).

2. Description of algorithms

2.1. Basis and assumptions of algorithms

Despite a wealth of empirical studies, understanding of the ontogenetic shifts in habitat use by reef fish is far from comprehensive (Shulman and Ogden, 1987; Birkeland, 1988; Birkeland and Amesbury, 1988; Sedberry and Carter, 1993; Ley et al., 1999; Nagelkerken et al., 2000b; de la Moriniere, 2002; Ley and McIvor, 2002; Nagelkerken et al., 2002; Nagelkerken and van der Velde, 2002; de la Moriniere et al., 2003b; Mumby et al., 2004). Although the study of Mumby et al. (2004) was not purely correlative in that it used a natural experiment and managed to discount alternative hypotheses that might plausibly explain the observed enrichment of fish biomass near mangroves, the quantification of nursery habitat was partly arbitrary. Any estimate of the availability of nursery habitat around a reef requires a specific catchment. But how large should this catchment be? Without comprehensive species- and size-level data on the migratory ability of reef fish, an arbitrary catchment size was used: that of the smallest whole-reef ecosystem unit in the study, Glovers Reef (Atoll) which has an area of about 200 km^2. At this scale, spatial variation in reef fish community structure and biomass could be quantified unambiguously in the absence of mangroves. The total perimeter of nursery habitat was then quantified within a region of this size in each of six reef systems in Belize and Mexico. Reefs, seagrass beds and mangroves were then sampled in at least three sites within each system, where sites were separated by kilometres (Mumby et al., 2004).

In the Caribbean, juvenile reef fish occupy the submerged prop roots of *Rhizophora mangle* and make frequent foraging runs into adjacent seagrass beds. The prop root environment of offshore mangroves in Belize ranges in depth from about 0.3 to 3 m and is rarely more than 4 m in width (i.e., occupies only the fringe of a mangal). Mangrove nursery habitat was therefore defined as any area of fringing *R. mangle* that bordered an aquatic habitat (usually seagrass) and was quantified in units of length (mangrove perimeter) rather than area. Each side of a fringing mangrove pixel with an aquatic border was included in the total for nursery habitat perimeter (i.e., a single-pixel promontory exposed to

water on three of four sides would contribute three pixel widths to the total). Mangroves were mapped using satellite imagery from the Landsat Thematic Mapper (30 m × 30 m pixels). Radiance data were converted from digital numbers to a measure of amount and physiological status using the Normalised Difference Vegetation Index. Mangroves were mapped using supervised classification with a maximum likelihood decision rule (overall thematic accuracy >80%, Mumby, unpubl. field data, n = 300). Further details on mangrove remote sensing are available elsewhere (Green et al., 1998a,b).

Adult reef fish generally exhibit their greatest density and diversity in structurally-complex forereef habitats (McCormick, 1994). In the Caribbean, the most complex habitat is built primarily by corals of the genus *Montastraea* (Mumby and Harborne, 1999) and all references to forereef hereafter refer to this habitat. *Montastraea* reefs were mapped using Landsat TM imagery. The influence of variable depth on bottom reflectance was minimised using the methods of Mumby et al. (1998). The *Montastraea* habitat was then mapped using unsupervised classification and two contextual decision rules (Mumby et al., 1998). The first classified relatively sheltered areas of forereef as *Montastraea* when located within 200 m of the escarpment. The second applied extensive field knowledge of the sites of *Montastraea* reefs based on about 1500 h experience surveying and mapping reefs in Belize.

The total perimeter of mangroves exceeded 70 km in the mangrove-rich systems and was less than 5 km in mangrove-depauperate systems. Therefore, observations from Belize and Mexico suggest that nursery impacts of mangroves differ greatly between 5 and 70 km of mangrove fringe within a region of 200 km^2. Whilst the upper level (70 km) could be used in an algorithm that searched for 'important nurseries', doing so may be unduly conservative: no data exist on the impact of intermediate levels of mangrove. To improve the criteria for the algorithm, a new threshold level of mangrove perimeter was derived based on the relationship between fish community structure on coral reefs and the availability of mangrove nursery within each reef system. The biomass of up to 162 species of reef fish was quantified at a minimum of three sites per reef system. Fish were censused using discrete group visual census (Green and Alevizon, 1989) and lengths were converted to biomass using the allometric scaling relationships of Bohnsack and Harper (1988). The mean biomass of each fish species was calculated for all sites in a reef system and square-root transformed to prevent common species overwhelming the analysis (Clarke, 1993). An ordination of community structure was then plotted using Principal Components Analysis (Fig. 1). The first principal component explained 39% of the variance in the data and was then plotted as a function of mangrove perimeter in each of the six reef systems (Fig. 2). The relationship is strongly non linear, possibly suggesting the existence of threshold levels of mangrove nursery, above which density-dependent processes on the reef (e.g., predation) may prevent further enrichment of the fish fauna. Whilst it is difficult to justify placing a line among such disparate points (Fig. 2), visual interpretation suggests that a lower threshold of about
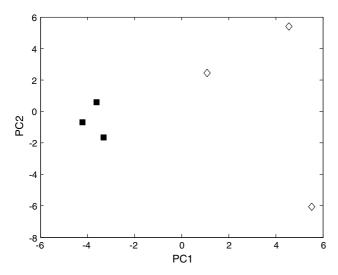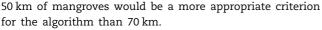
Fig. 1 – Principal Components ordination of the community structure of coral reef fishes in six reef systems throughout Belize and Mexico. Mangrove-rich systems (■) include Turneffe Atoll, Tobacco Range and Curlew Cay. Systems with scarce mangroves (◇) include Banco Chinchorro, Glovers Reef and Lighthouse Reef.

Fig. 2 – Relationship between availability of mangrove nursery habitat and the community structure of coral reef fish on outer *Montastraea* reefs. Community structure based on the mean biomass of 162 species in each reef system where each system was sampled in at least three locations. The first principal component explained 39% of variation in the data.

50 km of mangroves would be a more appropriate criterion for the algorithm than 70 km.

A criterion of 50 km of mangroves (within a region of 200 km²) needs to be set in the context of the units of measurement; in this case, pixels of 30 m × 30 m. This is because calculations of mangrove perimeter are highly sensitive to the pixel size employed; the fractal geometry of a structure leads to larger estimates of perimeter as the unit of measurement (pixel size) decreases (Sugihara and May, 1990). If mangroves were mapped using a sensor with higher spatial resolution, such as Ikonos (4 m), then a higher criterion for mangrove extent would be needed. A full list of algorithm assumptions is given in Table 2 and their implications are discussed later.
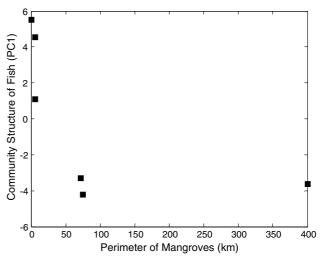
All algorithms operate on a pixel scale and can be implemented fairly swiftly when the total study area is modest (<1 million pixels). For example, the present case study from Belize was coded in Matlab and took 30 minutes to process an area of 30 km × 30 km. All algorithms provide *indices* of connectivity whose absolute values have no quantitative ecological interpretation at this stage.

Algorithm 1. Value of mangrove pixels as nursery habitats for reef fish

The first algorithm aims to identify areas of mangrove that might offer important nursery habitat for coral reef fishes and then plot the relative connectivity of such mangroves. The

Table 2 – Assumptions of algorithms for quantifying the connectivity of reef fish between mangroves and reefs	
Factor	Assumption
(1) Generality of algorithm	Caribbean-wide since the habitats and fish species concerned are generally found Caribbean-wide
(2) Nature of nursery habitat	Fringing prop roots of *Rhizophora mangle* that border submerged habitats (measured in units of length, perimeter)
(3) Nature of reef habitat	Applies to patch reefs, shallow forereefs and outer *Montastraea* reefs
(4) Fish migrations across connecting habitat	Migrating fishes can move directly between mangroves and reef habitats, passing over deep water and seagrass beds
(5) Local availability of fringing mangrove required to have net impact as a nursery	50 km per 200 km² region, where the region encompasses shallow (<30 m depth) submerged shelf around the reef. Shape is not constrained a priori and usually follows the continental shelf
(6) Maximum distance fish migrate between mangroves and reefs	10 km (based on the maximum distance observed between offshore mangrove cays and reef study sites in Belize)
(7) Scale of mangrove mapping	Carried out at ecologically-relevant scales and based on 30 m × 30 m pixels. Mangrove fringes will be overlooked at sub-pixel scales
(8) Local heterogeneity in mangrove habitat quality	Does not vary at the scale of 200 km² regions, though leeward versus seaward sites exert local influence (Mumby, unpub. data)

algorithm is implemented in five steps and provides a basis for all other algorithms.

(a) Identify fringing cells of R. mangle where at least one pixel edge borders a submerged habitat (typically seagrass).

(b) Assess each fringing cell and include as a nursery habitat if the total perimeter of fringing cells within a 200 km^2 window exceeds a critical threshold of 50 km. Dimensions of the window should conform to shallow lagoon habitats potentially capable of supporting mangroves (i.e., it would be inappropriate to include areas of deep water in preference to shallow banks). Windows applied in Belize measured approximately 10 km (longitude) by 20 km (latitude).

(c) Identify all reef cells (e.g., those of the Montastraea forereef habitat).

(d) Create a connectivity matrix between mangrove nursery cells (rows) and reef cells (columns). The connectivity, C, for cell ij is calculated using (1) where D is the maximum Euclidean migratory distance between mangroves and reefs (Table 2, assumption 6) expressed in units of pixel widths, x is the row coordinate of the mangrove cell m, and y is the column coordinate of the reef cell r.

$$C_{ij} = D - (\sqrt{(|m_{ix} - r_{ix}|)^2 + (|m_{jy} - r_{jy}|)^2}). \tag{1}$$

Connectivity is therefore weighted (linearly) such that shorter distances between mangroves and reefs result in greater connectivity. The sum of each row gives the total connectivity of mangrove cell C_{xy}, to coral reefs.

(e) Plot the total connectivity of mangrove cells to coral reefs (Fig. 3). Interpretation of this plot distinguishes mangroves that serve as important nurseries from those that do not, and identifies hotspots of nursery habitat.

The sensitivity of this algorithm to underlying assumptions (Table 2) depends largely on the seascape concerned. For example, relaxing the requirement of at least 50 km of nursery habitat within a region of 200 km^2 (assumption 5) to half this value (25 km) had no influence on the algorithm in many parts of Belize. It could, however, prove important in areas where mangroves are less abundant. Clearly, some assumptions are more important than others for any given seascape. Perhaps the most critical assumption is the migratory capacity of reef fish (assumption 6). Halving this distance from 10 to 5 km led to a virtually linear reduction (46%) in total mangrove connectivity in mangrove-rich areas of Belize such as Turneffe Atoll (total of 405 km of mangrove nursery habitat). However, areas such as Tobacco Range, which only has 75 km of nursery habitat were more sensitive to this assumption and the total connectivity of mangroves fell by 68%.

Algorithm 2. Reef connectivity to mangrove nurseries

The above algorithm assumes that fish move directly from nursery habitats to the nearest available reef (assumption 4, Table 2). In other words, those reefs closest to mangroves will tend to receive the greatest influx of new adults. This hypothesis has not been tested formally but limited field data provide qualitative support. The mean biomass of H. sciurus on patch reefs found within 1 km of a mangrove was 12-fold greater than that on patch reefs located 10 km from the same mangal (Mumby, unpubl. data from Belize). Similarly, the biomass of H. plumieri was five-fold greater in those patch reefs nearest mangroves. A formal test of this hypothesis is difficult because several factors influence the density of fish on patch reefs, such as patch shape and size (Acosta and Robertson, 2002), the density of predators, and availability of refugia (Hixon and Beets, 1993). A large-scale tagging study is required to quantify the dispersal of fishes from their nursery habitats. However, assuming that fish migrate directly between habitats, the total connectivity of each reef cell to mangrove nurseries, R, can be plotted as the sum of each column in the connectivity matrix (Table 3). Reefs with greater overall connectivity to mangroves are most likely to have higher rates of immigration from nursery habitats and potentially greater production.
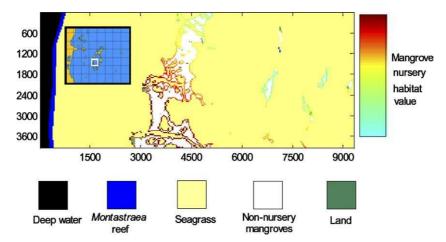

Fig. 3 – Plot of relative nursery habitat value for a section of reef on the western side of Turneffe Atoll (Belize). Plot shows major habitats plus linear interpolation for nursery habitat values from Algorithm 1. Numbers denote distances in metres.

	$R_{j=1}$	$R_{j=2}$	$R_{j=3}$	$R_{j=4}$	C_i	Calculation of MCC_i	MCC_i
$M_{i=1}$	13	13	13	13	52	$(13/81)^2 + (13/70)^2 + (13/69)^2 + (13/80)^2$	0.12
$M_{i=2}$	0	52	0	0	52	$(0/81)^2 + (52/70)^2 + (0/69)^2 + (0/80)^2$	0.55
$M_{i=3}$	68	5	56	67	196	$(68/81)^2 + (5/70)^2 + (56/69)^2 + (67/80)^2$	2.06
R_j	81	70	69	80			

Table 3 – Calculation of Mangrove with Critical Connectivity, MCC, showing a subset of a mangrove-reef connectivity matrix

Reef and mangrove areas are denoted as R and M, respectively. See text for equations.

Algorithm 3. Mangrove with Critical Connectivity (MCC)

Two areas of mangrove could have the same overall connectivity to coral reefs, C, but the form of such connectivity could be quite different. For example, one area may be positioned such that it contributes a minor level of nursery function to a large number of reefs (Table 3, $M_{i=1}$). A contrasting area may be connected to fewer reefs but contribute the majority of nursery functions to those reefs (Table 3, $M_{i=3}$). In the latter case, the mangrove provides critical nursery habitat albeit to relatively few reefs. The overall level of critical nursery habitat, MCC, for mangrove cell i can be calculated as the sum of each mangrove's proportional contribution (squared) to reef connectivity where there are n reef cells (columns) in the matrix (2). Each proportion is squared to increase the impact of larger proportions on the total.

$$MCC_i = \sum_{j=1}^{n} \left(\frac{C_{ij}}{R_j} \right)^2. \qquad (2)$$

In the worked example (Table 3), the first mangrove cell is equally connected to each reef cell but only provides a small proportion (16–18%) of the total nursery habitat to each reef cell, R. The second mangrove cell has the same overall connectivity but contributes 74% of the nursery habitat to the second reef. As a result, its overall MCC is substantially greater. The third mangrove cell has the greatest MCC because it contributes a high proportion of nursery habitat (>80%) to several reef cells. In short, the most critically-linked nursery habitats provide a high proportion of the nursery habitat to many coral reefs.

Algorithm 4. Priority sites for mangrove restoration

Mangrove restoration projects would usually aim to restore some of the ecosystem functions of mangroves which include the provision of habitat for mangrove-associated organisms, coastal defense, reduced runoff of sediments, and the provision of nursery habitat for coral reef fishes (Moberg and Ronnback, 2003). While a final selection of priority site would likely consider multiple criteria, the algorithms described here can help clarify the potential impact of restoring mangroves on the level of nursery habitat provided to coral reef fishes.

The first step is the identification of potential reclamation areas. Algorithm 1 can then be modified to treat each potential reclamation area (comprising a group of pixels) as another area of mangrove. The total mangrove connectivity of the region is then determined based on the inclusion of each

potential reclamation area in turn. Those reclamation areas that confer the greatest overall increase in region-wide mangrove nursery habitat may be considered more desirable than others. Alternatively, Algorithm 3 could be applied to each potential reclamation area thereby highlighting which reclamation sites (if any) provide critical new nursery habitat to coral reefs.

Note that potential reclamation areas would be excluded if they do not contribute to a sufficiently large perimeter of total mangrove within a region of 200 km². The main limitation of this approach is that it does not evaluate multiple arrangements of potential reclamation sites simultaneously. It requires, therefore, that potential reclamation plans can be fully specified a priori. The impact of each can then be compared having run the algorithm. If many (>20) potential reclamation sites exist and a large number of spatial arrangements are possible then an alternative approach would be required using optimisation methods such as simulated annealing (Possingham et al., 2000).

3. Discussion

The algorithms described here can be used directly for wetland, coral reef or integrated watershed management. Presenting outputs as maps allows a static interpretation and general management planning (e.g., which areas of mangroves would be highest priority to protect to maximise fisheries production on reefs). However, products of these algorithms can also be incorporated into dynamic conservation planning (Possingham, 1996). For example, the value of mangroves as nursery habitats for coral reef fish could be reconciled against a cost-surface for the prevention of coastal development within a dynamic optimisation program. Software packages that take a dynamic approach to planning and the selection of reserves include MARXAN (Possingham et al., 2000) and C-PLAN (Pressey, 1999; Margules and Pressey, 2000). Another dynamic approach would utilise the underlying connectivity matrix to establish connected corridors of habitat into a reserve design (sensu Siitonen et al., 2002). To do this, a candidate system of mangrove and reef sites is selected by the reserve selection algorithm (not described here) and then the total level of mangrove–reef connectivity evaluated from the connectivity matrix (i.e., the sum of a subset of the matrix confined to just those cells of mangrove and reef selected to be reserves). The reserve selection algorithm would attempt to maximise the overall level of connectivity for a given

constraint to reserve number and size. Whether achieving a high level of connectivity is assigned a greater weight than other conservation targets (e.g., number of habitats represented) will depend on the specific objectives of the planner, though it would seem that locking in a series of connected habitats would be a productive starting point for a reserve selection algorithm.

This paper attempts to translate the conclusions of an empirical study (Mumby et al., 2004) into practical tools for conservation. As the list of assumptions (Table 2) makes clear, understanding of mangrove–reef connectivity is limited. A mechanistic understanding of ontogenetic shifts in habitat use is required to complement emerging theory (Halpern et al., 2005). Specifically, the dynamics of reef fish communities need to be quantified within each habitat and with explicit consideration of the impact of habitat patch size and distribution. The latter requires new information on the migratory ability of fishes. How do fish search for new habitat? How far will a fish swim at a given size? What constitutes a barrier to connectivity (e.g., deep channels)? Given that settling fish larvae can hear reefs (Simpson et al., 2005), is it reasonable to assume that juveniles can swim directly between habitats rather than follow a random walk (i.e., is the use of Euclidean distance, assumption 6, justified)? With improved empirical data it will be possible to create spatially-realistic metapopulation models for coral reef fishes. A variety of spatially-realistic metapopulation models have been used in both marine and terrestrial systems (Lipcius et al., 2001; Hanski and Ovaskainen, 2003; DeWoody et al., 2005; Munzbergova et al., 2005). Outcomes of such models will highlight the sensitivity of populations to potential disturbance and management activities throughout the system (e.g., identify candidate sites for inclusion in a network of protected areas).

New information on the connectivity of reef fish among habitats will not only improve the accuracy of algorithms, but also improve their interpretation. At this stage, the outputs of algorithms are indices whose numerical value has no direct ecological interpretation. Whilst empirical data suggest that the standing crop of adult reef fish is elevated when access to nursery habitat is good, the effects on fisheries production are not yet clear. In the near term, it is certainly logical to establish connected corridors of habitat protection and the protection of adequate nursery habitat should help buffer impacts of fishing and contribute to trophic functioning of the ecosystem. However, the full ecological and economic benefits of such conservation measures are yet to be quantified and form a priority for further study.

Acknowledgements

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