

Primacy of seascape connectivity effects in structuring coral reef fish assemblages

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ABSTRACT: Connectivity has fundamental consequences for the productivity, persistence and management of coral reefs. The area and position of adjacent mangroves and seagrass can affect the demography of reef fish populations and the composition of reefal assemblages. To date, no studies have attempted to partition the influences of these habitats on reef fish assemblages. We used an exploratory seascape approach to separate the effects of connectivity with mangroves and seagrass on reef fish in Moreton Bay, Australia. We then compared the performance of seascape connectivity and reef complexity (i.e. coral cover, rugosity and area) in structuring these assemblages. Our results suggest a hierarchy of seascape connectivity effects, with reef fish assemblages being primarily distinguished by isolation (i.e. separation distance) from mangroves and secondarily by proximity (an index incorporating habitat isolation and area) to seagrass. Importantly, measures of reef complexity were only useful in separating reef fish assemblages within levels of connectivity with mangroves and seagrass. We demonstrate that neighbouring mangroves and seagrasses can exert different effects on reef fish assemblages, with 25 % of all species being primarily influenced by mangroves and a different 25 % being affected by seagrass. These findings have important implications for the design of marine reserve networks. They show that position in the seascape can be of greater significance than reef area or complexity to the composition of reef fish assemblages and highlight the value of incorporating seascape connectivity into conservation planning.

KEY WORDS: Landscape · Mangrove · Seagrass · Fish · Nursery · Australia

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INTRODUCTION

Coral reef seascapes are mosaics of seemingly disjointed habitat that are functionally connected by the movement and dispersal of organisms (Almany et al. 2009). Reefs lie within spatially heterogeneous seascapes (Pittman et al. 2011) that include other complex habitats, such as mangroves and seagrass. Reef organisms utilise a range of non-reef habitats during their lives, for example, as juvenile nurseries (e.g. Nagelkerken 2009), for foraging and sheltering (e.g. Valentine & Heck 2005) or for spawning and dispersal (e.g. Jones et al. 2009). The characteristics of the seascape (e.g. composition, arrangement and proximity of nearby habitats), therefore, can have a major

influence on the assemblages and population dynamics of organisms that inhabit coral reefs (e.g. Grober-Dunsmore et al. 2008). Connectivity between habitats may also confer reefs with resilience (Mumby & Hastings 2008), which is the capacity to absorb recurrent natural perturbations and regenerate without slowly degrading or changing state (Hughes et al. 2010). Consequently, maintaining connectivity is now a focus for the management of marine reserves (McCook et al. 2009), and the protection of seascapes with high connectivity is recommended (e.g. Adams et al. 2006). However, the combined effects of overfishing, declining water quality, habitat loss and climate change have led to the degradation of many coral reefs and may have fundamentally

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altered connectivity within seascapes (Knowlton & Jackson 2008, Bostrom et al. 2011). Accordingly, there is now a pressing need for the application of spatially explicit studies of connectivity in coral reef ecosystems (Wilson et al. 2010).

Broadly speaking, connectivity is a function of habitat area, quality and spatial arrangement and the dispersal capabilities of individual species (Hodgson et al. 2009). Landscape connectivity, which is the physical connectedness of patches in a particular landscape (Lindenmayer & Fischer 2007), can be quantified using structural connectivity metrics, which describe the spatial arrangement of habitats from benthic habitat maps (Grober-Dunsmore et al. 2009). For example, Meynecke et al. (2008b) examined multiple connectivity metrics to determine that wetland connectivity explained the greatest proportion of variation in nearshore commercial fish catches in Queensland, Australia. This approach is assumed to provide reasonable surrogates for multi-species conservation, and its inherent simplicity gives it great appeal for conservation planning and assessment (Calabrese & Fagan 2004).

The demographics of coral reef fish populations are influenced by the composition of the seascape and the spatial arrangement of habitat patches (reviewed by Grober-Dunsmore et al. 2009). This seascape connectivity can exert an influence across a range of scales, from 100s of metres for diel and tidal feeding movements (e.g. Grober-Dunsmore et al. 2007), to 10s of kilometres for ontogenetic migrations between habitats (e.g. Mumby 2006) and up to 1000s of kilometres for broader dispersal (e.g. Treml et al. 2008). Its implications for reef fish are best understood for the waters of the Caribbean, where the composition of assemblages and population demography are affected by linkages with seagrass (e.g. Grober-Dunsmore et al. 2008) and mangrove (e.g. Mumby et al. 2004) habitats. These connections can also influence other ecological aspects, namely the structure of reef food webs (e.g. Heck et al. 2008), the value of non-reef habitats as nurseries for juvenile reef fish (e.g. Nagelkerken 2009), the ecological processes on both reefs and adjacent habitats (e.g. Layman et al. 2007, Dorenbosch et al. 2009) and the performance of marine reserves (e.g. Huntington et al. 2010, Olds et al. 2012). In contrast to the Caribbean, there have been relatively few quantitative analyses of Pacific reef seascapes (Nagelkerken 2007, but see Unsworth et al. 2008 for an exception). Furthermore, no studies have yet attempted to partition the influences of connectivity with mangrove and seagrass habitats on the composition of reef fish assemblages.

Here, we adopted an exploratory seascape approach (sensu Grober-Dunsmore et al. 2008) to examine how seascape connectivity with mangrove and seagrass habitats affects reef fish assemblages in the Moreton Bay Marine Park in eastern Australia. Then, we contrasted the roles of seascape connectivity and reef complexity (i.e. coral cover, rugosity and area) in the composition of these assemblages. Moreton Bay is a large subtropical embayment south of the Great Barrier Reef (GBR) and adjacent to the city of Brisbane. It supports marginal, fringing coral reefs (Lybolt et al. 2011), dominated by massive *Favia*, *Goniastrea* and *Goniopora* colonies (Wallace et al. 2009). These reefs occur within a heterogeneous seascape that supports abundant adjacent seagrass and neighbouring mangroves (Stevens & Connolly 2005) and provide a useful study area for examining the role of seascape connectivity in structuring reef fish assemblages. We tested the hypotheses (1) that connectivity with neighbouring mangroves and seagrass will affect different components of the reef fish assemblages and (2) that the effects of seascape connectivity will exceed those of reef complexity in structuring fish abundance in Moreton Bay. We anticipated mangroves to affect the abundance of snappers (Lutjanidae), groupers (Serranidae) and bream (Sparidae) on reefs and expected seagrass to influence the abundance of sweetlip (Haemulidae), emperors (Lethrinidae), parrotfish (Scaridae) and rabbitfish (Siganidae) (based on Nagelkerken 2009, Sheaves 2009, Unsworth & Cullen 2010).

MATERIALS AND METHODS

Seascape analysis

We surveyed the fish and benthic assemblages of 16 fringing reefs in central Moreton Bay (Fig. 1), Australia (27° 15' S, 153° 15' E), between December 2009 and April 2010. Seascape connectivity was quantified from existing benthic habitat maps for Moreton Bay (source: Queensland Department Environment and Resource Management) using ArcGIS (Environmental Systems Research Institute). Coral reefs, mangrove forests and seagrass meadows in the region have been mapped to a depth of 10 m based on field surveys and interpretation of satellite and aerial imagery, at a spatial resolution of 500 m² (e.g. Dowling & Stephens 2001, Roelfsema et al. 2009). Deeper benthic assemblages (to 50 m) have been field mapped at a coarser (5 km) scale (Stevens & Connolly 2005). These differences in map scale preclude the calcula-

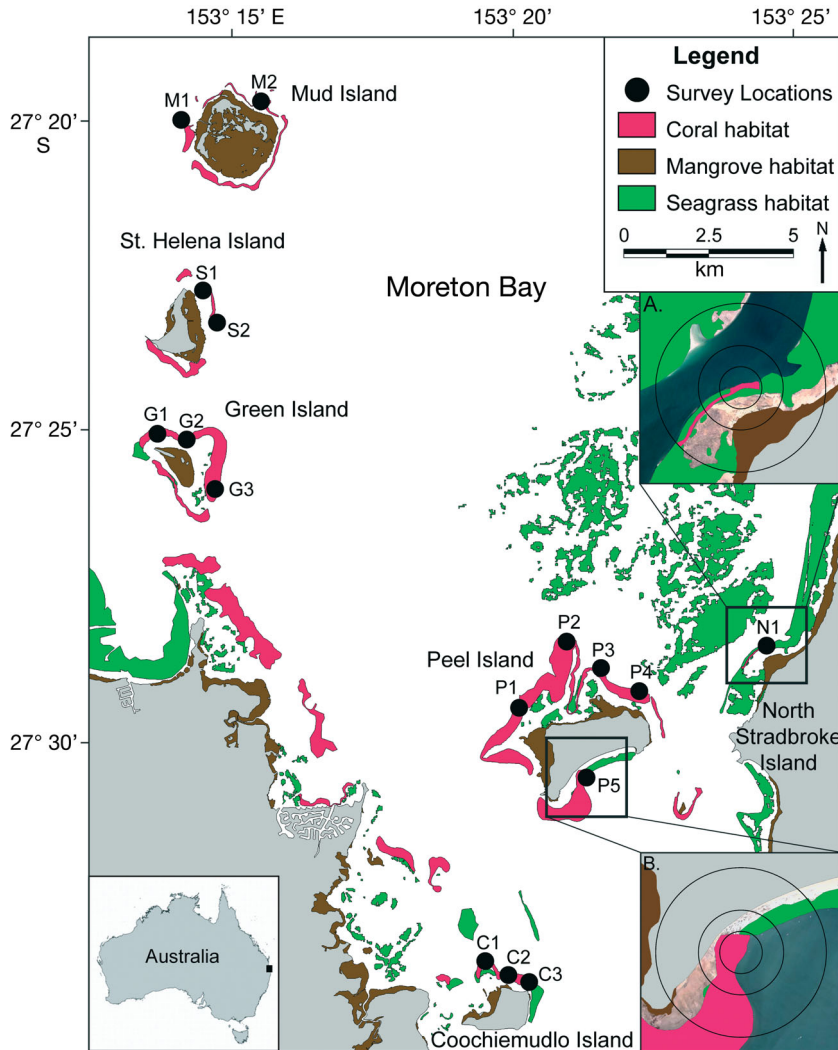


Fig. 1. Coral reef, seagrass and mangrove habitats of central Moreton Bay, Australia. Survey locations depicted as black dots over coral reef habitat. C: Coochiemudlo Island; G: Green Island; M: Mud Island; N: North Stradbroke Island; P: Peel Island; and S: St Helena Island. Insets: detailed seascapes and positioning of kernels around (A) Myora and (B) Horseshoe reefs

tion of spatial metrics across shallow and deep assemblages (sensu Kendall et al. 2011), and we focus on connectivity between shallow reefs, mangroves and seagrass. Seagrass communities support a heterogeneous mix of species but are dominated by *Zostera muelleri* (Skilleter et al. 2005). Sparse seagrass in the region declined in both cover and areal extent during the period between mapping and fish surveys (Lyons et al. 2011); consequently, all seagrass with <25% cover (cf. Roelfsema et al. 2009) was omitted from the analysis. Mangrove forests are dominated by *Avicennia marina*, with similar composition and tidal inundation across most sites surveyed (Olds et al. 2012); however, rubble banks (resulting from the prior extraction of limestone) have altered the bathymetry at

Mud and St Helena islands (Johnson & Neil 1998). Five spatial pattern metrics (Fig. 2) (reviewed by Wedding et al. 2011) were used to describe connectivity in reef seascapes: (1) isolation, the edge-to-edge distance from reefs to nearest habitats (Moilanen & Nieminen 2002), (2) area, the area of neighbouring habitats within kernels centred on each reef (Moilanen & Nieminen 2002), (3) proximity index, which incorporates the isolation and area of neighbouring habitats within kernels centred on each reef (McGarigal et al. 2002), (4) connectivity index, which incorporates the isolation and area of both reefs and neighbouring habitats within kernels centred on each reef (Kindlmann & Burel 2008) and (5) length of the connected edge (LCE), the length of shared edges connecting reefs and adjacent habitats (McGarigal et al. 2002).

Importantly, seascape studies need be scaled to the mobility of the species of interest (Grober-Dunsmore et al. 2009). We adopted a multi-scale analytical approach (sensu Pittman & Brown 2011), which is appropriate when there is insufficient information on movement and habitat use patterns and it is likely that species respond to seascape structure at different scales. We quantified connectivity metrics at scales of 250, 500 and 1000 m in kernels centred on each reef survey location (Figs. 1 & 2). These scales were chosen to encompass the daily home

ranges of many adult bream, emperor, grouper, parrotfish, rabbitfish and snapper, which are large resident components of the fish assemblages of coral reef seascapes in the western Pacific (e.g. Sheaves 1993, Zeller et al. 2003, Chateau & Wantiez 2009, Fox & Bellwood 2011). Ideally, home ranges of other species would also be included when selecting a spatial context, but movement data are lacking for other fish families in the region. The minimum scale for calculating connectivity metrics (i.e. kernel radii of 250 m) was restricted by the size of fish survey transects. It was not possible to examine seascape connectivity at larger scales to encompass ontogenetic shifts between juvenile nurseries (sensu Beck et al. 2001) and reef habitats (i.e. 10s of kilometres) (e.g. Nagel-

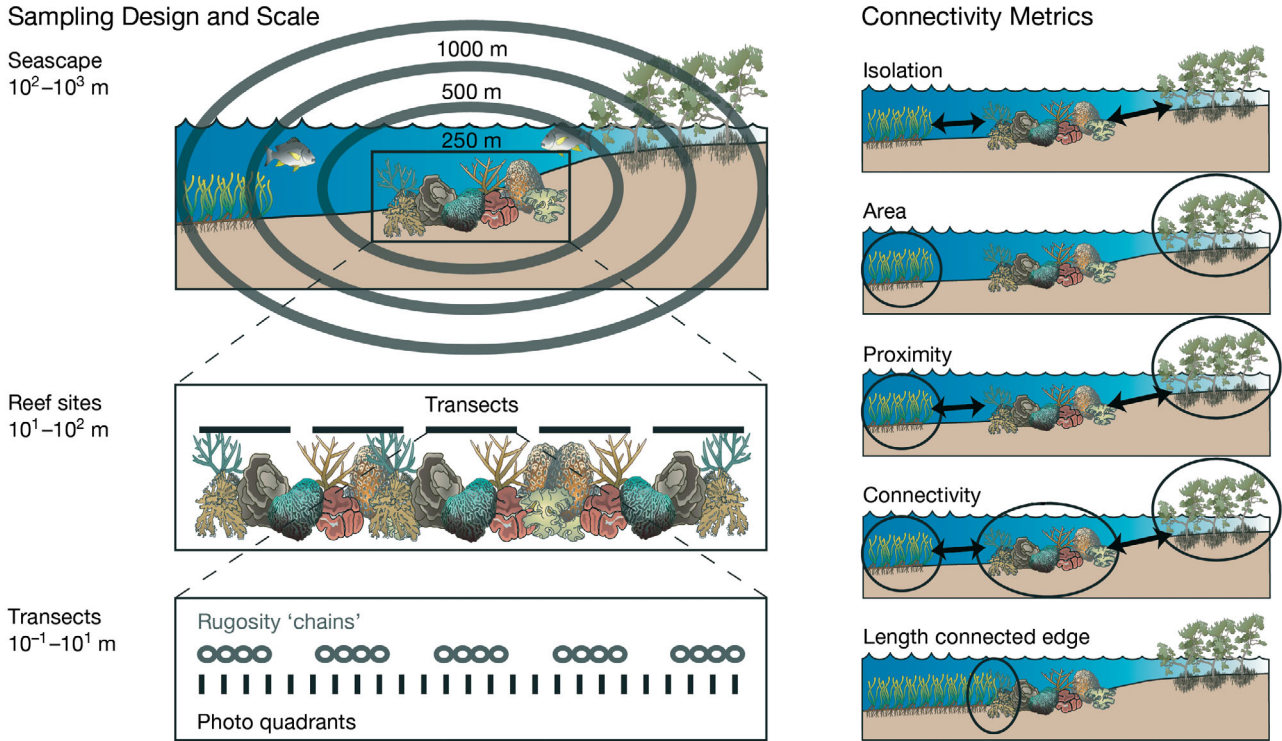


Fig. 2. Conceptual diagrams illustrating the sampling design (i.e. positioning of kernels around reefs and the nested scales of sampling) and the difference between seascape connectivity metrics (i.e. isolation, area, proximity index, connectivity index and length of the connected edge) (Symbols courtesy of the Integration and Application Network, ian.umces.edu/symbols/)

kerken 2009). The close proximity of reefs in the study area resulted in substantial overlap in the area of nursery habitats adjacent to reefs. This homogenised nursery connectivity metrics among sites at this broader (10s of kilometres) scale.

Fish surveys

Coral reef fish were surveyed using underwater visual census (UVC) (following Fulton et al. 2001). Five replicate 50×4 m belt transects were censused at each site within 2 h of low tide, when intertidal mangroves and seagrass were dry and not accessible and fish were concentrated over subtidal reefs. Transects were positioned in series along each reef and separated by a minimum of 50 m (Fig. 2). Each census consisted of a diver swimming parallel to the reef slope and recording the species and abundance of all fish with total length (TL) > 5 cm. All transects were surveyed by the same diver and positioned at depths of 1 to 3 m below the lowest astronomical tide. We examined the influence of seascape and coral reef variables on the composition of fish assemblages and assessed their effects on distribution of individual species to provide support for trends at the assemblage level.

Benthic habitat assessments

Coral reef rugosity and coral cover are important drivers of spatial variation in reef fish assemblages (e.g. Wilson et al. 2007) and were surveyed along the same belt transects used to quantify fish abundance, to describe intra-habitat variation in reef habitat among locations. Benthic assemblages were quantified by taking digital photographs of the benthos every 2 m along each transect from 0.5 m above the substrate (Fig. 2). Photographs were taken with a Canon Powershot digital camera in an Ikelite housing with an ultra wide-angle lens. Digital images were analysed for benthic cover using Coral Point Count v3.6 (Kohler & Gill 2006). A grid of 25 points was randomly overlaid on each 1 m^2 image, and the substrate underlying each point was classified as hard coral, soft coral, macroalgae, epilithic algae matrix (EAM), crustose coralline algae, coral rubble or sand. This broad classification precludes the detection of any relationships between fish assemblages and coral species composition; however, it was deemed appropriate for the fringing reefs of Moreton Bay, which support low coral diversity and are dominated by massive corals (Johnson & Neil 1998, Wallace et al. 2009, Lybolt et al. 2011). Rugosity

was assessed using the 'chain-link method' (Luckhurst & Luckhurst 1978). Briefly, a 6 m chain was draped over the substrate every 10 m along each transect to follow the natural reef contour (Fig. 2). Rugosity (r) was calculated as the ratio of distance along the reef surface contour (CD) to linear horizontal distance (LD) using $r = CD/LD$.

Data analysis and distribution modelling

Distributions of all recorded reef fish species were examined for relationships with seascape and coral reef variables using boosted regression trees (BRTs) (sensu Pittman & Brown 2011). BRTs are non-parametric machine learning algorithms that provide for sophisticated regression analyses of complex responses and are optimised for high predictive performance (Elith et al. 2008). This technique differs from conventional regression in that, rather than fitting a single 'best' model, it fits an ensemble of simple regression tree models by iteratively fitting new trees to the residual errors of their predecessors (De'ath 2007). BRTs provide superior predictive performance over conventional modelling techniques, such as generalised additive models and linear regression (Knudby et al. 2010). They can fit non-linear relationships and are robust to colinearity among predictors, their power is not reduced by the presence of irrelevant variables, and they can model interaction and threshold effects (Pittman et al. 2009). This enables the data for each species to be analysed in a single model that includes all predictor variables across the 3 spatial scales. Models were implemented using the R *dismo* software package (R Core Development Team 2012) and optimised with slow learning rates (0.0001 to 0.001) and low tree complexities (2 to 4), using 10-fold cross-validation (CV) (following Elith & Leathwick 2011) (Appendix 1). Predictor variables used to model fish distributions included reef complexity variables (i.e. coral cover, reef rugosity and reef area), seascape connectivity metrics (i.e. isolation, area, proximity, connectivity and LCE of mangroves and seagrass) and location (to account for the spatial structure of sites around islands). Interaction strength was estimated using the techniques of Elith et al. (2008). The relative contribution (%) of predictor variables to the model's predictive power and the overall patterns in fish abundance was determined using the variable importance score (Elith et al. 2008). Model discrimination was assessed using the area under the receiver operating characteristic curve (AUC) statistic. We followed Pittman and Brown (2011) and considered

AUC values of >0.9 outstanding, 0.8–0.9 excellent, 0.7–0.8 acceptable and a value of 0.5 as the predictive ability that could be achieved by chance alone.

Fish assemblage data were examined using the BEST and LINKTREE procedures with PRIMER (PRIMER-E). The BEST routine was used to identify seascape and coral reef variables that best explained patterns of similarity in reef fish assemblages (Clarke et al. 2008). Relationships between these variables and fish assemblages were then further examined using the LINKTREE test, which constructs a hierarchical dendrogram to relate environmental variables and patterns in assemblage composition, with each division being characterised by one or more variables that appear responsible for discriminating different assemblage groupings (Clarke et al. 2008). LINKTREE maximises the degree of separation between the 2 groups of samples formed at each division using the ANOSIM R statistic. Groups are, therefore, defined by similarities in their assemblage structure and separated by inequalities in associated environmental variables. Coherent groups of samples in the dendrogram were defined by SIMPROF tests at a significance level of 0.01. SIMPROF is a permutation test (we used 999 permutations) for evidence of multivariate structure among samples in clusters with no *a priori* grouping (Clarke et al. 2008). Analyses were applied to Bray-Curtis similarity matrices calculated on square-root transformed abundance data. Variables included in the environmental data matrix were the area of coral reef, reef rugosity, coral cover, reef isolation from mangroves and reef proximity to seagrass. Connectivity metrics were chosen on the basis of their performance in describing patterns in species abundance. The similarity matrix of environmental variables was calculated using normalised Euclidean distances.

RESULTS

Reef fish species and seascape connectivity

BRT provided acceptable (or better) model predictions for the distribution of 28 fish species (Table 1). Reef complexity variables were important predictors for the distribution of 14 species, including 5 butterflyfish (Chaetodontidae), 2 surgeonfish (Acanthuridae), 2 wrasse (Labridae), 2 damselfish (Pomacentridae), a cardinalfish (Apogonidae), a morwong (Cheilodactylidae) and a threadfin bream (Nemipteridae). Coral cover was of primary importance to all species and contributed between 23% (*Apogon li-*

Table 1. Important seascape connectivity and reef complexity metrics contributing to boosted regression tree (BRT) models of reef fish distribution, contributions of each predictor (%) and pairwise interactions between predictor variables. AUC: area under the receiver operating characteristic curve; CA: reef area; CC: coral cover; CR: reef rugosity; MA: mangrove area; MC: mangrove connectivity; MI: mangrove isolation; SA: seagrass area; SI: seagrass isolation; SL: seagrass length of connected edge (LCE); SP: seagrass proximity. Subscript numbers denote scale (metres). Only species with fitted models with acceptable predictive performance (i.e. AUC ≥ 0.7) are reported; all predictor variables that contributed $>10\%$ to BRT models are reported. Interaction values indicate degree of departure from additive effects, with zero indicating no interaction is present; interactions reported for all values > 1

Species	Family	AUC	Predictor 1	Predictor 2	Predictor 3	Interactions
Reef influence						
<i>Abudefduf bengalensis</i>	Pomacentridae	0.860	CC (34)	CR (20)	SP ₅₀₀ (11)	
<i>Acanthurus dussumieri</i>	Acanthuridae	0.707	CC (40)	CR (12)		
<i>Apogon limenus</i>	Apogonidae	0.867	CC (23)	CR (13)	SP ₅₀₀ (10)	
<i>Chaetodon auriga</i>	Chaetodontidae	0.826	CC (39)			
<i>Chaetodon flavirostris</i>	Chaetodontidae	0.886	CC (54)			CC & MI (1.9)
<i>Chaetodon melannotus</i>	Chaetodontidae	0.833	CC (31)	CR (21)	SL ₁₀₀₀ (11)	
<i>Chaetodon plebeius</i>	Chaetodontidae	0.824	CC (40)	CR (25)		
<i>Cheilodactylus vestitus</i>	Cheilodactylidae	0.881	CC (38)	CR (17)	SP ₅₀₀ (14)	CR & SP ₅₀₀ (1.5)
<i>Chelmon rostratus</i>	Chaetodontidae	0.891	CC (28)	CR (21)	CA ₁₀₀₀ (13)	
<i>Choerodon schoenleinii</i>	Labridae	0.704	CC (30)	SI (15)	SA ₁₀₀₀ (12)	
<i>Parma oligolepis</i>	Pomacentridae	0.904	CC (27)	CA ₅₀₀ (16)		CC & SA ₁₀₀₀ (1.6)
<i>Pentapodus paradiseus</i>	Nemipteridae	0.708	CC (31)	CA ₁₀₀₀ (10)	CR (10)	CC & CR (2.0)
<i>Prionurus microlepidotus</i>	Acanthuridae	0.715	CC (33)	CR (11)		CC & SP ₅₀₀ (1.1)
<i>Thalassoma lunare</i>	Labridae	0.903	CC (69)			CC & SC ₂₅₀ (2.3)
Mangrove influence						
<i>Acanthopagrus australis</i>	Sparidae	0.860	MC ₅₀₀ (36)	MI (11)	CC (11)	MC ₅₀₀ & MA ₅₀₀ (3.4)
<i>Atherinomorus vaigiensis</i>	Atherinidae	0.847	MC ₅₀₀ (54)	MI (18)		
<i>Epinephelus coioides</i>	Serranidae	0.827	MC ₁₀₀₀ (35)	MI (11)	CC (10)	
<i>Gerres subfasciatus</i>	Gerridae	0.927	MI (33)	MC ₅₀₀ (13)	CC (12)	MI & CR (10.4)
<i>Lutjanus fulviflamma</i>	Lutjanidae	0.895	MA ₅₀₀ (23)	CR (13)	SL ₂₅₀ (11)	
<i>Lutjanus russelli</i>	Lutjanidae	0.892	MC ₁₀₀₀ (35)	CC (13)	MC ₅₀₀ (11)	CC & CR (1.4)
<i>Siganus fuscescens</i>	Siganidae	0.871	MC ₅₀₀ (24)	MI (13)	CC (11)	MC ₁₀₀₀ & CC (1.1)
Seagrass influence						
<i>Choerodon cephalotes</i>	Labridae	0.728	SP ₅₀₀ (24)	SA ₁₀₀₀ (12)	CA ₅₀₀ (11)	
<i>Diagramma labiosum</i>	Haemulidae	0.820	SP ₁₀₀₀ (24)	CR (13)		
<i>Lethrinus laticaudis</i>	Lethrinidae	0.878	SP ₁₀₀₀ (39)	SA ₁₀₀₀ (18)	CC (11)	
<i>Lethrinus nebulosus</i>	Lethrinidae	0.837	SL ₁₀₀₀ (35)	SI (15)	CC (14)	
<i>Monacanthus chinensis</i>	Monacanthidae	0.823	SP ₅₀₀ (29)	SA ₁₀₀₀ (15)	CC (14)	SP ₅₀₀ & CC (8.5) CC & CR (3.5)
<i>Scarus ghobban</i>	Scaridae	0.865	SI (33)	CC (11)	SA ₁₀₀₀ (10)	
<i>Sphyaena obtusata</i>	Sphyraenidae	0.862	SP ₅₀₀ (57)	CR (11)		SP ₅₀₀ & CR (7.0)

menus) and 69% (*Thalassoma lunare*) to the distribution of each species. Reef rugosity was of secondary importance for 9 species (contributing 10 to 25%). Reef area (at the 500 and 1000 m scales) was also significant to 3 species (contributing 10 to 16%). In addition to reef effects, seagrass connectivity (i.e. area, isolation, LCE and proximity) was of low importance (contributing $<15\%$) to 5 species. Most species demonstrated a clear preference for reefs with high coral cover and rugosity (e.g. *Acanthurus dussumieri*; Fig. 3), but reef area and distance to seagrass were also of lesser importance to several fish. The effects of coral cover on reef fish abundance occurred over a narrow threshold, and abundance typically increased with coral cover between 10 and 30% (Fig. 3).

Connectivity with mangroves (at the 500 and 1000 m scales) was most important to the distribution of 7 reef fish species (Table 1). These included 2 snappers (Lutjanidae), a hardyhead (Atherinidae), a silver-biddy (Gerridae), a grouper (Serranidae), a rabbitfish (Siganidae) and a bream (Sparidae). Mangrove connectivity (i.e. separation distance and area of both habitats) was most important to 4 species and contributed between 35% (*Epinephelus coioides*) and 53% (*Atherinomorus vaigiensis*) to fish distributions on the reef. Mangrove isolation was also important for 4 species (contributing 11 to 33%), and mangrove area was significant to *Lutjanus fulviflamma* (contributing 23%). Reef complexity (i.e. coral cover and reef rugosity) was less important for all species (con-

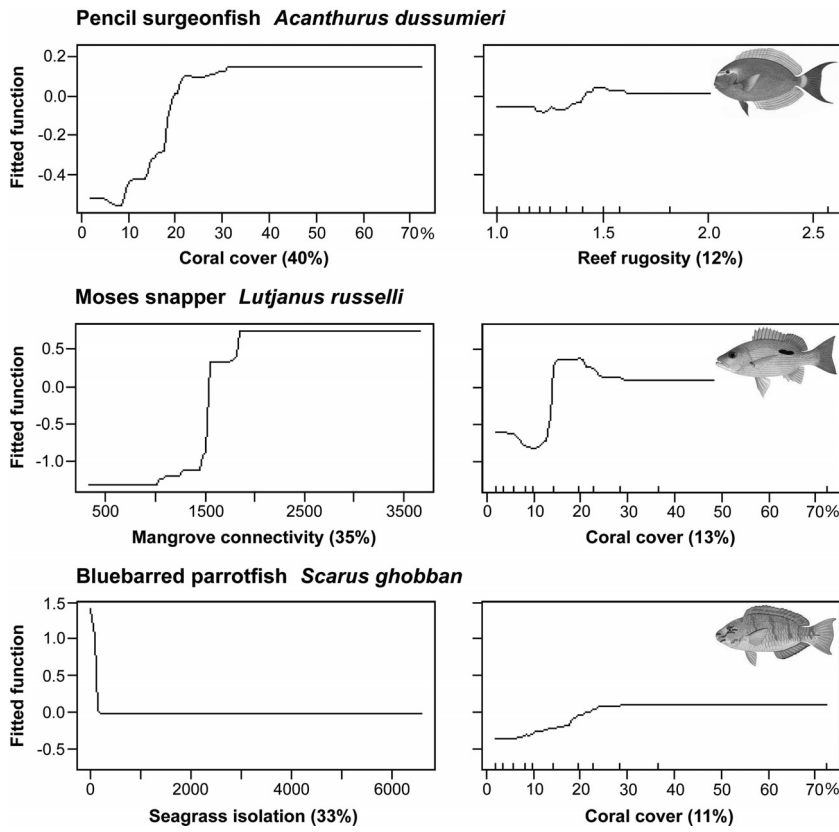


Fig. 3. Functions fitted in boosted regression trees (BRT) models relating the distribution of *Acanthurus dussumieri*, *Lutjanus russelli* and *Scarus ghobban* to the most important seascape connectivity and reef complexity metrics. The relative importance (percentage contribution) of each variable to BRT models is shown in parentheses on the x-axis (fish illustrations sourced from www.efishalbum.com)

tributing <13%). The LCE of reef with seagrass was also important to *L. fulviflamma* (contributing 11%). The distribution of these mangrove-influenced species was centred on reefs with high connectivity to adjacent mangroves, and reef complexity was less important (e.g. *Lutjanus russelli*; Fig. 3). The effects of mangroves on reef fish abundance were manifest across a narrow threshold, and abundance declined sharply as mangrove isolation increased from 350 to 500 m.

Connectivity with seagrass (at the 500 and 1000 m scales) was most important to the distribution of 7 species on reefs (Table 1). These included 2 emperors (Lethrinidae), a sweetlip (Haemulidae), a tuskfish (Labridae), a leatherjacket (Monacanthidae), a parrotfish (Scaridae) and a barracuda (Sphyraenidae). Seagrass proximity (i.e. separation distance and area of seagrass) was primarily important to 5 species and contributed between 24% (*Diagramma labiosum*) and 57% (*Sphyraena obtusata*) to fish distributions on

the reef. Seagrass area (at 1000 m) was important for 4 species (contributing 12 to 18%), seagrass isolation was significant for 2 species (contributing 15 to 29%), and seagrass LCE was important (contributing 35%) to the distribution of *Lethrinus nebulosus*. Reef complexity was less important for all species (contributing <14%). The distribution of these seagrass-influenced species was centred on reefs with high connectivity to adjacent seagrass, and reef complexity was less important (e.g. *Scarus ghobban*; Fig. 3). The effects of seagrass on reef fish abundance operated across a small range, with fish abundance increasing rapidly within 250 m of seagrass (Fig. 3).

Interactions between reef complexity and seascape connectivity predictors led to a more ecologically meaningful understanding of how multiple predictors interact to determine habitat suitability. Interactions were common among related seascape connectivity metrics (i.e. area and connectivity index) and reef complexity variables (i.e. coral cover and reef rugosity). Aside from this expected outcome, the models for *Gerres subfasciatus*, *Monacanthus chinensis* and *S. obtusata* involved the strongest interactions among predictors (Table 1). Interactions occurred

between mangrove isolation and reef rugosity for *G. subfasciatus*, seagrass proximity and coral cover for *M. chinensis* and seagrass proximity and reef rugosity for *S. obtusata*. Interactions were relatively weak for the other species examined. Fish were characterised as reef-, mangrove- or seagrass-influenced species on the basis of BRT models (see Table 1). These categories were also used for interpretation of assemblage analyses.

Reef fish assemblages and seascape connectivity

Connectivity across the reef seascape correlated well with the overall composition of reef fish assemblages. Assemblages were best explained by their isolation from mangroves and coral cover at a scale of 250 m (BEST R value = 0.373, $p = 0.01$) and by their isolation from mangroves, proximity to seagrass and coral cover at scales of 500 ($R = 0.520$, $p = 0.01$) and

1000 m ($R = 0.441$, $p = 0.01$). Importantly, the maximum assemblage correlation (i.e. greatest R value) occurred at a scale of 500 m, and this provided the focus for subsequent LINKTREE analyses.

LINKTREE analysis produced a 7-leaf dendrogram to describe the influence of environmental variables (i.e. connectivity and reef complexity metrics) on the composition of reef fish assemblages (Fig. 4). Overall, the analysis demonstrated strong agreement with the BEST analyses but also illustrated a hierarchy in the relative importance of seascape connectivity and reef complexity variables. Highest order divisions among fish assemblages reflected isolation from mangroves, middle order splits related to proximity to seagrass, and all lower order partitions correlated with reef habitat variables (refer to coloured separations in Fig. 4). This suggests that reef fish assemblages in Moreton Bay were characterised first by their isolation from mangroves and then by their proximity to seagrass. This is visualised by the separation of sites into clusters based on their spatial relationship with

both mangroves and seagrass. For example, reef fish assemblages at 4 sites (M2, S1, P1 and P4) were distinguished by being close to mangroves (<250 m) and far from seagrass (Fig. 4: *high mangroves, low seagrass* clusters). Assemblages at 3 sites (N1, C2 and G2) were characterised by being close to mangroves and close to large seagrass meadows (Fig. 4: *high mangroves, high seagrass* clusters) (site N1 was closer to a larger seagrass meadow). In contrast, assemblages at 4 sites (C1, C3, G1 and P5) were distinguished by being far from mangroves (>500 m) and close to large seagrass beds (Fig. 4: *low mangroves, high seagrass* clusters) (site C1 was further from mangroves and closer to a larger seagrass meadow). Assemblages at 5 sites (M1, S2, G3, P2 and P3) were characterised by being far from mangroves and far from seagrass (Fig. 4: *low mangroves, low seagrass* clusters).

Reef complexity (i.e. reef area and coral cover) had a lesser effect than seascape connectivity on the composition of reef fish assemblages (i.e. these variables

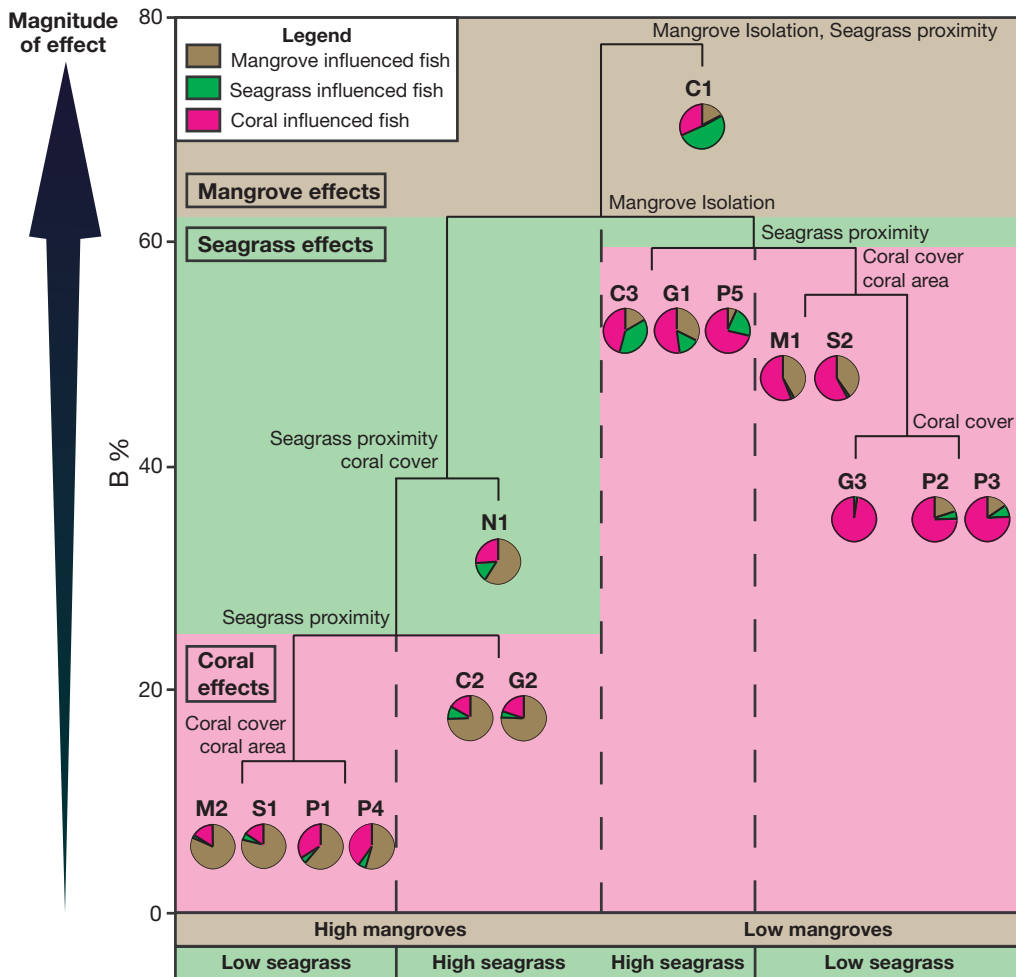


Fig. 4. Linkage tree (LINKTREE) of fish abundance from 16 reef locations. Plot displays tree divisions for which SIMPROF tests were significant ($p < 0.01$); factors responsible for divisions are provided above each division. B% (between-group separation scaled to 100) provides an absolute measure of group differences across divisions and a measure of the relative strength of seascape effects. Pie charts below terminal nodes display proportions of assemblages influenced by each habitat. High/low mangrove and high/low seagrass divisions denote reef assemblages with high/low connectivity to mangroves and seagrass, respectively. C: Coochie-mudlo Island; G: Green Island; M: Mud Island; N: North Stradbroke Island; P: Peel Island; and S: St Helena Island

were responsible for splits lower on the dendrogram) but had a greater influence on reefs further from mangroves (Fig. 4). The magnitude of this effect is visualised in Fig. 4 using pie charts, which represent the proportion of total fish abundance comprised of mangrove-, seagrass- and reef-influenced species. There were clear differences in assemblage composition among locations with different levels of connectivity with mangroves and seagrass, but little variation among locations on the basis of differences in coral cover or reef area.

DISCUSSION

The importance of adjacent habitats to reef fish populations has long been recognised. Early studies examined the ecology of off-reef feeding migrations (e.g. Randall 1965); more recently, research has focused on the role of seascape ecology in structuring reef fish assemblages (Grober-Dunsmore et al. 2009). Our findings show that there is a hierarchy in the correlation of reef fish assemblages with seascape connectivity. The composition of reef fish assemblages in Moreton Bay is primarily distinguished by their isolation from mangroves, secondarily by their proximity to seagrass, and only by reef habitat variables within each level of seascape connectivity. This result supports studies from the Caribbean, which have shown that the abundance, biomass and richness of reef fish species can be influenced by linkages with adjacent seagrass (e.g. Valentine et al. 2007, Nagelkerken et al. 2008) and mangrove habitats (e.g. Mumby et al. 2004, Nagelkerken 2007). It agrees with the conclusions of Grober-Dunsmore et al. (2008), who found that the area of neighbouring seagrass was more important to reef fish abundance than reef complexity. It also supports the findings of Pittman & Brown (2011), who demonstrated that a reef's cross-shelf location can be more important to fish distributions than its topographic complexity. This finding cautions against management approaches that seek to conserve fish assemblages by focusing on reef structural complexity and is particularly relevant to the broader utility of remotely sensed fish-habitat relationships in coral reef ecosystems (reviewed by Mellin et al. 2009). We provide evidence that mangrove and seagrass habitats can indeed exert different effects on reef fish assemblages. This is manifest through species-specific relationships with different habitats and scales of seascape connectivity. Consequently, the magnitude of these effects might be expected to vary across different seascapes. In par-

ticular, reef habitat variables might be more important on reefs that are more isolated or support greater coral diversity. However, we hypothesise that their effects may also be additive, with reefs in highly heterogeneous seascapes with high connectivity to both mangrove and seagrass habitats and high coral cover supporting greatest fish diversity and abundance. To strengthen this evidence for connectivity, we would ideally have also examined reefs lacking adjacent mangroves and seagrass, but this arrangement of habitats was not present in the studied system. Nevertheless, our findings support recommendations for adopting multi-scale hierarchical approaches when characterising the environmental drivers of reef fish biomass and diversity (e.g. MacNeil et al. 2009, Mellin et al. 2010a, Pittman & Brown 2011). They have obvious implications for how we visualise connectivity in reef seascapes and important ramifications for how connectivity is coalesced into a management framework that seeks to both promote connectivity (Steneck et al. 2009) and enhance reef resilience (Hughes et al. 2010). This assertion is supported by recent findings that fish assemblages on small, isolated reefs may have higher temporal variability and lower resilience than those from larger, more connected reefs (Mellin et al. 2010b).

Our results imply that the principles of landscape ecology (*sensu* Forman & Godron 1986), which have been applied in the reef seascapes of the Caribbean, warrant further investigation in the Pacific region. The spatial context of reefs relative to mangrove and seagrass habitats is important for the composition of reef fish assemblages in the Caribbean and Indian Ocean (reviewed by Grober-Dunsmore et al. 2009, Berkström et al. 2012), but there have been few comparable quantitative analyses on Pacific reefs (Nagelkerken 2007). Beger & Possingham (2008) determined that isolation from the nearest estuary was a good predictor of reef fish distribution in Papua New Guinea. Similarly, Olds et al. (2012) demonstrated that connectivity with mangroves promoted the ability of marine reserves in Moreton Bay to enhance fish abundance. The focus of other studies in the Pacific, however, has been on assemblages in the seagrass (e.g. Jelbart et al. 2007, Unsworth et al. 2008) and mangrove (e.g. Pittman et al. 2004, Payne & Gillanders 2009) habitats themselves. Our results suggest that seascape influences in the Pacific may affect reef fish from the same families as in the Caribbean (i.e. Haemulidae, Lutjanidae and Scaridae) (e.g. Nagelkerken 2007). It seems logical, therefore, that seascape connectivity may also structure ecological processes (e.g. Mumby & Hastings 2008) and food webs (e.g.

Heck et al. 2008, Nagelkerken et al. 2008) on Pacific reefs. However, given the geographic imbalance in studies of seascape connectivity (Nagelkerken 2007), there is now a need for further research testing the validity of these concepts across the wider Pacific. Furthermore, our results illustrate thresholds in the effects of mangrove and seagrass connectivity on reef fish abundance, with dramatic changes in fish abundance occurring with small decreases in mangrove (from 350 to 500 m) and seagrass (below 250 m) isolation. These thresholds concur with the scale at which diel and tidal connectivity is known to influence reef fish assemblages in the tropical Caribbean and Indian Ocean (e.g. Bostrom et al. 2011, Berström et al. 2012) and have important implications for conservation planning and marine reserve design (sensu Olds et al. 2012).

For reefs in Moreton Bay, the primacy of mangrove connections over seagrass linkages and the performance of different metrics in describing these connections (i.e. isolation and connectivity with mangroves and proximity to seagrass) point to differences in their roles as fish habitat. Mangroves in Moreton Bay are used tidally by adult and sub-adult mangrove-influenced reef fish but support few juveniles of these species (e.g. Tibbetts & Connolly 1998, Olds et al. 2012). Blackspot snapper *Lutjanus fulviflamma*, Moses snapper *L. russelli* and goldspotted rockcod *Epinephelus coioides* recruit to mangrove-lined creeks and shallow reefs as juveniles and migrate tidally to feed in mangroves before moving to offshore reefs at larger body sizes (e.g. Blaber 2000, Sheaves & Molony 2000, Newman 2002, Meynecke et al. 2008a). Juvenile *L. fulviflamma* are also common in seagrass (Igulu et al. 2011). Yellowfin bream *Acanthopagrus australis* and black rabbitfish *Siganus fuscescens* recruit to seagrass, move to reefs (and other structurally complex habitat) as sub-adults (e.g. Griffiths 2001, Mellin et al. 2007, Meynecke et al. 2008a) and migrate tidally to feed in mangroves in Moreton Bay (Olds et al. 2012). Common hardyhead *Atherinomorus vaigiensis* and common silverbiddy *Gerres subfasciatus* also migrate tidally into mangroves to feed and seek refuge from predators (e.g. Laegdsgaard & Johnson 2001). These fish use tidal streams to maximise time at the mangrove fringe, a pattern of mangrove use that is common for large mobile fish in tidal systems the world over (e.g. Sheaves 2009). Juvenile seagrass-influenced reef fish are common in seagrass adjoining the reefs in Moreton Bay, as are juveniles of some mangrove-influenced species (e.g. Tibbetts & Connolly 1998, E. Stone unpubl. data). Juvenile purple tuskfish

Choerodon cephalotes, grass and spangled emperor *Lethrinus laticaudis* and *L. nebulosus*, fanbelly leatherjacket *Monacanthus chinensis* and yellowtail barracuda *Sphyraena obtusata* occur in seagrass and migrate to reefs (and other structurally complex habitat) at larger sizes but often forage over seagrass (e.g. Blaber & Blaber 1980, Warburton & Blaber 1992, Wilson 1998, Fairclough et al. 2008). Similarly, painted sweetlip *Diagramma labiosum* and bluebarred parrotfish *Scarus ghobban* recruit to shallow seagrass and adjacent reefs, move to reefs as adults and feed in adjacent seagrass and soft-bottom habitats (e.g. Dorenbosch et al. 2005a,b, Mellin et al. 2007, Grandcourt et al. 2011). It is difficult to separate the potential drivers of these seascape linkages (e.g. ontogenetic or feeding migrations), but given the size distribution of fish in each habitat (and the habitat requirements of each species), we speculate that mangroves in Moreton Bay are important foraging locations for reef fish, while the value of seagrass primarily reflects its use as a juvenile nursery (sensu Beck et al. 2001). A potential differentiation of ecological roles among these 2 nursery habitats, however, would have significant implications for the way we conceptualise and manage nurseries for juvenile reef fish.

Our results suggest a hierarchy in the correlation of reef fish assemblages with seascape connectivity, with composition being primarily driven by isolation from mangroves, secondarily by proximity to seagrass and then by reef habitat variables within each of these connectivity groups. We demonstrate that mangrove and seagrass habitats can exert different effects on reef fish assemblages and have more influence on reef fish abundance than the complexity of the reef itself. These findings have important implications for the design of marine reserve networks, the way we conceptualise nursery habitats for juvenile reef fish and the management of mobile exploited populations across reef seascapes. They show that position in the seascape can be more significant than reef area or complexity to the composition of reef fish assemblages and highlight the value of incorporating seascape connectivity into conservation planning.

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Appendix 1. Optimal settings and predictive performance of boosted regression tree (BRT) models. NT: number of trees; LR: learning rate; TC: tree complexity; AUC: area under the receiver operating characteristic curve. Only species with fitted models with acceptable predictive performance (i.e. $AUC \geq 0.7$) are reported. The bag fraction was set at the default 0.50 for all models (bag fraction controls the level of stochasticity in BRT models and specifies the proportion of data to be selected at each step)

Species	NT	LR	TC	AUC	Species	NT	LR	TC	AUC
<i>Abudefduf bengalensis</i>	5700	0.0007	3	0.860	<i>Epinephelus coioides</i>	2550	0.0009	2	0.827
<i>Acanthopagrus australis</i>	5800	0.0006	3	0.860	<i>Gerres subfasciatus</i>	9400	0.0005	3	0.927
<i>Acanthurus dussumieri</i>	1000	0.0009	3	0.707	<i>Lethrinus laticaudis</i>	3800	0.0005	3	0.878
<i>Apogon limenus</i>	5200	0.0007	3	0.867	<i>Lethrinus nebulosus</i>	6350	0.0004	4	0.837
<i>Atherinomorus vaigiensis</i>	9250	0.0002	2	0.847	<i>Lutjanus fulviflamma</i>	6050	0.0005	3	0.895
<i>Chaetodon auriga</i>	3800	0.0006	3	0.826	<i>Lutjanus russelli</i>	3950	0.001	3	0.892
<i>Chaetodon flavirostris</i>	8700	0.0003	3	0.886	<i>Monacanthus chinensis</i>	8000	0.0005	3	0.823
<i>Chaetodon melannotus</i>	6150	0.0004	3	0.833	<i>Parma oligolepis</i>	7950	0.0007	3	0.904
<i>Chaetodon plebeius</i>	3200	0.0008	3	0.824	<i>Pentapodus paradiseus</i>	2050	0.0009	3	0.708
<i>Cheilodactylus vestitus</i>	5950	0.0006	3	0.881	<i>Prionurus microlepidotus</i>	4000	0.0006	3	0.715
<i>Chelmon rostratus</i>	3850	0.0009	3	0.891	<i>Scarus ghobban</i>	6500	0.0006	3	0.865
<i>Choerodon cephalotes</i>	1500	0.001	2	0.728	<i>Siganus fuscescens</i>	8350	0.0005	3	0.871
<i>Choerodon schoenleinii</i>	8850	0.0001	4	0.704	<i>Sphyaena obtusata</i>	9650	0.0004	3	0.862
<i>Diagramma labiosum</i>	6800	0.0003	3	0.820	<i>Thalassoma lunare</i>	3850	0.0009	3	0.903