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Defining critical habitats of threatened and endemic reef fishes using a multivariate approach

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Abstract: *Understanding critical habitats of threatened and endemic animals is essential for mitigating extinction risks, developing recovery plans and siting reserves but assessment methodologies are generally lacking. Here, we evaluated critical habitats of eight threatened or endemic fish species on coral and rocky reefs of subtropical eastern Australia, by measuring physical and substratum-type variables of habitats at fish sightings. We employed nMDS, mMDS, ANOSIM, SIMPER, PERMDISP and other novel multivariate tools to distinguish critical habitats. Niche breadth was widest for two endemic wrasses and reef inclination was important for several species, often found in relatively deep microhabitats. Critical habitats of mainland reef species included small caves or habitat-forming hosts such as gorgonian corals and black coral trees. Hard corals appeared important for reef fishes at Lord Howe Island and red algae for mainland reef fishes. A wide range of habitat variables are required to assess critical habitats owing to varied affinities of species to different habitat features. We advocate assessments of critical habitats matched to the spatial scale used by the animals and a combination of multivariate methods. Our multivariate approach furnishes a general template for assessing the critical habitats of species, understanding how these vary among species and determining differences in the degree of habitat specificity.*

Keywords: critical habitat, extinction risk, conservation planning, coral reef, sponges, algae, threatened species, marine

Introduction

Critical habitats: a key to marine conservation

In recent decades, the protection of habitats that are essential to threatened and exploited marine species has become integral to an ecosystem approach to management (Hagen & Hodge 2006). Habitat loss is one of the key factors associated with known extinctions and near extinctions of marine species (Dulvy et al. 2003; Reynolds et al. 2005). Knowledge about critical habitats is vital for conservation planning. For example, optimal places to site marine reserves should be in locations that encompass much of the critical habitat for a species or groups of species (Lindeman et al. 2000). Comparisons of critical habitats across species at risk could identify groups of species that are likely to benefit from protection of the same habitat.

Certain microhabitats may be at elevated risk from broad-scale threats, such as climate change effects, or localised threats such as anchor damage or pollution discharge. Understanding critical habitats of marine biota thus underpins conservation measures for habitat protection that aim to reduce extinction risk in threatened species (Reynolds et al. 2005) and recovery plans to restore populations (Lundquist et al. 2002). Protecting critical habitats of threatened species can also be a legal requirement of resource managers but designating these for marine animals has often proved complex and contentious (Hagen & Hodge 2006).

Some endemic fishes with restricted ranges are relatively uncommon and/or ecologically specialised, thereby exposing them to greater risks of extinction (Hobbs et al. 2011). Coral reef fishes are potentially at risk to losses in coral cover and reef structures through ocean acidification, and thermally-induced coral bleaching events (Hoegh-Guldberg et al. 2007). On subtropical reefs, loss of kelp and other habitat-forming algae from rising seawater temperatures also poses a significant threat to benthic habitats (Hobday et al. 2006).

One conservation objective is to identify critical habitats or areas of particular importance for threatened taxa (Pogonoski et al. 2002). Information on critical habitats of threatened species within subtropical eastern Australia (24–38°S) is a significant knowledge gap (Rule et al. 2007). Within this region, a mosaic of habitat types supports high endemism and diversity of species (Harriott et al. 1994), and threatening processes like climate change are especially serious (Hobday et al. 2006). For example, Lord Howe Island (159°E, 31°S) is a World Heritage site that hosts around 16 endemic reef fishes (Hobbs et al. 2009).

Evaluating critical habitats of marine species

An important research need for conservation is the evaluation of whether habitats used by a species are varied or quite specific (Hobbs et al. 2010). Narrow niche breadth, reflecting ecological specialisation (Krebs 1999), is known to predispose fishes to greater risks of extinction (Munday 2004; Wilson et al. 2006). Hence, niche breadth among species from a habitat-use perspective can be a useful indicator of comparative extinction risk.

Assessment of critical habitats requires measurement of a range of environmental and biotic variables. Surface structural complexity ('rugosity') appears to improve species richness and fish community biomass in some cases (Gratwicke & Speight 2005; Friedlander et al. 2007). Reef slope and depth can also be key determinants for certain marine animals (e.g. Ingram & Rogan 2002). Fish communities may also relate to the coverage of various sessile biota and substratum types on reefs (Friedlander et al. 2007).

We consider *critical habitats* as the specific microhabitats selected by the threatened and endemic species as places to live in, breed or settle (*sensu* Pogonoski et al. 2002). Descriptions of critical habitats

at a coarser resolution of macrohabitats are arguably too general because fish associate with habitat features at a finer scale and conservation management may need to act upon finer scales (Friedlander et al. 2007; Lindsay et al. 2008). However, because scales of habitat niches (*sensu* 'ecological neighbourhoods', Wiens 1989) differ among species, studies of interactions between species and their environment may be particularly sensitive to scaling. Thus conservation of key species or critical habitats may target particular microhabitats or landscape fragments for management (Wiens 1989). Critical habitats are defined by a combination of biophysical variables; hence field measurements and analyses that identify them need to apply a multivariate approach. Few examples exist of how this can be achieved for specific threatened and endemic fishes, which can be uncommon or rare and not conducive to sampling by randomly placed quadrats or transects within suitable macrohabitats.

Our study aimed to demonstrate the utility of a novel approach for assessing critical habitats of threatened or endemic reef fishes, employing a combination of existing and new multivariate statistical tools, and exemplified for two localities from subtropical eastern Australian reefs. We consider *threatened* species to include species listed as critically-endangered, endangered and vulnerable (IUCN 2010) and include species legislated by state or national bodies as protected, vulnerable or threatened. We studied a range of fish species from six families but our multivariate approach will furnish a template more generally for assessing the critical habitats of species, understanding how these vary among species and determining differences in the degree of habitat specificity.

Materials and methods

Study sites

We collected data at two subtropical localities: the mainland coast of northern New South Wales (NSW) and the Lord Howe Island (LHI) offshore reefs (Fig. 1). We selected the totality of field sites on the basis of accessibility and reported sightings of the focal species by recreational and research divers, and were then able to verify sightings of focal species and measure habitat features during our dives.

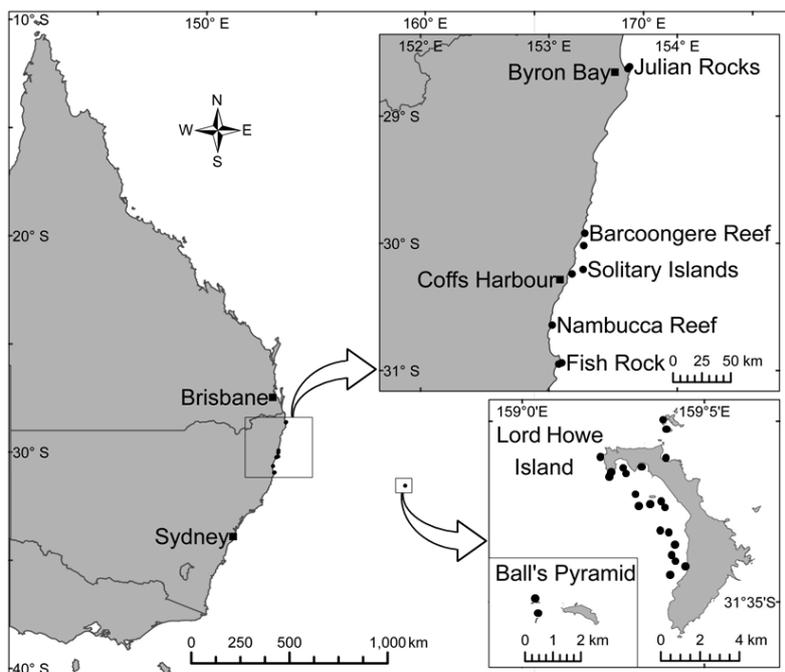


Figure 1. Map of study sites along the mid-eastern mainland coast of Australia and at Lord Howe Island. Sites could have one or multiple surveys of habitats of the focal species.

The mainland coast sites comprised rocky subtidal reefs, including boulder reefs, semi-exposed steep and shallow reef slopes and soft-bottom zones. For a few mainland-coast reef surveys, photographs of focal species from other researchers and recreational divers confirmed the precise sighting location (to ± 20 cm), which we later surveyed even if the fish was no longer present. Searches and surveys at LHI were spread over various subtidal reef macrohabitats, including protected lagoon reefs, reef passages, rocky reefs, semi-exposed steep and shallow reef slopes, seagrass beds and soft-bottom zones. At both localities, we attempted to spread survey effort similarly across all available reef macrohabitat types and depths. Both localities have rocky reefs with corals but only LHI has true coral reefs (Harriott et al. 1995). Otherwise, both localities experience a comparable range in annual seawater temperatures, have reefs with algae and various sessile invertebrates, caves and crevices, and reef habitats at various depths and with varying slopes. Searches for any of the focal fish species comprised SCUBA dives across depth profiles of 2–30 m and tows of divers behind boats in 1–8 m to cover large tracts of reef and lagoon habitats. Based on published life-history information (e.g. Kuitert 1993), the searched habitats comprised those used by both adults and juveniles. Apart from some specific locations within sites where rare species have been previously observed, our study sites were not chosen for particular species and we searched for all of the eight focal species at each site. When one of the focal species was found, it was observed and its habitat surveyed (described below). Including the search and survey periods, the sampling effort on the mainland coast reefs was 71 person dive hours and at LHI was 108 person dive hours.

Focal species

Selection of our fish species was based on their listing as threatened or protected under the NSW Fisheries Management Act 1994, or whether they were endemic to the study region. Although we searched for all eight species at both localities (replication given below, [*n*]), four species occur predominantly, and were found, at the mainland coast sites and the other four occur predominantly, and were found, at LHI reefs and nearby offshore reefs.

Species on mainland coast reefs: Most seahorse and pipefish species (Syngnathidae) and ghost pipefishes (Solenostomidae) are ‘data deficient’ (IUCN 2010) and protected under state legislation. We pooled data on seahorse species, *Hippocampus* spp. [3]. Ornate ghost pipefish, *Solenostomus paradoxus* [7], is widely distributed but uncommon in the subtropics (Kuitert 1993). Sawtooth pipefish *Maroubra perserrata* [14] and eastern blue devil *Paraplesiops bleekeri* (Plesiopidae) [14] are endemic to subtropical eastern Australia (Kuitert 1993) and protected by state legislation.

Species on LHI reefs: Double-header wrasse *Coris bulbifrons* (Labridae) [26] is considered vulnerable (IUCN 2010), and is endemic to LHI, Norfolk Island and offshore reefs (Randall & Kuitert 1982). Elegant wrasse *Anampses elegans* (Labridae) [17] is protected and found predominantly at LHI (Randall & Kuitert 1982) with limited sightings at Northern New South Wales reefs. Lord Howe Island butterflyfish *Amphichaetodon howensis* (Chaetodontidae) [9] and half-banded angelfish *Genicanthus semicinctus* (Pomacanthidae) [3] are endemic to LHI and may be vulnerable due to small population size, restricted distribution and reliance on vulnerable habitats (Hobbs et al. 2009).

Measurements of critical habitats

Delineating habitat areas

The study species on the mainland coast were site attached and did not move more than 1.5 m from sighting points during daytime observations. Two 3-m-long transect lines were laid in a cross in north-

south and east-west orientation centred on each sighting point. All data for each replicate sighting were collected within a circular area bounded by the transects.

At LHI sites, we located and immediately observed the fishes for 6 min, indicated as an optimal duration by a pilot study (Appendix S1). We visually estimated their fork length (FL) subsequent to diver training (Appendix S2). These estimates allowed us to partition, and assess whether separate analyses were required for, juveniles and adults. Apart from one juvenile *P. bleekeri*, we only found and observed juveniles of *C. bulbifrons* (<18 cm FL, via distinctive colour morphs) and *A. elegans* (<12 cm FL, approximated size-at-first-maturity). We observed fish movement during the 6-min periods while maintaining a distance of at least 4 m from the fishes, which appeared to not affect their normal behaviour. Fish that swam large distances during the observation period were followed discretely at a distance of about 8–10 m. Thereafter, we placed perpendicular measuring tapes on the substratum to delineate an elliptical area in which the fish moved, which was then used for measurements of habitat variables. A minimum habitat diameter of 3 m was employed for relatively stationary fish.

Physical variables

At each sighting, at both the mainland coast and LHI, we recorded depth, surface structural complexity and reef slope. Depth was measured to nearest 0.1 m with a dive computer, and surface structural complexity using the ‘rope and chain’ method (Luckhurst & Luckhurst 1978). Following another pilot study (Appendix S3), a maximum length of 15 m was used for either axis. For site axes <15 m, the complexity measurement was taken along the entire length and divided by the actual length of the axis. The average of the two axis measures was used for analyses.

Reef slope (inclination), at the scale of >1 m, was measured using an inclinometer, consisting of a 1-m rod attached to a protractor and a pivoting spirit level. The maximum slope at each sighting point was determined to the nearest degree from horizontal. For areas >3 m diameter, we used an average of measurements from the four site markers and at the transects’ intersection. For areas of 3 m diameter, one measurement was taken.

Substratum-type variables

Using an Olympus C-5050 digital camera, we took ten photographs (after Harrison & Smith 2012) of the substratum at pre-defined random coordinates within each delineated habitat area, re-scaled approximately to the dimensions of each habitat area. A 50-cm rod attached to the camera housing maintained a constant distance to the substratum with an image size of 0.2 m².

Photographs were analysed using Coral Point Count (CPCe) software by allocating 20 random points per photo and visually identifying one of 11 substratum types underlying each point. Recently dead hard corals were categorised here as bare substratum. This photographic sampling characterises the entire area used by the fish. In cases where the fish was attached, or hovering within 10 cm to a single habitat-forming plant or animal, the ‘host’ was identified and its height measured to ± 1 cm.

Statistical analyses

All variables were square-root transformed and physical variables were placed on comparable units to substratum-type variables by individually rescaling them to (0–10). Ranges for 11 substratum-type variables totalled 75, and for physical variables 30, implying a weighting of 2.5:1 in favour of the former in similarity calculations.

The appropriate similarity measure for quantitative cover data is Bray-Curtis (Clarke et al. 2006). In contrast, continuous physical variables are not ‘quantities’ and are on different scales, so normalised

Euclidean distance is usually appropriate. However, rescaling of the physical variables allows the merged variable set to be input to Bray-Curtis computation. Bray-Curtis similarities also permit a natural breakdown of variable contributions to within-species similarities (SIMPER, Clarke 1993), a breakdown with no natural counterpart for Euclidean distances.

ANOSIM tests (Clarke 1993) were used to demonstrate differences in occupied habitats (niche overlap) between focal species and, for two species, between juveniles and adults. There were sufficient replicates for all but two species for viable pairwise tests, even with Bonferroni corrections (i.e. utilising a severe $p < 0.001$ criterion). As replication is unbalanced, the pairwise R statistic itself is more revealing than its significance in assessing extent of niche overlap (Clarke & Warwick 2001). SIMPER identified habitat variables strongly associated with each species (to a cumulative contribution of $>50\%$ to average within-species similarity); high average similarity of habitat within species indicates greater specialisation (narrower niche breadth). Such differences (in multivariate dispersion) were formally tested by PERMDISP (Anderson et al. 2008) and displayed by nMDS ordination at the replicate level.

To summarise mean differences in habitat type for the eight species, a metric-MDS (mMDS) ordination was constructed from averages of transformed habitat variables over all samples for each species. This fits linear regression of between-sample distances in the ordination against matching resemblances, rather than using the monotonic regression of nMDS, and avoids the problem here of nMDS 'collapsing' the eight points unrealistically into three groups. This is a well-known difficulty with nMDS when all dissimilarities between groups of points are larger than any within-group dissimilarities, since the rank orders of the dissimilarities (the only information used by nMDS) will then not provide sufficient constraints to determine the ordination positions. With such few points, the generally inferior mMDS is often acceptable, judged by standard criteria (Clarke & Warwick 2001).

Superimposed on the mMDS is a segmented bubble plot, with segment sizes representing averaged variable values (on original scales) for each species, allowing juxtaposition of habitat variables distinguishing the different species. This allows more accurate interpretation than for conventional vector plots, which unrealistically assume linear relationships of habitat variables to ordination axes.

Standard multivariate analyses, nMDS, ANOSIM, SIMPER and PERMDISP, were performed with the PRIMER-6 software (Clarke & Gorley 2006) and its PERMANOVA+ add-on (Anderson et al. 2008); the novel combination of mMDS and segmented bubble plots used an alpha development version of PRIMER-7.

Results

Critical habitats

The eight fish species had widely different associations with habitat variables and the nMDS illustrates both overlap and segregation in their critical habitats (Fig. 2). ANOSIM revealed significant preferences for specific habitats on a global test ($R=0.35$, $p<0.001$), with paired comparisons showing large differences for many species (Table 1). However, *P. bleekeri*, *S. paradoxus* and *M. perserrata* were only separated with low pairwise R values, at weak significance levels (and not at all if Bonferroni corrections were made). Similarly, though ANOSIM indicated a significant difference between *A. elegans* and *C. bulbifrons*, resulting from the large numbers of replicates of both species, this is again a weak effect (low R), the most notable feature of their habitat associations being the wide niche breadths seen in Fig. 2. This is also evident from PERMDISP, which significantly separated just two groups of species in terms of dispersion of their habitat variables: (in rank order) *A. elegans*, *C. bulbifrons*, *S. paradoxus* and *A. howensis*, with wide niche breadths, and *P. bleekeri*, *M. perserrata*, *Hippocampus* spp. and *G. semicinctus*, with a greater niche specificity. Microhabitat use did not differ

significantly between adult and juveniles for *C. bulbifrons* ($R=0.06$, $p=0.22$) and *A. elegans* ($R=-0.12$, $p=0.89$).

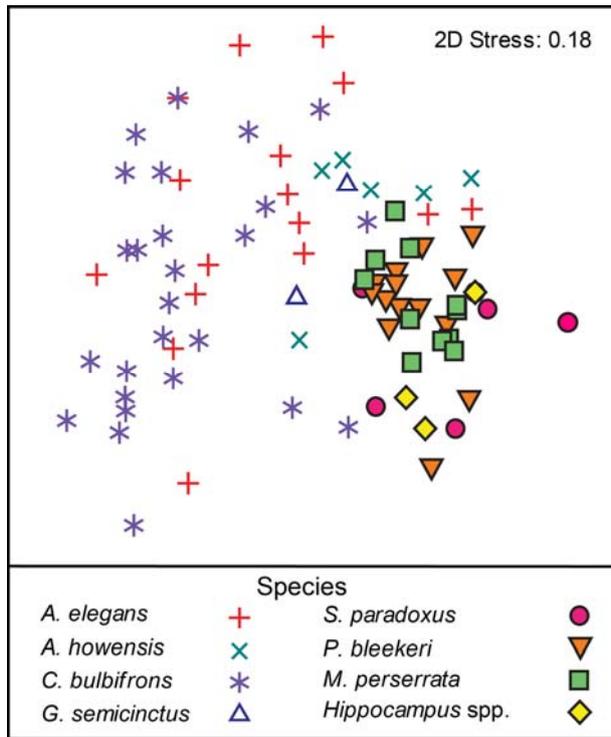


Figure 2. Non-metric multidimensional scaling (nMDS) of the Bray-Curtis resemblance matrix for the habitat data collected for eight focal species at the mainland coast (open symbols) and Lord Howe Island (closed symbols). The ordination displays the separation in critical habitats of the focal species. Sighting points close to one another have similar critical habitats.

Table 1. Pairwise R values and significance levels from the analysis of similarities (ANOSIM) test of occupied habitats between the eight fish species.

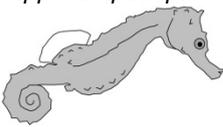
	<i>A. howensis</i>	<i>C. bulbifrons</i>	<i>G. semicinctus</i>	<i>S. paradoxus</i>	<i>P. bleekeri</i>	<i>M. perserrata</i>	<i>Hippocampus</i> spp.
<i>A. elegans</i>	0.22*	0.13**	0.02ns	0.43***	0.54***	0.53***	0.40**
<i>A. howensis</i>	-	0.43***	0.02ns	0.46***	0.58***	0.71***	0.74**
<i>C. bulbifrons</i>	-	-	0.22ns	0.58***	0.58***	0.62***	0.65***
<i>G. semicinctus</i>	-	-	-	0.49*	0.83***	0.98***	1.00ns
<i>S. paradoxus</i>	-	-	-	-	0.24*	0.29*	0.03ns
<i>P. bleekeri</i>	-	-	-	-	-	0.10*	0.65**
<i>M. perserrata</i>	-	-	-	-	-	-	0.58**

ns = not significant, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

The SIMPER analysis indicated the dominant variables whose relatively consistent values define the habitat for each species (Table 2), and the mean values of those variables are seen on the mMDS ordination as superimposed bubble segments summarising mean habitat conditions for each species (Fig. 3). The focal species at LHI (*C. bulbifrons*, *A. elegans*, *A. howensis*, and *G. semicinctus*) were all consistently associated with hard coral, which averaged 12–14% cover across those four species. *A. elegans* and *C. bulbifrons* were found in relatively shallow waters with turf algae, hard coral and shallow reef slopes (averaging 23° and 17°, respectively), but *A. elegans* tended to occur with red algae (Fig. 3a) whereas *C. bulbifrons* were commonly found in sandy habitats (Table 2; Fig. 3a). *A. howensis* and

G. semicinctus also occupied roughly similar habitats, typified by depth, turf algae and hard coral (Fig. 3; Table 2). Habitats occupied by *A. howensis* tended to have steeper reef slopes (52°) and were structurally complex (Fig. 3a) compared to those at sightings of *G. semicinctus*, which had high percentage coverage of other invertebrates (Table 2; Fig. 3b).

Table 2. SIMPER analysis of the key habitat variables that contributed 50% of the similarity contributions among replicates within each fish species.

Species	Group % similarity	Key variables	% Similarity contribution
<i>A. elegans</i> 	61.7	Turf algae Red algae Hard coral Reef slope	15.6 13.9 13.3 11.7
<i>C. bulbifrons</i> 	62.6	Sand Turf algae Hard coral Reef slope	20.1 15.7 12.8 8.5
<i>S. paradoxus</i> 	69.0	Depth Reef slope Red algae	21.7 19.7 13.3
<i>A. howensis</i> 	73.1	Depth Turf algae Reef slope Hard coral	18.2 14.1 12.6 10.3
<i>Hippocampus sp.</i> 	75.5	Depth Red algae Sponge	23.8 19.5 10.0
<i>P. bleekeri</i> 	78.5	Reef slope Depth Red algae Sponge	22.8 16.7 9.9 8.9
<i>M. perserrata</i> 	79.8	Reef slope Depth Red algae Sponge	17.9 15.7 12.6 9.3
<i>G. semicinctus</i> 	84.5	Depth Other Inverts Hard coral Turf algae	24.8 10.7 10.1 10.0

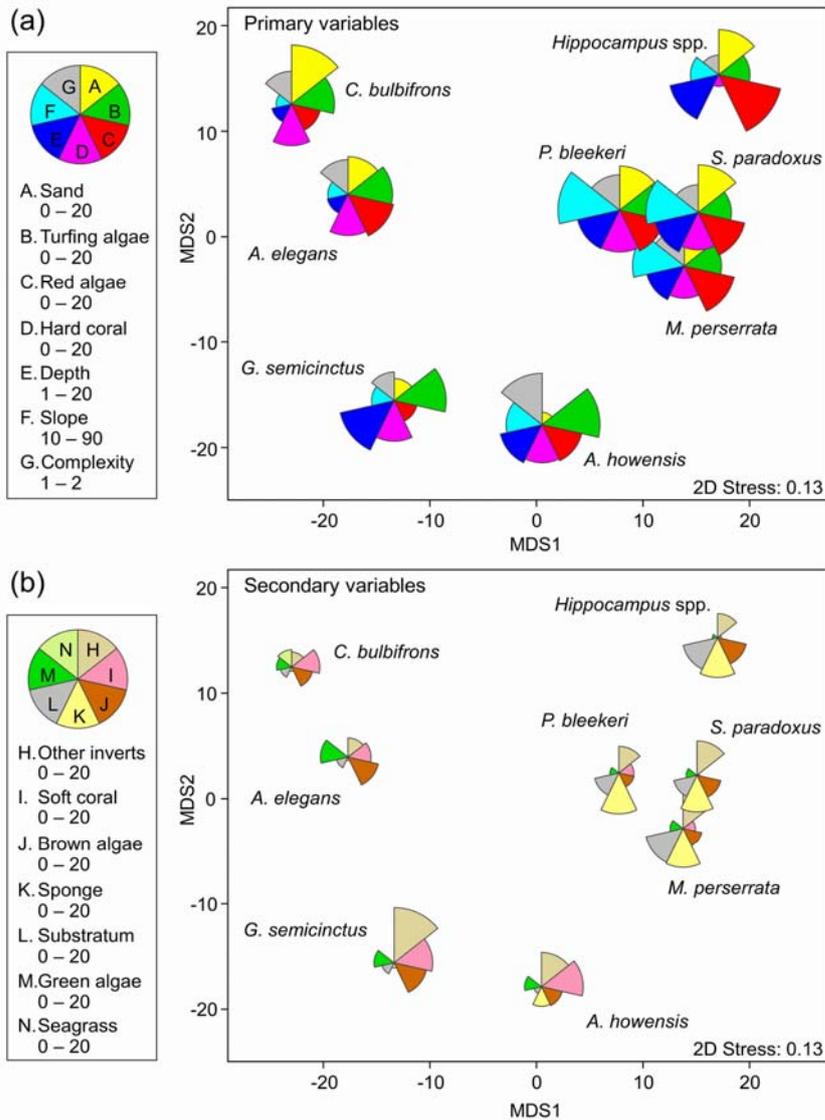


Figure 3. Segmented bubble plots on a metric multidimensional scaling (mMDS) ordination of ‘average habitat’ for each species, the latter based on Bray-Curtis similarities from habitat variables that were transformed, rescaled, then averaged across all surveyed sightings for each of the 8 focal species. (a) Primary variables, those 4 substratum variables with the largest cover overall, plus the 3 physical variables; (b) secondary variables, the remaining 7 cover variables (though less dominant overall, some are good discriminators between species). Segment sizes are proportional to averaged habitat variable values on original scales, and therefore in the original units. The ‘substratum’ category is a composite of bare rocks, rubble and recently dead coral.

Three of the mainland reef species occurred in relatively similar habitats, with strong associations with depth, steep reef slopes (many of them greater than 90°, denoting an overhang or cave), and high surface coverage of red algae and sponges (Table 2; Fig. 3). However, sightings of *P. bleekeri* were generally in shallow caves (<2 m wide) whereas *M. perserrata* were mostly observed in shallow crevices in reef walls. Hard corals were common at some sightings of *M. perserrata*, *S. paradoxus* and *P. bleekeri* (averages: 9–15% cover; Fig. 3a), but did not greatly discriminate their critical habitats (Table 2). *Hippocampus* spp. and *S. paradoxus* were found in relatively deep waters, averaging 16 m (SE 2) and 20 m (SE 4), respectively.

Habitat-forming ‘host’ organisms were poorly represented by photographic data because they were solitary and thus occurred in, at most, one of ten photographs per sighting. Five of the six *S. paradoxus* and two of the three *Hippocampus* spp. were adjacent to black coral trees (*Antipathes* spp.) or gorgonian sea fans (e.g. f. Isididae, Plexauridae, Subergorgiidae). Black coral trees hosting *S. paradoxus* averaged 94 cm in height.

Habitat specificity

Habitat generalists can be described as those species with a broad spread of observations in the nMDS (Fig. 2) and relatively low group similarity from SIMPER (Table 2). Relative to the other species, the two wrasses were habitat generalists and their wide niche breadths overlapped considerably in habitat space. This finding is probably most reflective of adults, which comprised the majority of our replicates. In contrast, *G. semicinctus*, *M. perserrata* and *P. bleekeri* had the narrowest niche breadths.

Niche overlap and segregation is illustrated in the nMDS ordination (Fig. 2) and pairwise ANOSIM *R*-values (Table 1). For example, habitats occupied by *M. perserrata* were most similar to those occupied by *P. bleekeri* ($R=0.10$) and most different from habitats at sightings of *G. semicinctus* ($R=0.98$). Caution is needed in interpreting the *R*-values and significance levels in cases of low replication, e.g. comparisons involving *G. semicinctus*. For unbalanced cases, the significance level reflects the very different numbers of sightings for each of these species, and a better guide to distinctiveness of their habitat variables is given by the *R* values themselves.

Discussion

Assessment of critical habitats

Both physical and substratum-type variables were important in describing the key features of critical habitats of the fishes. Our study shows the utility of habitat variables that are widely measurable such as reef slope, which varied greatly among habitats of the eight species (Fig. 3). Standardisation of habitat variables across geographic localities and species allows comparisons of habitat breadth and overlap among all focal species. We also advocate that habitat measurement scales should ideally match the spatial habitat-use scales for each species. With an understanding of their relation to fish communities, microhabitat features that are measurable in the field can provide a basis for locating marine reserves (Friedlander et al. 2007; Lindsay et al. 2008).

The key variables in defining critical habitats in this study were depth, reef slope, and areal coverage of hard coral, red algae and sponge. Depth was the easiest variable to measure. Reef slope was also rapid to measure *in situ*. Underwater photography offers a fantastic tool for estimating substratum types but office-based processing can incur significant human-resource costs (Molloy et al. 2013). Optimal replication of photographs and points per frame will depend on the scale and diversity of the habitats, the photographic area covered and the required resolution of habitat classifications.

Surface structural complexity can be a strong predictor of reef fish communities (McCormick 1994; Friedlander et al. 2007), but this was not the case in this study and we note that surface complexity measurements are time consuming. The coverages of soft coral and brown algae were also relatively unimportant in discriminating critical habitats, despite being common at the study sites.

A suite of multivariate analyses was needed to understand critical habitats of species and how they differ within and among species. Previous work has linked fish communities to reef habitat types, via ANOSIM tests and other routine multivariate analyses, in the context of conservation planning (e.g. Friedlander et al. 2007; Lindsay et al. 2008). Here, though, we have employed standard multivariate routines combined with novel, or rarely seen, techniques, such as: a) merging ‘quantity-type’ cover variables with physical ones in a single matrix with common scaling (whilst maintaining natural differential weighting of cover variables); b) mMDS for accurately displaying relationships among a small number of (averaged) samples; c) associated segmented bubble plots, allowing both visualisation of a holistic multivariate analysis, in the ordination points, and the contributions of individual variables to that synthesis.

More typically, population survey methods are applied to link habitats to certain communities or species, in which fish are counted and habitat variables are measured along randomly placed belt transects (e.g. Friedlander et al. 2007; Lindsay et al. 2008; Hobbs et al. 2009). The mismatch of randomly placed transects and rare/uncommon species is obvious. Moreover, a fish may associate with habitats at one end of a transect but not the other, leading to false correlations with habitat variables. In contrast, we employed a distinctive ‘reverse architecture’ of sampling, in which habitats are measured where the fish are found and the multivariate analyses are a synthesis of habitat variables associated with a specific fish, rather than of species variables associated with a specific habitat. The SIMPER analysis identifies key variables contributing to similarity of microhabitat within species, and therefore does not require random samples of surrounding habitats, which would at least double the sampling effort.

Different variables define critical habitats for different species

Critical habitats could be typified by affinities of our fish species to certain algae, habitat-forming fauna, reef structures and depth. A key finding is that a diverse array of variables needs to be measured because species have widely different affinities to features of marine habitats.

Habitat-forming fauna were important features for a majority of the fishes in this study. Hard corals were prominent in the habitats occupied by the fishes at LHI. These species may seek shelter under them and might be vulnerable to climate-related losses of hard coral in the future (Wilson et al. 2006; Hoegh-Guldberg et al. 2007). For example, 95–98% of LHI lagoon hard corals were seriously affected by a recent thermal bleaching event (Harrison et al. 2011).

S. paradoxus and *Hippocampus* spp. associated closely with gorgonian sea fans or black coral trees, likely for refuge. Black corals and gorgonian sea fans have slow life histories and are susceptible to physical damage (Bavestrello et al. 1997; Carreiro-Silva et al. 2013). Hence, the threatening processes are more likely to be from divers, anchors and fishing traps and nets.

Steep topographic (structural) features and depth were the most influential physical variables. This finding could be used in marine reserve planning if resource managers have fine-scale information on reef topography at candidate sites. Likewise, such information could improve the design of artificial reef structures to include steep slopes and caves of various sizes.

Habitat segregation and specialisation

This study showed broad overlap and distinct segregation of the habitats occupied by threatened and endemic reef fishes. We did not collect the threatened and endemic fishes to examine dietary resources, so our interpretations concern only habitat niches. Our ‘reverse architecture’ of sampling and analysis differ from classical methods of measuring niche breadth using proportions of individuals found in, or using, a resource category (Levins 1968; Krebs 1999).

The widest niche breadths were found in two fishes most locally abundant: *A. elegans* and *C. bulbifrons*. At local scales, microhabitat specialisation in wrasses correlates with low abundance (Berkström et al. 2012). We acknowledge that the broad habitat specificity of the two wrasses studied may be partially explained by ontogenetic variation in habitat selectivity, as also shown for reef damselfishes (Wilson et al. 2008). Nonetheless, our results concur with the notion that abundant endemic species are often not ecologically specialised and this may confer some resilience to extinction (Hobbs et al. 2010). However, these endemics with small geographic distributions may still be at risk from stressors operating at larger scales (Hobbs et al. 2010).

Habitat specialists are especially prone to biotic disturbances on reefs (Munday 2004; Wilson et al. 2006). *M. perserrata* and *P. bleekeri* were relatively specialised but associated strongly with crevices

and small caves, which are not under threat. Hence, species with such associations with abiotic features of coarse reef structure might be more resistant to disturbances that affect sessile benthic communities.

Limitations

The habitat areas used by these fishes are probably larger than estimated here. We did attempt to sample evenly across resource states (Krebs 1999), i.e. available habitats. However, other habitats not assessed (e.g. deeper than 30 m) may be used by the animals at other times of the day or year.

The determination of critical habitats is limited by the resources and technological capacity of the data collection program. A large range of variables to describe habitats means less replication of individuals for analyses: choice of habitat variables is a trade-off between time, cost, usefulness and practicality. For example, while current regime and average wave surge could have been useful discriminating variables, field costs of deployed instruments and revisits to sites precluded this. However, a wide range of variables should be used where data can be acquired cost-effectively.

Management implications

Principal conservation uses of information on critical habitats are: (1) a better understanding of a species' vulnerability to population decline; (2) mitigation measures to preserve critical habitats; and (3) siting of reserves; as part of (4) recovery plans for affected or threatened species. Threatening processes that can degrade critical reef habitats include: climate change effects on sessile flora and fauna; pollution, increased nutrients and sediment discharge; physical damage through natural events and human disturbances; and invasive and alien species (Pogonoski et al. 2002; Wilson et al. 2006). In this regard, knowledge on the affinities of threatened species to biotic features of habitats provides justification for investment in mitigation measures to preserve these habitat features. Our findings show that both algal and invertebrate communities need protection to safeguard critical habitats of a range of threatened and endemic reef fish species.

In the context of this study, planning of management measures to mitigate habitat degradation on reefs should especially consider potential effects on hard corals, red and turfing algae and sponges. Protection of sensitive habitat-forming biota such as black coral trees and gorgonian corals through restrictive use of anchors and potentially destructive fishing gears is also legitimized by our findings. Comparisons of habitat affinities using multivariate tools can better assign species to niche groups (e.g. *M. perserrata*, *S. paradoxus*, *P. bleekeri*) and might aid in prioritizing regulatory measures and siting of reserves that benefit multiple species at risk. In the present study, fishers only target *C. bulbifrons* and illegal extraction of other species by aquarists is probably minimal. However, more importantly, our work gives support to the siting of marine reserves to include critical habitats of threatened species that are exploited, with marine reserves also serving to restrict other local stressors such as pollution discharge or anchoring, which can affect biotic habitats.

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Supporting Information

Pilot studies determining appropriate observation durations for fish-monitoring (Appendix S1), fish-length estimation (Appendix S2) and measuring reef complexity (Appendix S3) are available online. Queries should be directed to the corresponding author.

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