



Microhabitat selectivity underpins regional indicators of fish abundance and replenishment



Christopher J. Fulton^{a,*}, Mae N. Noble^a, Ben Radford^{b,c}, Christopher Gallen^d, David Harasti^d

^a Research School of Biology, The Australian National University, Canberra, ACT 2601, Australia

^b Australian Institute of Marine Science, Crawley, 6009 WA, Australia

^c School of Earth and Environment, University of Western Australia, Crawley, 6009 WA, Australia

^d NSW Department of Primary Industries, Port Stephens Fisheries Institute, Locked Bag 1, Nelson Bay, NSW 2315, Australia

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ABSTRACT

Species with specialized resource use can display strong spatial heterogeneity in abundance according to the availability of their preferred habitats. If these preferences shift with ontogeny, then a wide range of habitats may need to be protected in order to support both adult populations and their replenishment. We explored whether microhabitat selectivity interacts with habitat availability to provide an effective suite of indicators for regional fish abundance and replenishment, using offshore rocky reefs in south-eastern Australia as a case study. We examined generalized additive mixed models (GAMMs) in a full subsets approach to infer the best predictors for adult and juvenile fish density in four diverse families (Labridae, Odacidae, Pomacentridae, Serranidae), based on rapid underwater visual surveys across transects (~500 m²), wave exposures (0.3–1 km), and sites (0.3–48 km). We then examined whether these regional fish-habitat models aligned with the microhabitat electivity of individuals (at scale of <1 m²). Microhabitat selection by reef fishes at the local scale underpinned the most effective habitat indicators for regional heterogeneity in fish abundance, and pointed to critical nursery habitats that support hotspots of juvenile recruitment. Strong species-habitat relationships, such as these, can be combined with broad-scale habitat mapping to assess the potential carrying capacity of focal areas, spatial management zone placements, and nursery habitats that warrant special protection. A number of emerging threats to these key habitat types indicates an urgent need for habitat-based protection and monitoring as a key part of holistic marine ecosystem conservation and management.

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1. Introduction

Understanding how environmental heterogeneity shapes patterns of biodiversity across local to regional scales remains an ongoing priority for ecologists and natural resource managers (Malcolm et al., 2012; Smale et al., 2010; Werner et al., 2014). Alongside the need to understand species assembly rules in ecosystems, rising concerns over climate change and habitat loss (e.g. marine heatwaves, Wernberg et al., 2013; tropicalization, Vergés et al., 2014) are driving an urgency to identify key indicators that can inform spatial conservation, management and monitoring approaches (e.g. Gladstone, 2007; Malcolm et al., 2012; Werner et al., 2014). However, a crucial challenge has been uncovering scal-

able mechanisms that link environmental heterogeneity with the patterns and processes that maintain populations and communities (Kneitel and Chase, 2004; Ricklefs, 1987).

In diverse assemblages where species exhibit specialized resource use, their patterns of distribution and abundance should reflect spatial and temporal variations in their preferred resource (Brown et al., 1995; Gregory and Gaston, 2000). Among marine fishes, we often find a diversity of preferences for different biotic and abiotic habitats (e.g. Choat and Ayling, 1987; Jones, 2013; Morton and Gladstone, 2011). When there is spatial heterogeneity in habitat availability, such habitat selection can shape species abundances over local to regional scales (Morris, 1988; Resetarits, 2005). Fish habitat preferences can also shift with ontogeny, where fishes utilize a range of habitats to complete tripartite life cycles (e.g. Green, 1996; Harasti et al., 2014). Accordingly, juvenile-preferred microhabitats can identify critical nursery habitats that

* Corresponding author.

E-mail address: christopher.fulton@anu.edu.au (C.J. Fulton).

support population replenishment (Beck et al., 2001; Sheaves et al., 2015).

Evidence-based planning and management of ecosystems often requires spatial indicators of biodiversity (Gladstone, 2007; Malcolm et al., 2012), which have often been investigated at coarse scales via remote sensing and large-scale mapping of species over broad abiotic gradients (e.g. wave exposure, depth; Leaper et al., 2012) and/or mesohabitat categories (e.g. “reef”, “sand”; Moore et al., 2011). In reef fishes, these studies have revealed significant relationships between abundance, diversity and coarse spatial habitat heterogeneity. Although this has illustrated the utility of such species-habitat modeling, large amounts of unexplained variation often remain in many coarse-scale models. Fine-scale models that encompass habitat variation at local scales where microhabitat selection occurs (e.g. individual foraging ranges spanning 10 s or 1000 s of metres) could help resolve much of this unexplained variation (e.g. Cameron et al., 2014; Curley et al., 2002; Tuya et al., 2011). Moreover, the potential for ontogenetic microhabitat shifts suggests life history stage-specific models may be needed to reveal the range of mechanisms by which habitat availability can provide a multi-scale predictor of reef fish community structure.

Here, we explore the extent to which measures of microhabitat occupation and availability can provide effective indicators for understanding and managing regional patterns of rocky reef fish diversity, abundance, and replenishment. Using the Port Stephens region (New South Wales, Australia) as a case study, we utilized rapid underwater visual surveys at scales relevant to the patchiness of rocky reef benthic habitats and fish foraging ranges (Barrett, 1995; Jones and Andrew, 1990; Morton and Gladstone, 2011), to assess multi-scale variations in fish density and habitat availability within and among transects (~500 m²), wave exposures (0.3–1 km), and offshore reef sites (0.3–48 km). We focused upon four reef-associated fish families (Labridae, Odacidae, Pomacentridae, Serranidae) that encompass species of ecological and/or fisheries importance, and have previously been found to be good surrogates for representing the majority of rocky reef fish diversity (Malcolm and Smith, 2010). We applied full-subsets model selection to (1) determine which types of habitat availability can best explain the distribution and abundance of adult and juvenile fishes across these spatial scales, and then (2) examine whether species-specific fish habitat-abundance relationships aligned with patterns of microhabitat selectivity from our observations of fish microhabitat use (<1 m²).

2. Materials and methods

2.1. Study region

Twelve offshore sites (0.3–48 km apart) were selected within the Port Stephens Great Lakes Marine Park to encompass eight offshore reefs spread across 48 km of coastline (Fig. 1a). Sites were balanced among wave exposed (south-east aspect) or sheltered (north-west aspect) positions, since wave exposure strongly influences rocky reef fish community composition in this region (Fulton and Bellwood, 2004). Sites were also chosen for their similar bathymetry and hard substratum complexity within the target depth range (6–9 m), which was typically a moderate to steeply sloping reef face dominated by bedrock and/or boulders.

2.2. Field surveys

Visual surveys were conducted in March 2013 to estimate benthic habitat composition alongside the density of demersal reef fishes from four families (Labridae–20 species, Odacidae–2 species, Pomacentridae–8 species, Serranidae–3 species; Fig. 1b–e). Surveys

were done at this time of year because it is typically when new fish recruits are present in this region (Curley et al., 2002; Lincoln Smith et al., 1991; Morton and Gladstone, 2011). Surveys involved a triple-pass belt transect method developed after Lincoln Smith (1989) that started with a diver taking a 10 min timed swim along the reef contour within a depth strata of 6–9 m, which is the zone of greatest overlap in reef fish species and habitat types (Curley et al., 2002; Fulton and Bellwood, 2004; Morton and Gladstone, 2011), to record the estimated total length (TL, to nearest cm) of all conspicuous fish individuals encountered within a 5 m wide band. A return pass over the same transect area was used to record the estimated TL of cryptic fishes encountered by systematically searching within the macroalgae canopy, corals and/or rocky crevices within the same 5 m band. Benthic habitat composition was estimated and recorded on a third pass of the transect, using the plan view method of Wilson et al. (2007). This method involved the diver visually estimating the percent cover of all habitat categories visible beneath them in a 5 m wide by 10 m long section (when hovering 3 m above the reef) at the beginning, middle and end of each transect, which were aggregated to yield a single percent cover estimate for each benthic habitat category per transect. Eleven functional categories of habitat were recorded, including the biotic components of erect macroalgae (>30 cm canopy height, principally *Ecklonia*, but also some *Phyllospora* and *Sargassum*), foliose macroalgae (2–30 cm canopy height, mainly *Haliptilon*, *Amphiroa*, *Delisea*, *Lobophora*), turf macroalgae (<2 cm canopy height), sponges, corals (*Pocillopora*), and pyurids (*Pyura*, *Herdmania*), as well as the abiotic sediment classes of bedrock, boulders, rocks, gravel, and sand (following Wentworth, 1922). A prominent marker was placed at the beginning and end of each transect on the first pass to facilitate repeat passes. Measurements by tape measure indicated a mean transect length of 107 ± 8 m (± standard error, n = 6), hence each replicate surveyed ~535 m² of reef. Three replicate sets of belt transects, separated by a minimum of 50 m, were performed by the same observer (CJF) at each site during daylight hours (08:00–16:00) when underwater visibility was at least 7 m.

Concurrent assessments of fish microhabitat use were made across the same sites by three SCUBA divers, which involved swimming a non-overlapping path across the reef and recording the fish species, estimated TL and nearest benthic habitat type immediately beneath each individual encountered, following Fulton et al. (2001). If fish were in a school, only one observation was recorded for a random individual in the school. A total of 3396 individual records were made across all sites for 20 fish species (<10 total records were made for the 13 rare species in the assemblage). During each day of surveys the observers used a cross-check method to validate their underwater size estimates, which involved estimating the length of six or more benthic features (e.g., rock, coral head) to the nearest cm and comparing this against the actual size (measured by ruler) to check there were no significant differences in estimated versus actual lengths.

2.3. Data analyses

Of the 33 species recorded in the visual surveys, the three tropical vagrants *Macropharyngodon meleagris* (Valenciennes 1839), *Cheilio inermis* (Forsskål 1775), *Chrysiptera notialis* (Allen 1975), and *Coris sandageri* (Hector 1884) were represented by just a single individual, and so were excluded from further analyses. Spatial structure in rocky reef habitat composition and the fish community were examined using permutational multivariate analyses of variance (PERMANOVAs; Anderson et al., 2008), where wave exposure (exposed, sheltered) was a fixed factor, and reef site (n = 8 islands/headlands) was a random factor in an unbalanced design (only 4 reefs had sites across both levels of exposure, Fig. 1). All PERMANOVAs were conducted using models with Type III sum of

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