

# Microhabitat selectivity underpins regional indicators of fish abundance and replenishment



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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 m<sup>2</sup>), 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 m<sup>2</sup>). 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; Reserits, 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

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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 m<sup>2</sup>), 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 m<sup>2</sup>).

## 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

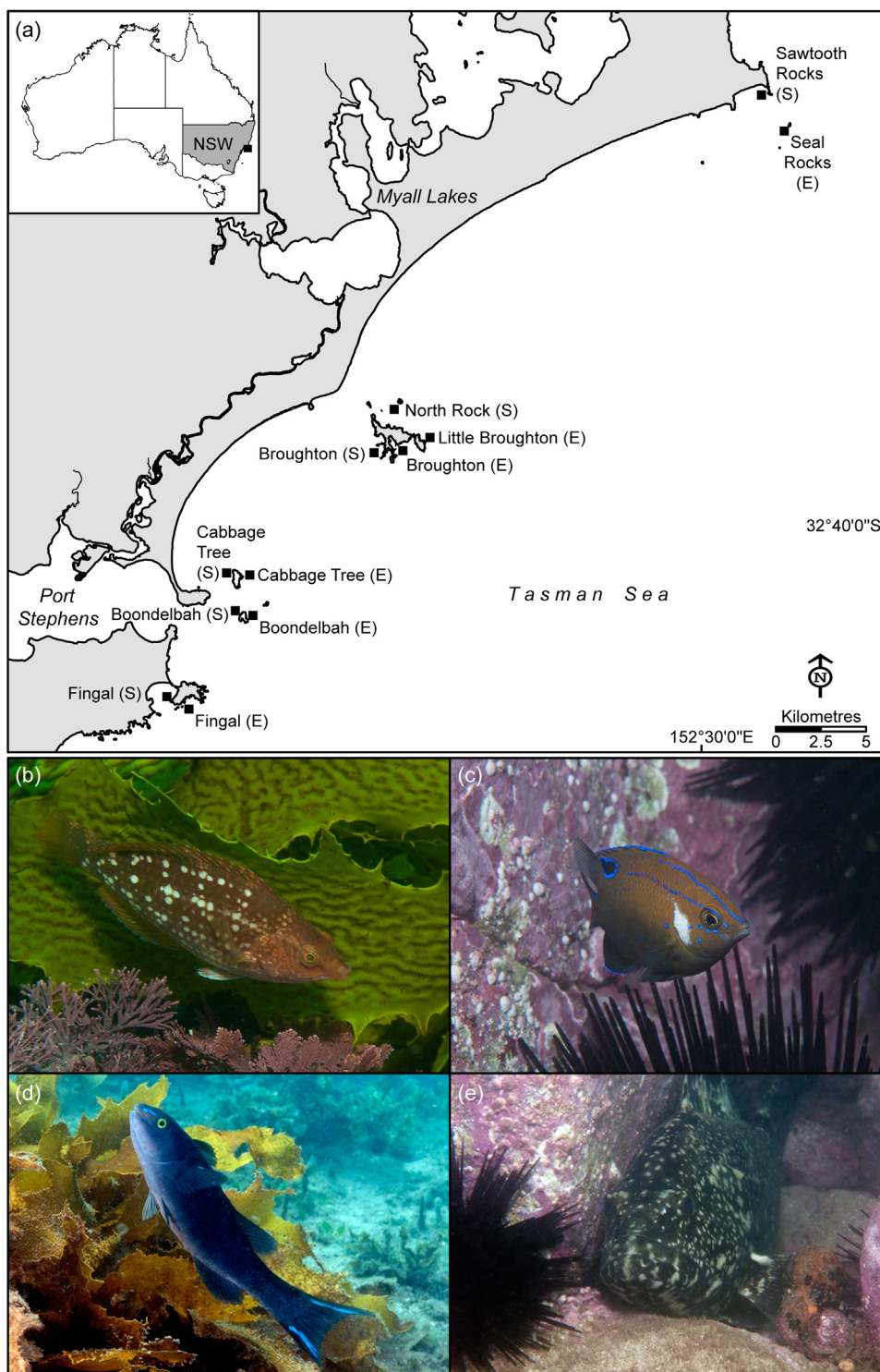
Visual surveys were conducted in March 2013 to estimate benthic habitat composition alongside the density of demersal reef fishes from four families (Labridae–20 species, Odacidae–2 species, Pomacentridae–8 species, Serranidae–3 species; Fig. 1b–e). Surveys

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 *Halimnion*, *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  $107 \pm 8$  m ( $\pm$  standard error,  $n = 6$ ), hence each replicate surveyed ~535 m<sup>2</sup> 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* (Forsskal 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



**Fig. 1.** (a) Study area and location of survey sites among wave exposures (E=exposed, S=sheltered) and offshore reefs near Port Stephens, New South Wales (NSW). Fishes from the four focal families: (b) *Notolabrus gymnogenis* (Günther 1862) (Labridae), (c) *Parma microlepis* Günther 1862 (Pomacentridae), (d) *Olisthops cyanomelas* Richardson 1850 (Odacidae), and (e) *Epinephelus daemeli* (Günther 1876) (Serranidae). All photos are by D. Harasti.

squares and 9999 permutations on resemblance matrices created from estimates of percent cover for each habitat category and density of each reef fish species across the 36 transects. Resemblance matrices were constructed using a modified Gower (base 2) distance measure (which weights a doubling in abundance equal to a change in species composition) for the fish species, and a Bray Curtis similarity measure for benthic habitats, on square-root transformed data (Anderson et al., 2008; Clarke et al., 2014). Principal

coordinates analysis (PCO; Anderson et al., 2008) performed on the same Gower (base 2) resemblance matrix was used to visualize structure within the reef fish community, with overlays of significant (SIMPROF test with  $\alpha=0.05$ ) Bray-Curtis similarity clusters, and vectors for the benthic habitat categories and fish species that were highly correlated (Pearson's  $r > 0.5$ ) with the ordination structure.



Fish-habitat relationships were explored using generalized additive mixed models (GAMMs) and a full subsets approach to infer the best habitat predictors for variations in the density of adult and juvenile fishes from each family (Zuur et al., 2009). Fish individuals were coded as adults or juveniles above and below a size threshold of 4 cm TL, respectively, which was based on the different pigmentation of individuals (Kuitert, 1993; Lincoln Smith et al., 1991). One exception was the large-bodied species *Achoerodus viridis* (Steindachner 1866), which attains >80 cm TL and individuals <20 cm TL are considered juveniles (Gillanders and Kingsford, 1998). Full-subsets GAMM analyses was also used to explore environment-density relationships for each of the 20 species on which we were able to analyze microhabitat electivity (details below). All possible combinations of predictors were considered, which included the two spatial factors of wave exposure (fixed) and site (random, to account for potential spatial autocorrelation) for 11 benthic habitat variables. The best model for each group was selected as that with the fewest variables within two AICc (Akaike Information Criterion corrected for finite samples) of the lowest AICc for all possible models (Burnham and Anderson, 2002). Relative importance of each habitat predictor was further explored by summing the AICc model weights across all models containing that variable (Burnham and Anderson, 2002).

Microhabitat selectivity was explored via electivity indices (Vanderploeg and Scavia, 1979) for 20 species that were recorded with 10 or more individuals across our 12 sites (which matched the species examined in the species-specific GAMMs above). Electivity indices ( $E_i^*$ ) were calculated as  $E_i^* = [W_i - (1/n)]/[W_i + (1/n)]$ , where  $n$  is the number of microhabitat categories;  $W_i$  is the selectivity coefficient for microhabitat category  $i$ , calculated as  $W_i = (r_i/p_i)/[\sum_i (r_i/p_i)]$ , where  $r_i$  is proportional use and  $p_i$  proportional availability of microhabitat category  $i$  at each site. Electivity indices were then averaged across all sites for each species to explore patterns of microhabitat association across the region. Categories were the same as for the habitat surveys, although two pairs of similar abiotic categories (Boulders/Rocks and Gravel/Sand) were merged for presentation. Electivity values of zero indicate random use of a microhabitat, while above and below zero suggest preference and avoidance, respectively (Lechowicz, 1982).

All PERMANOVA analyses and ordinations were made using PRIMER (version 6.1.16) with PERMANOVA+ (version 1.0.6). GAMM analyses were completed in R (v 3.2.1, R core development team) using the function “*gamm*” from library *mgcv* (Wood, 2015) and “*gamm4*” from the library *gamm4* (Bates et al., 2013).

### 3. Results

Significant heterogeneity was apparent in both benthic habitat composition and reef fish community structure among offshore reef sites and wave exposures (Table 1, Fig. 2). Spatial structure in the benthic habitat was fine grained, with adjacent transects separated by 50 m within a site often distinctly different in biotic cover (e.g. *Ecklonia* forest interspersed with urchin barrens). Erect macroalgae (typically *Ecklonia* kelp forest) was generally the most abundant habitat-forming organism overlaying the predominantly boulder/rock substratum at these sites (overall mean of 21% that ranged 0–58%; Fig. 2a). Where erect macroalgae was absent, either pyurids or hard coral (typically *Pocillopora*) were the next most prominent biotic habitat types (Fig. 2b). While fish species richness was relatively consistent across sites (Fig. 2d), three distinct groups of reef fish community composition were apparent – these groups spanned a mixture of wave exposures and/or sites up to 48 km apart (Fig. 3a and b), but were correlated strongly with whether the benthic habitat within transects was dominated by erect macroalgae, coral/boulders/sediment, or pyurids/turf/bedrock (Fig. 3c).

**Table 1**

Summary of PERMANOVAs comparing (a) benthic habitat composition and (b) reef fish densities among eight offshore reefs and two wave exposures. Differences are significant for  $p$ -value <0.05.

Source	df	SS	MS	pseudo-F	p-value
(a) Habitat					
Exposure	1	8680	8680	7.23	0.03
Site	7	23382	3340	6.05	<0.01
Exposure × Site	3	3603	1201	2.18	0.06
Residual	24	13241	552		
Total	35	44779			
(b) Reef Fish					
Exposure	1	1.04	1.04	2.09	0.14
Site	7	3.55	0.51	3.01	<0.01
Exposure × Site	3	1.50	0.50	2.96	<0.01
Residual	24	4.05	0.17		
Total	35	10.14			

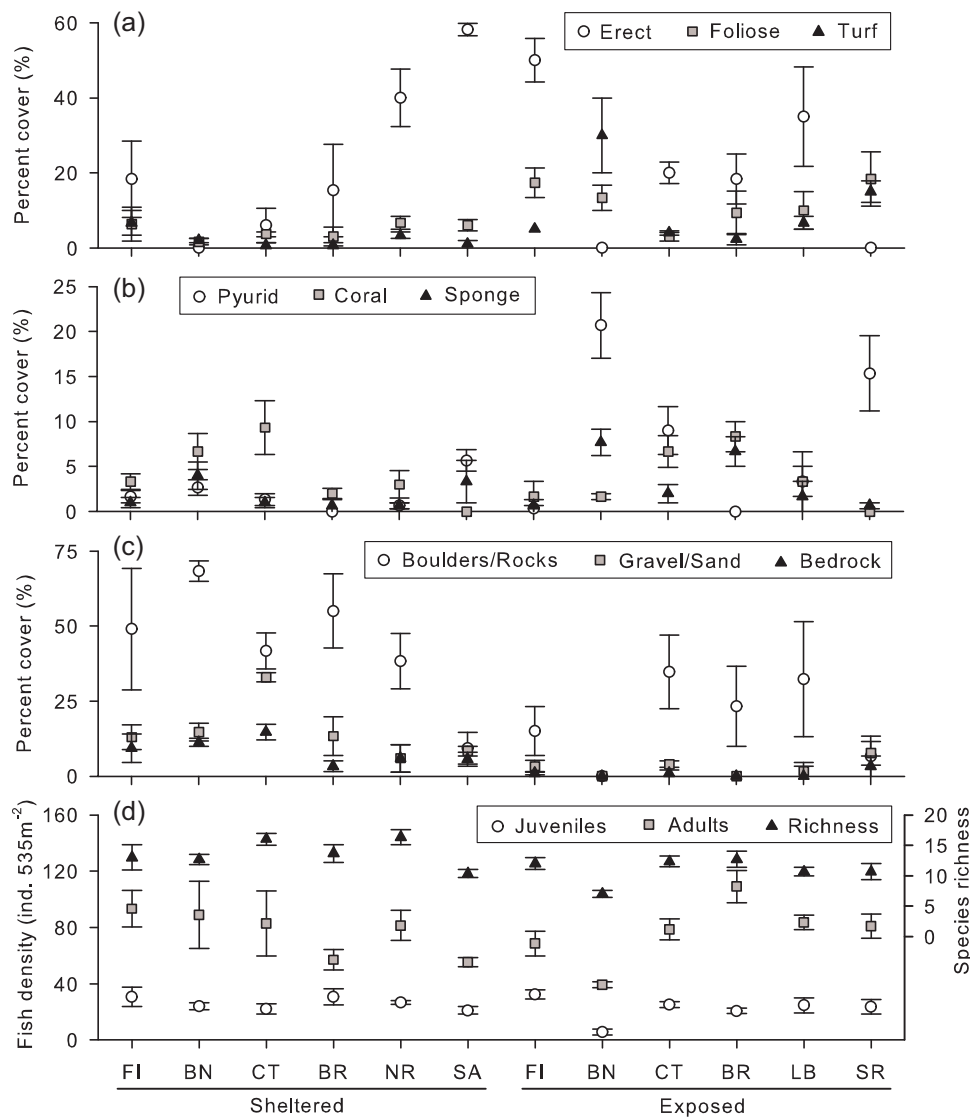
**Table 2**

Models selected from mixed-effects GAMM full subsets analyses to identify the best benthic habitat and/or spatial (Exposure/Site, in parentheses) predictors for the density of adult and juvenile reef fishes from the families (a) Labridae, (b) Odacidae, (c) Pomacentridae, and (d) Serranidae. Best models were selected as those with the fewest variables and lowest AICc (Akaike Information Criterion for finite samples) among all of the top models (see Appendix A). MA = macroalgae.

Model terms	AICc	r <sup>2</sup>
(a) Labridae		
Adults ~ Erect MA + Turf MA + Sand	17.8	0.66
Juveniles ~ Erect MA	53.6	0.58
(b) Odacidae		
Adults ~ Erect MA + Pyurid + (Exposure)	128.3	0.82
Juveniles ~ Foliose MA + Sponges + Sand + (Exposure)	80.5	0.52
(c) Pomacentridae		
Adults ~ Coral	68.2	0.36
Juveniles ~ Boulders	69.9	0.17
(d) Serranidae		
Adults ~ Boulders + (Exposure)	77.0	0.40
Juveniles ~ Turf MA + (Exposure)	105.4	0.40

Benthic habitat availability provided some of the best predictors for family-level variations in adult and juvenile fish density, with increases in fish density often positively related to increases in percent cover of certain habitat types (Table 2, Fig. 4). The best habitat predictor for adult fishes varied according to family, such as percent cover of erect macroalgae for labrids (Fig. 4a,c) and odacids (Fig. 4d,f), coral for pomacentrids (Fig. 4g,i), and boulders for serranids (Fig. 4j,l). For juveniles, a different habitat type often emerged as the best predictor, with percent cover of erect macroalgae important for both adult and juvenile labrids (Fig. 4b and c), but foliose macroalgae emerged as more important for juvenile odacids (Fig. 4e and f), boulders for juvenile pomacentrids (Fig. 4h and i), and turf macroalgae for juvenile serranids (Fig. 4k,l). Wave exposure was also informative for some families (Fig. 4c,f,i), with higher fish densities in sheltered reefs compared to exposed reefs for labrid adults (mean ind.  $535 \text{ m}^{-2} \pm \text{SE}$ ,  $2.7 \pm 0.6$  and  $1.3 \pm 0.6$ , respectively) and juveniles ( $14.9 \pm 1.6$  and  $11.6 \pm 1.3$ ), as well as serranid adults ( $7.6 \pm 0.9$  and  $4.1 \pm 0.9$ ) and juveniles ( $3.9 \pm 0.5$  and  $1.6 \pm 0.5$ ). However, the converse was apparent for odacid adults ( $1.2 \pm 0.7$  and  $2.9 \pm 0.8$ , sheltered and exposed, respectively) and juveniles ( $0.02 \pm 0.3$  and  $0.9 \pm 0.2$ ).

Species-specific models revealed a similar suite of habitat predictors to the family-level models (Table 3), which also aligned with species-specific patterns of fish microhabitat electivity (Fig. 5). For most species, the models identified habitats to which species displayed strong preferences (positive electivity, Fig. 5), including: macroalgae for most labrids and odacids, such as *Ophthalmolepis lineolata* (Valenciennes 1839), *Pictilabrus laticlavius* (Richardson 1840), and *Olisthops cyanomelas* Richardson 1850; coral for many



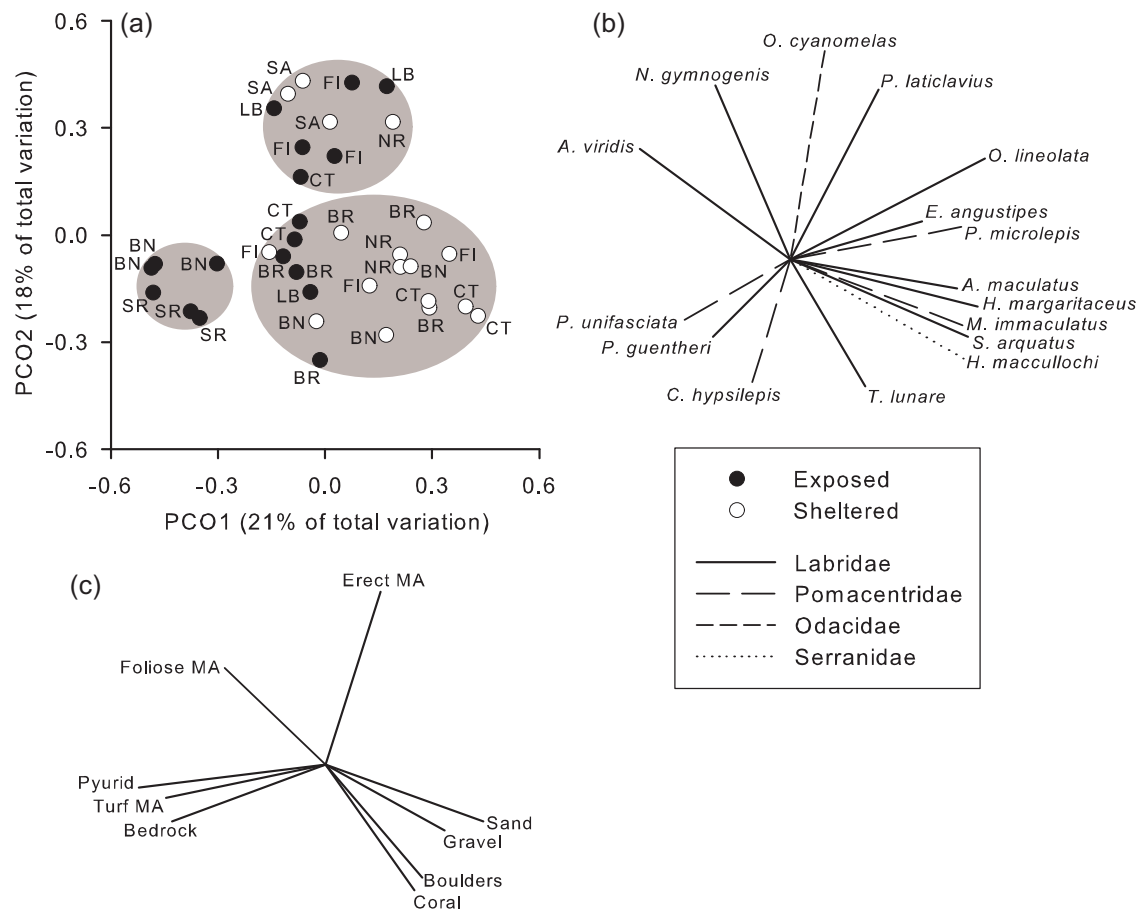
**Fig. 2.** Mean percent cover of (a) macroalgae groups, (b) other benthic organisms and (c) abiotic microhabitats, alongside (d) fish density and species richness on offshore reefs (FI = Fingal Island, BN = Boondelbah, CT = Cabbage Tree, BR = Broughton, NR = North Rocks, LB = Little Broughton, SA = Sawtooth, SR = Seal Rocks) arranged by wave exposure (Sheltered, left; Exposed, right). Errors are standard errors of the mean (n = 3 per site).

pomacentrids, such as *Chromis hypsilepis* (Günther 1867), and *Pomacentrus coelestis* Jordan & Starks 1901; and predominantly abiotic sediments for both serranids and pomacentrids, such as *Acanthistius ocellatus* (Günther 1859), *Parma microlepis* Günther 1862, and *Mecaenichthys immaculatus* (Ogilby 1885). However, in some cases the model selection process identified habitats to which species displayed strong avoidance (negative electivity, Fig. 5), such as: sand for *Thalassoma lunare* (Linnaeus 1758) (Table 3a), erect macroalgae for *Parma unifasciata* (Steindachner 1867) (Table 3c), and turf macroalgae for *Hypoplectrodes maccullochi* (Whitley 1929) (Table 3d). Overall, the biogenic microhabitats of canopy-forming macroalgae (erect, foliose) and coral were positively selected by the most species (48% and 40%, respectively), while boulders/rocks were the most positively selected abiotic habitat (80% of species, Fig. 5). In terms of spatial factors, site was uninformative, but wave exposure was one of the best predictors of density in 50% of the species (Table 3).

#### 4. Discussion

Habitat-based approaches to conservation and fisheries management are being recognized as a key part of sustaining

biodiversity and marine ecosystem goods and services (Malcolm et al., 2012; Smale et al., 2010; Werner et al., 2014). In recognizing the potential for strong associations between reef fish diversity and habitat composition (e.g. Levin and Hay, 1996; Pérez-Matus and Shima, 2010), we find that fine-scale habitat availability provides a key predictor for the abundance of both adult and juvenile rocky reef fishes over local to regional scales. Underpinned by diverse patterns of fish microhabitat selection, there is no single habitat predictor for all taxa, rather a suite of habitats arranged in a spatially heterogeneous mosaic (typically at scale of ~500 m<sup>2</sup> or more) that supports most of the conspicuous fish taxa found on rocky reefs. However, a few key habitat types do appear to shape the abundance of most adult and juvenile fishes, particularly canopy-forming macroalgae (erect/foliose), corals, and the mid-range abiotic sediment grades of boulders and rocks. In the context of an overarching influence of wave exposure, these multi-scale fish-habitat relationships provide key indicators of the scale and location of offshore fish recruitment areas (i.e. juvenile nurseries), and point to the range of habitats that are needed to support a diversity of healthy fish populations. As such, these key indicators can be used in concert with broad-scale mapping methods (e.g. towed video, drop cameras, aerial/satellite imagery) to inform

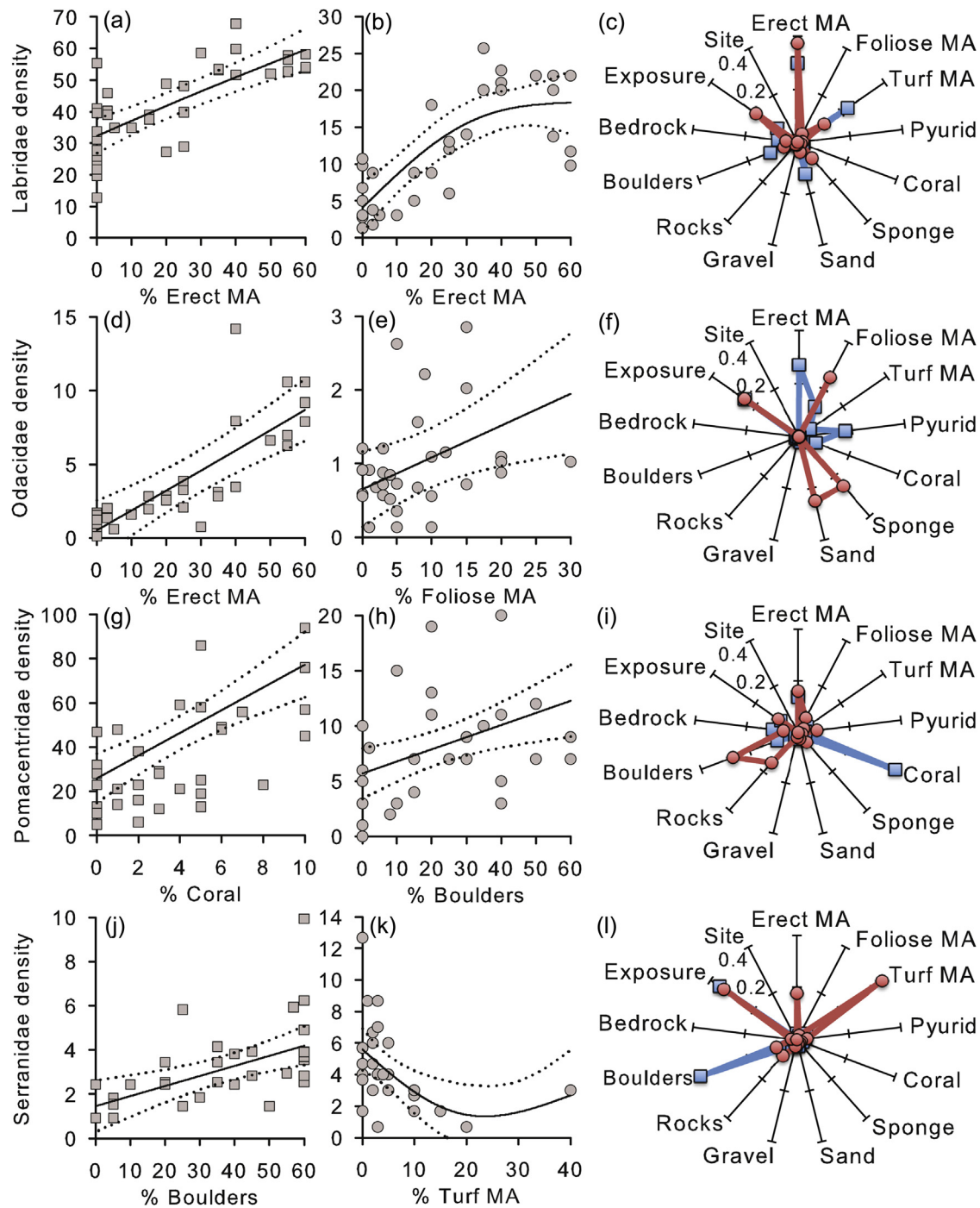


**Fig. 3.** (a) Principal coordinates (PCO) ordination of the offshore reef fish community, indicating significant Bray-Curtis hierarchical clusters of transects (grey ellipses) that include multiple sites (abbreviations as in Fig. 2) and wave exposures, alongside the (b) fish species (vectors coded by family, see legend) and (c) benthic habitat components (MA = macroalgae) that are strongly correlated ( $r > 0.5$ ) with this ordination structure. Full species names are given in Table 3.

**Table 3**

Models selected from mixed-effects GAMM full subsets analysis to identify the best benthic habitat and/or spatial (Exposure/Site, in parentheses) predictors for the density of 20 reef fish species from the families (a) Labridae, (b) Odacidae, (c) Pomacentridae, and (d) Serranidae. Best models were selected as those with the fewest variables and lowest AICc (Akaike Information Criterion for finite samples) among all of the top models (see Appendix A). MA = macroalgae.

Model terms	AICc	$r^2$
<b>(a) Labridae</b>		
<i>Achoerodus viridis</i> ~ (Exposure)	96.4	0.29
<i>Austrolabrus maculatus</i> ~ Erect MA + Foliose MA + Sand	115.9	0.78
<i>Coris picta</i> ~ (Exposure)	146.1	0.01
<i>Eupetrichthys angustipes</i> ~ Erect MA + (Exposure)	108.8	0.30
<i>Halichoeres margaritaceus</i> ~ (Exposure)	132.0	0.10
<i>Notolabrus gymnogonis</i> ~ Erect MA + Foliose MA	30.2	0.70
<i>Ophthalmolepis lineolata</i> ~ Erect MA + Sand	68.9	0.58
<i>Pictilabrus laticlavus</i> ~ Foliose MA + Coral + (Exposure)	108.1	0.34
<i>Pseudolabrus guentheri</i> ~ Erect MA	130.1	0.03
<i>Pseudolabrus luculentus</i> ~ Turf MA + Sponge + Pyrid + Rocks	118.9	0.07
<i>Suezichthys arquatus</i> ~ (Exposure)	135.9	0.04
<i>Thalassoma lunare</i> ~ Sand	144.0	0.18
<b>(b) Odacidae</b>		
<i>Olisthops cyanomelas</i> ~ Erect MA + (Exposure)	131.9	0.59
<b>(c) Pomacentridae</b>		
<i>Chromis hypsilepis</i> ~ Coral	120.9	0.26
<i>Mecaenichthys immaculatus</i> ~ Coral + Sponge + Rocks + Gravel + (Exp.)	115.8	0.88
<i>Parma microlepis</i> ~ Rocks	107.2	0.20
<i>Parma unifasciata</i> ~ Erect MA	99.3	0.17
<i>Pomacentrus coelestis</i> ~ Coral + Boulders + Sand + (Exposure)	52.0	0.19
<b>(d) Serranidae</b>		
<i>Acanthistius ocellatus</i> ~ Coral + Boulder + Rocks	67.6	0.27
<i>Hypoplectrodes maccullochi</i> ~ Turf MA + (Exposure)	81.5	0.44



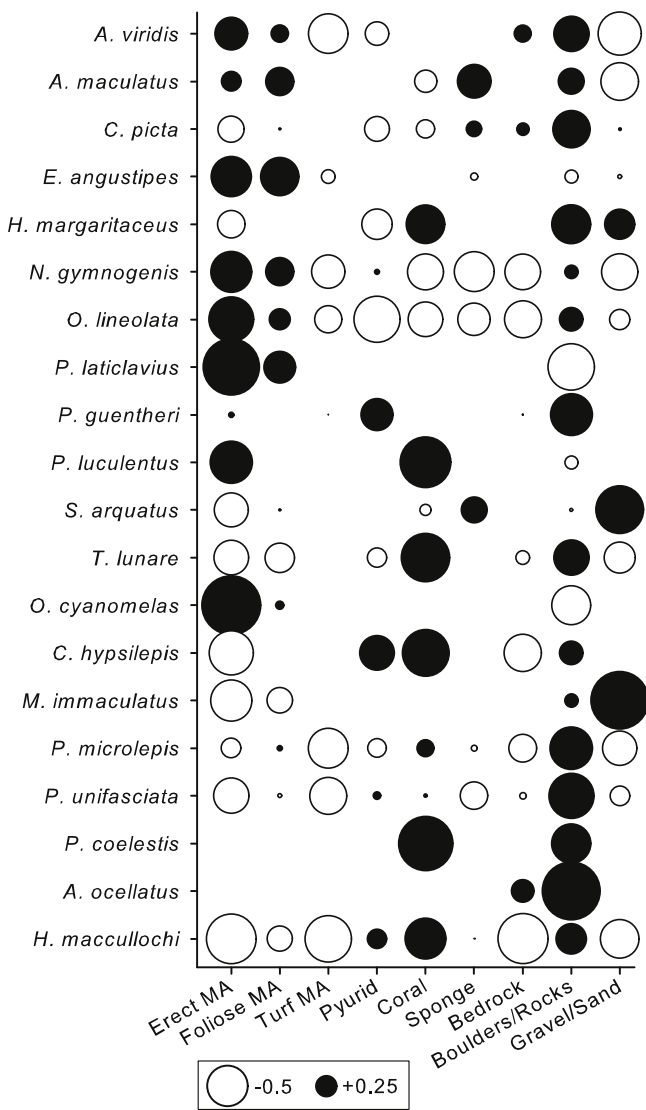
**Fig. 4.** Relationships between benthic habitat availability and fish density (adults = squares, juvenile = circles) for the families (a, b) Labridae, (d, e) Odacidae, (g, h) Pomacentridae, and (j, k) Serranidae. Solid lines are GAMM partial response fits, dotted lines are 95% confidence limits. Relationships are shown for habitat types in the best models (Table 2) that have the highest summed AICc weights (y-axis of radar plots) for adults (blue squares) and juveniles (red circles) of each family (c, f, i, l, respectively). Fish densities are ind. 535 m<sup>-2</sup>. MA = macroalgae. (Please see web version of this article to interpret references to colour in this figure legend.)

habitat-based monitoring of fish populations for both conservation and ecosystem-based fisheries management (Malcolm et al., 2012; Smale et al., 2010; Werner et al., 2014).

Several mechanisms may be driving these patterns of fish-habitat association on temperate rocky reefs. Predator-prey linkages can often shape patterns of habitat association (e.g. Choat and Ayling, 1987; Gillanders, 1995; Morton and Gladstone, 2011). In our assemblage, some direct trophic explanations appear likely, such as that between herbivorous odacids and the percent cover of fleshy macroalgae that they consume (Jones and Andrew, 1990).

For other taxa, habitat may have indirect relevance to trophic ecology, such as carnivorous wrasses targeting macroalgae-associated invertebrate prey (Morton and Gladstone, 2011). Similarly, interstitial spaces between boulders and rocks may be necessary for resident serranids to undertake ambush predation (Hixon and Beets, 1993). However, it can be difficult to fully disentangle trophic influences from the benefits habitats provide as shelter from predation (Jones, 1984) and/or disruptive water motion (Johansen et al., 2008). Indeed, the influence of wave exposure must be considered alongside these fish-habitat relationships, due to the different





**Fig. 5.** Electivity of 20 reef fish species towards benthic microhabitats on offshore rocky reefs near Port Stephens, NSW. Bubble sizes are scaled to mean electivity index values across all sites and coded to either preference (positive = filled) or avoidance (negative = open). Full species names and families are given in Table 3.

capacity of fishes to tolerate and thrive in wave exposed conditions according to their swimming ability, body size, and/or adaptive swimming behaviours (Fulton, 2010; Fulton and Bellwood, 2004; Heatwole and Fulton, 2013).

Certain nursery habitats emerge as important from the quantitative juvenile fish-habitat relationships, which can be used to identify and monitor recruitment hotspots within a bioregion. Juvenile reef fishes are often more specialized in their habitat association than adult conspecifics/conspecifics (Jones, 1984; Morton and Gladstone, 2011), which can produce the strong habitat-fish recruitment relationships found here and elsewhere (e.g. Levin and Hay, 1996; Pérez-Matus et al., 2007) due to gregarious habitat-specific settlement and/or habitat-mediated mortality (Félix-Hackradt et al., 2013). The complex habitat provided by canopy-forming seaweeds (e.g. *Ecklonia*) appears to be a particularly important nursery habitat for supporting rocky reef fish diversity around the world. For instance, the availability of giant kelp is positively correlated with the local abundance of juvenile fishes in California (Holbrook et al., 1990), and higher abundances of labrid new recruits are found in areas of high algal cover in the Mediterranean and across Australasia (García-Rubies

and Macpherson, 1995; Pérez-Matus and Shima, 2010). Notably, the abundance of many fished species, such as *A. viridis*, *Noto-labrus gymnogensis* (Günther 1862), and *O. lineolata* (Rowling et al., 2010), are among the most strongly correlated to the availability of canopy-forming macroalgae habitat. Collectively, this suggests that canopy-forming macroalgae habitats are particularly important for facilitating the fundamental process of reef fish population replenishment on offshore rocky reefs.

Spatial heterogeneity in these reef fish-habitat associations can also directly inform the scale and composition of spatial conservation and management zones on temperate rocky reefs. Major variations in habitat availability and fish community structure occurred primarily among transects (~500 m<sup>2</sup>), with distinct groups of macroalgae-associated, coral and sediment-associated fishes spanning multiple sites and wave exposures. Considering this, and the spectrum of foraging range sizes recorded for these reef fishes (e.g. 2–12 m<sup>2</sup> *H. maccullochi*, 175 m<sup>2</sup> *P. laticlavus*, 50–1700 m<sup>2</sup> *O. lineolata*; Barrett, 1995; Kingsford and Carlson, 2010), it is unlikely that zones smaller than 1 km<sup>2</sup> will adequately encompass a range of habitat types and areas that are sufficient to support the breadth of rocky reef fish diversity found within a bioregion (Gladstone, 2007; Malcolm et al., 2012). In seeking a representative area approach, both habitat and wave exposure should be salient factors in determining the placement of spatial management zones for rocky reef ecosystems, alongside key considerations of the scale of connectivity among nursery and adult habitats (Gillanders et al., 2003). In balancing the scale and composition of habitats available, this spatial management approach will support the full breadth of fish diversity in no-take zones, and ensure that habitats within open (fished) zones will support both new fish recruits and adult fish populations. Targeted habitat-based monitoring via cost-effective methods (e.g. towed video, AUVs) can then be used to assess not only the representative nature of the zoning plans as the reefs may change, but also the potential capacity of spatial zones to sustain the desired population sizes and replenishment of harvested reef fish species.

Emerging threats to these key habitats provides urgent motivation for adopting habitat-based protection and monitoring. Specialization by juvenile reef fishes towards erect macroalgae habitat suggests a strong dependency and sensitivity of recruitment success to macroalgae habitat availability (Levin and Hay, 1994; Pérez-Matus and Shima, 2010). Moreover, the complex habitat provided by canopy-forming macroalgae is a facilitator of broader rocky reef biodiversity, analogous to that provided by corals in tropical reef ecosystems (Filbee-Dexter and Scheibling, 2014; Nagelkerken et al., 2015). Worryingly, macroalgae-dominated habitats are under threat from marine heatwaves, tropicalization, and ocean acidification, through either direct effects upon taxa such as *Ecklonia* (Mabin et al., 2013; Wernberg et al., 2013; Vergés et al., 2014), or via changes in the abundance of sea urchins and other key modifiers of macroalgae habitats (Filbee-Dexter and Scheibling, 2014; Ling, 2008). In the face of such climate-driven habitat loss, we may see deleterious effects on many macroalgae-associated fish species, especially those whose population replenishment depends on the presence of these nursery habitats (Filbee-Dexter and Scheibling, 2014; Nagelkerken et al., 2015). Therefore, as critical facilitators of biodiversity and population replenishment, the highest priority should be placed on the protection and monitoring of *Ecklonia* and other canopy-forming macroalgae (e.g. *Cystophora*, *Phyllospora*, *Sargassum*), whose loss can cause ecosystem-wide phase shifts and biodiversity loss (Filbee-Dexter and Scheibling, 2014; Nagelkerken et al., 2015). In doing so, we must move beyond recognizing just mangroves and seagrass as important fish nurseries in temperate coastal ecosystems (Beck et al., 2001; Sheaves et al., 2015), and extend this to include the canopy-forming seaweeds on offshore reefs that facilitate the population replen-



ishment and maintenance of fish biodiversity in temperate reef ecosystems around the world.

### Conflict of interest

The authors declare that they have no conflict of interest.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolind.2016.06.032>.

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